The Impact of Climate Change on the Small Island Developing States of the Caribbean

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To Kishore, Jenty and Marcus

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Small Island Developing States (SIDS) of the Caribbean are one of the world's 'hottest' 'biodiversity hotspots'. However, this biodiversity continues to be threatened by habitat loss, and now, by climate change.

The research reported here investigated the potential of species distribution modelling (SDM) as a plant conservation tool within Caribbean SIDS, using Trinidad as a case study. Prior to the application of SDM, ancillary analyses including: (i) quantification and mapping of forest cover change (1969 to 2007) and deforestation rates, and (ii) assessment of the island's vegetation community distribution and associated drivers were carried out.

Community distribution and commercial importance and global/regional rarity were used to generate a list of species for assessing the potential of SDM within Trinidad. Species occurrence data were used to generate species distribution models for present climate conditions within the SDM algorithm, MaxEnt. These results were assessed through expert appraisal and concurrence with results of ecological analyses. These models were used to forecast suitable species climate space forty years into an SRES A2 future. Present and future models were then combined to produce a 'collective change map' which showed projected areas of species' range expansion, contraction or stability for this group of species with respect to Trinidad's Protected Areas (PAs) network.

Despite the models being indicative rather than accurate, it was concluded that species' climate space is likely to decrease or disappear across Trinidad. Extended beyond Trinidad into the remainder of the Caribbean region, SDM may be a crucial tool in identifying which PAs within the region (and not individual islands) will facilitate future survival of given target species. Consideration of species conservation from a regional, rather than an individual island perspective, is strongly recommended for aiding the Caribbean SIDS to adapt in response to climate change.

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Contents

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Glossary of terms

AOGCM Atmosphere-Ocean General Circulation Model.
AR4 Fourth Assessment Report.
AR5 Fifth Assessment Report.
ASCII American Standard Code for Information Interchange.
AT Assisted Translocation.
AUC Area Under the Curve.

Bioclim Bioclimatic.
BRAHMS Botanical Research and Herbarium Management System.
BRT Boosted Regression Tree.

CANARI Caribbean Natural Resources Institute.
CARICOM Caribbean Community.
CBD Convention on Biological Diversity.
CCCCC Caribbean Community Climate Change Centre.
CMIP5 Climate Intercomparison Project 5.

DBH Diameter at Breast Height.
DEM Digital Elevation Model.
DGLM Department of Geomatics Engineering and Land Management.
DPSOX Department of Plant Sciences, University of Oxford.

ECLAC Economic Commission for Latin America and the Caribbean.
EMA Environmental Management Authority of Trinidad and Tobago.
ENFA Ecological Niche Factor Analysis.
ENSO El Niño-Southern Oscillation.
ESA Environmentally Sensitive Area.
ESRI Environmental Systems Research Institute.

FAO Food and Agriculture Organization of the United Nations.

GAM Generalised Additive Model.
GARP Genetic Algorithms for Rule Production.
GCM General Circulation Model.
GEF Global Environment Facility.
GIS Geographic Information System.
GLM Generalized Linear Model.

GOTT Government of Trinidad and Tobago.
GPS Global Positioning System.

IADB Inter-American Development Bank.
ICL Institutional Consultants (International) Ltd..
IDW Inverse Distance Weighted.
IKONOS is a commercial earth observation satellite from India.
IPCC Intergovernmental Panel on Climate Change.
IUCN International Union for Conservation of Nature.

LZ Longitudinal Zone.

MA Millennium Ecosystem Assessment.
MACC Mainstreaming Adaptation to Climate Change.
MONARCH Modelling Natural Resource Responses to Climate Change.

NCGIA National Center for Geographic Information and Analysis.
NGO Non-Governmental Organisation.
NHZ Northern Horizontal Zone.
NMDS Non-Metric Multidimensional Scaling.

OECS Organisation of Eastern Caribbean States.

PA Protected Area.
PAN Protected Areas Network.
PES Payments for environmental services.
PRECIS Providing REgional Climates for Impacts Studies.
PSP Permanent Sample Plot.

RBS Rapid Botanical Survey.
RCF Rate of Change in Forest cover.
RCM Regional Climate Model.
RCP Representative Concentration Pathway.
ROC Receiver Operating Characteristic.

SCP Systematic Conservation Planning.
SDC Soil Drainage Capacity.
SDM species distribution modelling (most times verb).
SHZ Southern Horizontal Zone.
SIDS Small Island Developing States.
SIMPER Similarity Percentage.
SIMPROF similarity profile test.
SM species distribution model (always a noun).
SPACC Special Programme for Adaptation to Climate Change.
SPSS Statistical Package for the Social Sciences.
SRES Special Report on Emissions Scenarios.

TIN Triangulated Irregular Network.

UNDP United Nations Development Programme.
UTM Universal Transverse Mercator.
UWI University of the West Indies.

WBG World Bank Group.
WGS World Geodetic System.
WWF World Wildlife Fund.

Chapter 1

Introduction

1.1 Background

1.1.1 Islands, biodiversity and climate change

The Earth's surface is sprinkled with many islands which vary dramatically in terms of size, geology and degree of isolation (from neighbouring continents or other islands). The seminal work on island biogeography during the 1960s (MacArthur and Wilson 2001) proposed that the ecosystems within undisturbed islands exist in fragile, yet dynamic states within which species richness depends upon immigration and extinction – which are in turn influenced by distance from a source of colonists (e.g., a neighbouring continent). Within remote islands, long periods of isolation have given rise to evolutionary adaptive radiation resulting in the genesis of endemic species (Carlquist 1980). Hence, unlike continental biotas, islands generally consist of fewer species, of which significant portions may be endemic. The highest proportions of endemics are frequently associated with ancient continental islands (e.g., Madagascar) as well as larger, higher oceanic islands which are located within warm-temperate and tropical regions (e.g., Hawaii). Much smaller floras (and usually lower proportions of endemics) are found within smaller oceanic islands (Carlquist 1980; Wagner and Funk 1995; Whittaker and Fernández-Palacios 2007). Islands hence contribute a disproportionate proportion of global biodiversity relative to their surface area. For example, one sixth of the world's plant species are located within islands – as are one third of all threatened plants (globally) (Groombridge 1992).

However, today, the natural rate of attrition of island biotas discussed by early island biogeographers (e.g., MacArthur et al. 1972; MacArthur et al. 1973) is being accelerated as a consequence of human activities such as: habitat destruction/loss, the introduction of exotic species and diseases, and more recently, climate change. The impacts of these disturbances when combined with evolutionary traits developed by island biota such as a decreased dispersal potential (relative to their continental counterparts) (Carlquist 1965; Carlquist 1966a, 1966b) may further decrease the ability of many island species to respond in a timely and effective manner.

Impacts of human induced climate change upon island biotas and ecosystems across the globe have already been observed; for example, global warming has been extensively documented to enhance conditions necessary for the spread of exotic species within species poor sub-Arctic/Antarctic islands (Chapuis et al. 2004; Frenot et al. 2005) as well as mid-latitude islands (Kudo et al. 2004) leading to changes in ecosystem function and extensive loss of local biodiversity. Additionally, the spread of disease vectors such as mosquitoes is forecasted to further threaten island biotas (Freed et al. 2005) while the cumulative impacts of more frequent and intense natural disasters such as hurricanes are expected to both severely affect the biodiversity of forests within islands and slow the adaptation responses of these systems (Ostertag et al. 2005). Moreover, altitudinal species range contractions and shifts have been recorded within high islands, with the upward shifting of tree lines and some associated faunal species along areas of high altitude in response to warming conditions (Benning et al. 2002). Further, within larger islands such as Madagascar, both altitudinal and horizontal species range shifts have been projected for the future, with more species forecasted to experience suitable climate space contractions instead of expansions (Consiglio et al. 2006; Hannah et al. 2008; Schatz et al. 2008). Most importantly, such impacts are forecasted to become more acute as, in conjunction with past habitat loss, climate continues to change (Benning et al. 2002; Mimura et al. 2007). It has therefore been suggested that efforts to conserve biodiversity within islands as climate changes should be based upon (i) an understanding of the past; (ii) monitoring of current species responses to climate change and (iii) modelling future biological responses to projected future climate change scenarios (Hannah et al. 2008).

1.1.2 Vulnerability of the Caribbean

Almost two decades ago, representatives of small island states coined the phrase Small Island Developing States (SIDS) to define, and draw attention to, island nations with limited resources due to their small size, economic vulnerability and fragile ecosystems (Pelling and Uitto 2001). Like many other developing nations, most of the Caribbean SIDS suffer from a variety of limiting factors. These range from insufficient human, technological and institutional resources to finite natural resources delimited within a small, fixed geographic space. In addition to increasing population densities (ECLAC 2009; Walling et al. 2006), these islands are highly vulnerable to international trade patterns and global developments (Nurse et al. 2001; Pulwarty and Hutchinson 2009). These limitations impinge on the abilities of the populations within these islands to respond to challenges such as climate change and associated loss of biodiversity.

1.1.3 A biodiversity hotspot threatened

During the late 1980s, Norman Myers coined the term ‘biodiversity hotspot’ to describe regions across the globe which contained large numbers of endemics within relatively small geographic regions under significant threats of habitat destruction (Myers 1988, 1990). Of these, the Caribbean region has been identified as one of the ‘hottest’ ‘biodiversity hotspots’ because it contains a high percentage of endemic species which occupy increasingly threatened habitats (Myers et al. 2000). Stretching over just 0.15% of the earth’s surface, it is estimated that this region hosts approximately 7,000 endemic vascular plant species within just 11.3% of its remaining primary vegetation (Mittermeier et al. 2005; Myers et al. 2000). This amounts to approximately 2.3% of the world’s known vascular plant species within a diversity of important ecosystems which range from montane cloud forests to coral reefs (Mittermeier et al. 2005). Apart from the traditional drivers of this habitat loss such as the expansion of industry, agriculture, commerce and tourism, the effects of climate change have also been acknowledged as an increasing threat to the biodiversity of these islands.

The Intergovernmental Panel on Climate Change (IPCC) expects the Caribbean region to be particularly vulnerable to the effects of climate change, with projected (A1, A2, B1 and B2 scenarios) average surface air temperature increases ranging between 0.48 °C to 1.06 °C (2010 to 2039), 0.79 °C to 2.45 °C (2040 to 2069) and 0.94 °C to 4.18 °C (2070 to 2099) (Mimura et al. 2007). Additionally, rainfall patterns are likely to be altered, in conjunction with decreased precipitation and increased aridity within most of the southern Caribbean (Mimura et al. 2007). This increased aridity is likely to be exacerbated due to increased evaporative demand (e.g., evapotranspiration) resulting from increased temperatures. Furthermore, the frequency and intensity of hurricanes is expected to increase

(Day 2009; Lee and Jetz 2008; Mimura et al. 2007), in addition to sea level rise ranging between 0.18 m to 0.59 m and 0.5 m to 1.4 m towards the end of the 21st century (Day 2009; Rahmstorf 2007).

Indeed, over recent decades sequences of significant climate events have already been experienced within this region. These include increased impacts from the El Niño-Southern Oscillation (ENSO) event (1997 to 1998), consecutive years of abnormally high hurricane activity (2004 and 2005) and severe, widespread drought (2009 to 2010) (Chen et al. 2008; Pulwarty et al. 2010). Based on the above observations, researchers believe that the transient response of climate system within Caribbean environments will be significant (Mimura et al. 2007; Pulwarty et al. 2010).

Apart from adversely affecting food (agriculture and fishing) and economic security (e.g., through tourism), climate change impacts are expected to threaten biodiversity, as the limited geographic space and steep climate gradients, which characterise many Caribbean SIDS, leave species with very little room to shift or adapt. It is possible that such biodiversity loss would in turn serve to further undermine the adaptive capacity of ecosystems within these islands by increasing their vulnerabilities to environmental stress and natural disasters.

1.1.4 Initiatives for addressing the threat of climate change

National and international initiatives have been introduced to increase the adaptive capacity and resilience of the Caribbean SIDS to anticipated impacts of climate change. The majority of these are focused upon the strengthening of water resources, agriculture and food security, and in particular, the protection of coastal zones and ecosystems. Recent examples of such initiatives include the Mainstreaming Adaptation to Climate Change (MACC) (2004 to 2008) and the

Special Programme for Adaptation to Climate Change (SPACC) (2007 to 2011), both of which were supported by the Global Environment Facility (GEF). While these have been successful in the raising of awareness among decision makers and contributed to greater regional co-operation and the articulation of a united position under frameworks such as the Kyoto Protocol, there has been very little focus on terrestrial biodiversity and ecosystem services.

A search for literature on anticipated impacts of climate change upon the terrestrial biodiversity within the Caribbean SIDS revealed, with the exception of Cuba, no relevant studies and very little cartographic information. This observation has been echoed both by the findings of several published reports (over the last five years) which focused on the identification of knowledge gaps for addressing climate change within the region (Cambers et al. 2008; Chen et al. 2008; Day 2009; Suárez et al. 2008); and at the IPCC's Expert Regional Meeting for Small Islands in Belize earlier this year (2011).

Although most Caribbean states are signatories to several biodiversity conventions, such as the Ramsar Convention and the Convention on Biological Diversity, only three countries (Jamaica, Dominican Republic and Cuba) within the region presently have national plans that specifically link biodiversity with climate change. However, there is thus far, no available information available on whether these have yet been implemented in Jamaica and the Dominican Republic. Very limited information on a Cuban initiative revealed that Cuba has since conducted a study reviewing the climate change impacts upon its biodiversity. This revealed a negative correlation between rainfall and the aridity index and plant composition – hence suggesting that the composition of its endemic flora would change significantly with climate change.

The current national adaptation plans of most other states do promote the conservation of biodiversity as a tool for reducing vulnerability and increasing resilience to climate change. However these objectives are not effectively linked to each other nor are they well integrated or practically implemented into broader national development and planning programmes. One of the main reasons for this is the unavailability of robust data and supporting analyses that are necessary to inform decision making and the implementation of such strategies. Required data include baseline species inventories and ecosystem assessments which are necessary for making informed decisions on habitat protection with respect to climate change (Rivera-Monroy et al. 2004).

Another obstacle that prevents implementation is the need for the use of scenario-based approaches in conjunction with more traditional simulation (and optimisation) studies in order to develop climate risk and adaptation strategies for this region (Pulwarty et al. 2010). The lone biodiversity impact study found to employ a small number of climate scenarios [from General Circulation Models (GCMs)] is one which reviewed climate change impacts, vulnerability and potential adaptation of the floristic composition of six phytogeographic regions in Cuba (Suárez et al. 2008). More climate scenario data (downscaled from GCM) that can be adequately used at an island scale is imperative in order to inform development and contribute to the implementation of adaptive strategies to preserve island biodiversity within the region. Finally, there appears to be limited human capacity for adopting multi-disciplinary approaches that integrate ecology/conservation science with climate science, environmental economics and social sciences in order to develop more effective conservation strategies (Day 2009).

1.1.5 Protected Areas as conservation tools within the Caribbean

Chape et al. (2008) estimated that some 749 Protected Areas (PAs) exist within the Caribbean archipelago, covering approximately 67,719 km^2. However there is a considerable variation in the proportion of area that is protected across the islands that make up the archipelago, ranging from 20% of Dominica's territory (inclusive of marine sites) to less than 1.7% within countries such as Haiti and Grenada (Chape et al. 2008). The biodiversity within many of these PAs are considered to be at risk due to climate change. For example, the species of the elfin forests within PAs that occur at high elevations in many islands such as Jamaica, St. Vincent and St. Kitts and Nevis are expected to be severely impacted – as there is little room left for them to migrate upwards as conditions begin to warm.

It has also become clear that greater investment and focus have been placed upon biodiversity conservation within marine rather than terrestrial PA systems in this region. For example, the Caribbean Challenge is an on-going initiative whereby Caribbean governments have committed to expand their marine PA systems to encompass at least 20% of their near-shore territory by 2020 in conjunction with developing sustainable financing for their upkeep. This initiative has thus far secured in excess of 45 million US dollars from the international and conservation community; such emphasis is in direct contrast to the poorly developed and financed efforts for biodiversity conservation within terrestrial regions of these islands.

Most Caribbean islands have not traditionally established their PAs in a systematic approach. However, countries such as Jamaica, the Bahamas, the Dominican Republic and members of the Organisation of Eastern Caribbean States (OECS) (e.g., Grenada, St. Kitts and Nevis, Dominica and St. Lucia) have recently begun to conduct gap analyses of their Protected Areas Network (PAN) with the aim of creating frameworks of sustainable management for the present and future. These analyses have highlighted that many PANs do not comprehensively cover all ecosystem types, with key ecosystems missing or under-represented. Further, many PANs contain PAs which are too small and scattered to be considered viable in the long term or aid in enhancing connectivity among the larger PAs (Suárez et al. 2008). Moreover, apart from Cuba and the Dominican Republic, PAN management is weak and ineffective, lacking strong, well-coordinated and centralized management mechanisms (Day 2009). There is also a lack of political will to support establishment of new PAs, as well as of efforts to link existing PAs to create coherent, effective and viable landscapes for sustaining biodiversity (Day 2009). Finally, other hurdles exist such as the issue of squatting upon private lands which, because of vague legislation, may impede the establishment of new PAs or the linking of existing ones due to (i) continuous conflict between the squatter and legal land owner and (ii) insecure tenure rights of the squatter (Driver 2001).

Apart from the Caribbean islands being highlighted as a top priority for the expansion of the global PAN, some authors maintain that the linking of existing PAs in conjunction with the establishment of new PAs will buffer against the stress that climate change is expected to place upon the biodiversity of these islands (Brown et al. 2007; Chape et al. 2008). However, there is an urgent need for more scenario and empirical-based studies to determine if this suggestion is a viable adaptation option at the small island scale. Thus far, there have been no studies which have sought to investigate whether the PANs within these islands will be able to facilitate future species range shifts and sustain the survival of important species, such as endemics, as climate changes. It is also well known that: (i) the establishment and management of PANs in smaller, less developed countries have been less successful and (ii) traditional terrestrial PA models have not been designed for small ecosystems with weak management and institutional capacities (Brown et al. 2007; Parsram 2007). Hence more research is needed using terrestrial PA models specifically designed to address PAs within small islands which incorporate management uncertainty and multi-stakeholder involvement.

1.1.6 Species Distribution Modelling as a potential conservation tool for the Caribbean

The biodiversity conservation and adaptation strategies of the Caribbean SIDS presently require up-dating – by the incorporation of potential impacts of climate change upon species distributions. Such an endeavour would require the forecasting of potential species distributions within these islands; this would offer critical insight into the effectiveness of the PANs to protect valued species into the future as climate continues to change. This thesis employs one of the most recognised and well used tools for such analyses: species distribution models (Box 1981; Elith and Graham 2009; Franklin et al. 2009; Heikkinen et al. 2006; Pearson and Dawson 2003). These are correlative models which first analyse and identify environmental conditions important to the current distribution of a given species; this information is then used to define suitable areas for the species survival under future climate conditions. However, to use the results of these models effectively, knowledge of both the ecology and natural habitat availability within the study area is necessary.

1.2 Objectives

The main aim of this thesis is to evaluate the use of species distribution modelling (SDM) (in combination with assessments of forest cover (change) and vegetation ecology) as a tool to aid the development or updating of biodiversity conservation strategies for adapting to climate change within the Caribbean SIDS.

This thesis has four research objectives, using Trinidad as a case study:

(i) Document forest cover change at varying spatial scales within Trinidad between 1969 and 2007; and assess the effectiveness of the PAN in maintaining forest cover during this period.

(ii) Assess the distribution of the island's vegetation to develop a list of important tree species for SDM analysis.

(iii) Develop species distribution models (SMs) of potential distribution ranges of these tree species within the present climate using the SDM algorithm MaxEnt.

(iv) Develop SMs forecasting suitable climate space (henceforth referred to as 'potential future distribution range') of these tree species; and combining SMs (for present and future) to produce a 'collective model', which highlights areas across Trinidad and its PAN which are expected to lose, maintain and gain species forty years into the future.

(v) Assess the usefulness of SDM applied within an island context, and its potential for contributing to regional biodiversity conservation strategies

1.3 Approach

This thesis integrates the application of Geographic Information System (GIS), biogeography, ecological multivariate analyses and spatial ecology at the small island scale with SDM techniques that have, thus far, been applied mainly within continental settings.

Because of (i) a paucity of up-to-date assessments of forest cover across Trinidad and (ii) only out-dated ecological assessments of its vegetation being available, no pre-existing ecological concepts or description of forest cover within the island or its PAN were integrated. The initial chapters are devoted to the assessment of spatial and geographic limits as well as the ecological status of the existing forests within the island. These assessments were then used to support and contribute to interpretation of the SDM analyses (Chapters 4 and 5).

The majority of the data used for this thesis were either collected or derived from Trinidad (species distribution data and GIS data) or specifically generated for use within the Caribbean region [the PRECIS Caribe Regional Climate Model (RCM)]. The main exception to this trend, due to unavailability of alternative regional or local data, was the WorldClim climate data for the present period. Finally, the SDM techniques used were adapted from the international literature and applied to the small island scale.

Additionally, because of the paucity of SDM analyses at a small island scale, there was no template for the comparison and assessment of these results. Hence, concurrence with results from the ecological analyses in conjunction with expert assessment of the SMs was used as an alternative.

Because of its independence from reliance upon pre-existing ecological concepts within a given island, this study is designed as a potential template that can be adopted by the conservation authorities within any Caribbean island, irrespective of whether past assessments of the island's ecology, forest cover and species distribution data are available.

1.4 Thesis Structure

Chapter 2: GIS analyses. This chapter briefly describes the history of forest cover change across Trinidad from the post-independence era in 1969 to 2007. It begins by introducing the case study (Trinidad) and describing its PAN and the potential drivers which may threaten forested areas within the island. The analyses quantify and describe both the rate and area of change in forest cover across Trinidad at the island, PAN and buffer (internal and external to the PAN) scales between 1969 and 1994 and between 1994 and 2007. The discussion highlights the increasing vulnerability of the remaining forested areas across the island in the face of increasing anthropogenic development. These vulnerable areas are later linked with the SDM results to assess the effectiveness of the PAN to protect these species in the future.

Chapter 3: Ecological Analyses. This chapter assesses the distribution and ecology of Trinidad's forest vegetation (excluding mangrove and swamp forests) based on data from an up-to-date survey of Trinidadian vascular plants. Non-metric multivariate techniques describe community structure and highlight the main environmental parameters which are believed to influence this structure. The final product of the chapter is the generation of a list of 21 important tree species (based on the integration of ecological and commercial importance with global/regional rarity) to be used in SDM analyses.

Chapter 4: Development of bioclimatic species distribution models. This chapter introduces the theoretical issues of SDM and the generation of SMs based upon present climatic conditions. It also points out the uncertainties and limitations involved, especially with respect to the use of spatially-biased species occurrence data. It describes the preparatory work that was necessary for model generation including the details of the 1 km^2 species occurrence and present climate data, as well as how they are treated, parameterised and selected for modelling within the MaxEnt algorithm. SMs representing the potential distribution of each tree species within the present climate are generated and mapped [across both the entire island and areas of remaining forest cover (from Chapter 2)], and details are provided on how they are evaluated and short-listed for further analyses (generation of SMs within future climate). The potential of such analyses being used as a conservation tool within the Caribbean is discussed.

Chapter 5: Assessment of the potential impacts of climate change

upon the effectiveness of Trinidad's PAN to conserve the selected tree species forty years into an Special Report on Emissions Scenarios (SRES) A2 future. This chapter first defines the differences between SMs that are built based upon present versus future climatic data. It then describes the details involved in the preparation of the future climate data that are required for the forecasting of suitable climate space for 11 selected tree species forty years into an SRES A2 future. The SMs for the present (Chapter 4) and future climates of each of these species are then combined to produce change maps which illustrate the expected contraction, expansion or stable areas of each species' climate space. Individual change maps are combined to illustrate the anticipated change in the 'collective presence' of these species. The collective presence map is used to assess the effectiveness of Trinidad's existing PAN to secure the collective species survival. These results are used to discuss the implications of climate change for conservation planning at a regional versus an island scale.

Chapter 6: Conclusion. This chapter summarises the findings of the thesis and also highlights the challenges that were faced in trying to apply traditionally continental-scale SDM techniques to a small island scale. Suggestions of future work which may help to resolve these issues are made together with a discussion of a regional rather than island based approach to biodiversity conservation within the Caribbean SIDS. The development of 'Novel Community Arks' is suggested as a means of facilitating regional biodiversity conservation by enhancing the (generally disturbed) vegetation of regional PAs with high value, resilient species.

1.5 Summary and contributions of this study

This study represents the first attempt to explore the potential impacts of climate change upon terrestrial plant species diversity within a Caribbean SIDS, as well as its implications for conservation strategies which seek to incorporate future climatic conditions into its planning and management.

The following research gains are offered:

(i) An updated and quantitative assessment of changes in forest cover across the island of Trinidad from 1969 to the present.

(ii) The first reported description of the community structure of the forests on Trinidad based upon the vascular vegetation across the island. This differs from traditional assessments which have focused solely on the use of dominant timber species across state-owned lands.

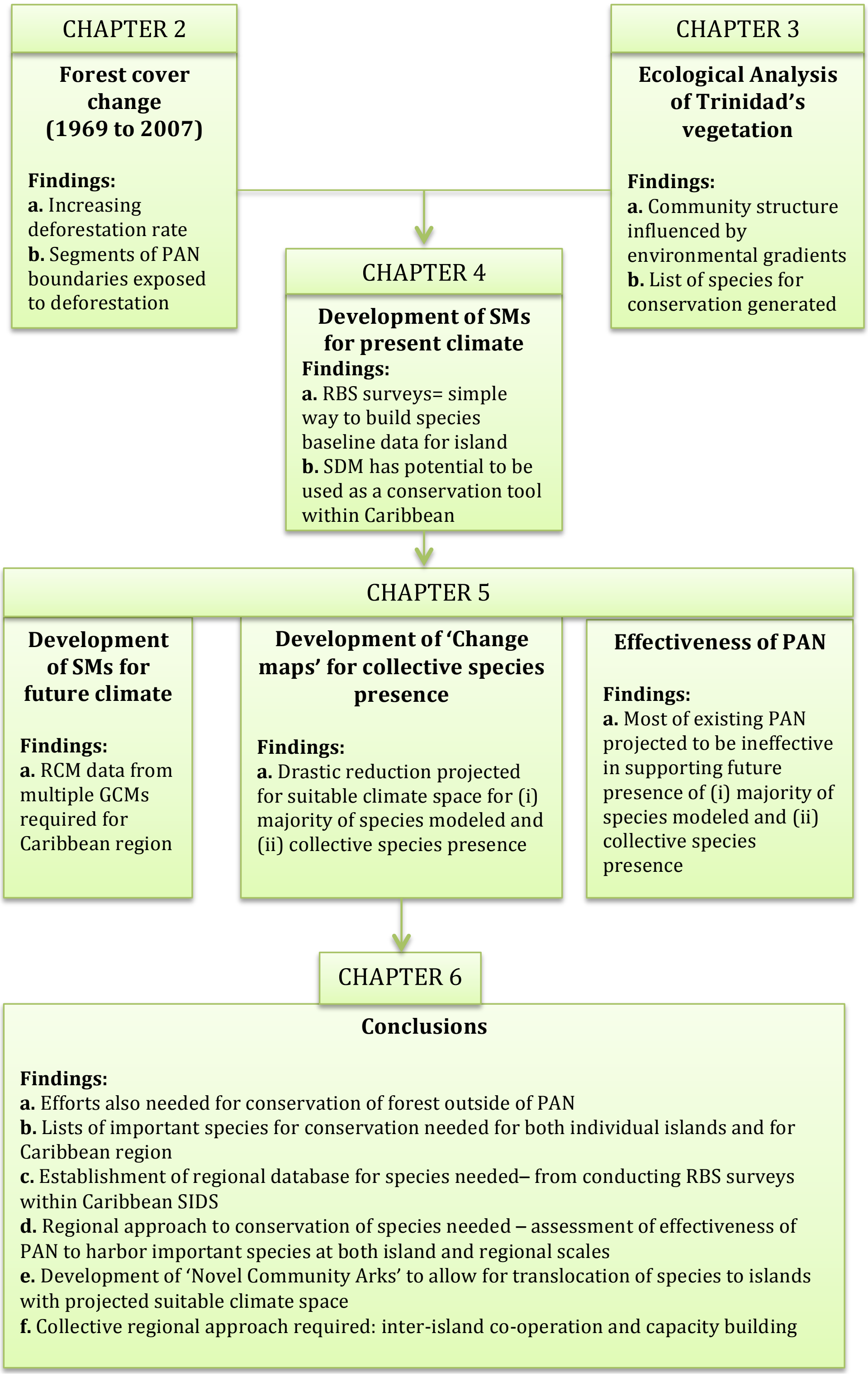
(iii) Original analyses that apply ecological understanding of terrestrial plant species at a small island scale to species distribution modelling techniques.

(iv) First reported quantification of expected change in the climate space of terrestrial plant species in response to climate change within the Caribbean SIDS.

(v) First reported assessment of the expected change in effectiveness of the PAN within a small island developing state as a result of expected changes in climate.

This study provides a template which can be built upon by both conservation planners and researchers to develop SDM, as an important tool for enhancing the region's biodiversity conservation measures by integrating climate change into these strategies.

1.6 Theoretical Framework



CHAPTER 2

Forest cover change (1969 to 2007)

Findings:
a. Increasing deforestation rate
b. Segments of PAN boundaries exposed to deforestation

CHAPTER 3

Ecological Analysis of Trinidad's vegetation

Findings:
a. Community structure influenced by environmental gradients
b. List of species for conservation generated

CHAPTER 4

Development of SMs for present climate

Findings:
a. RBS surveys= simple way to build species baseline data for island
b. SDM has potential to be used as a conservation tool within Caribbean

CHAPTER 5

Development of SMs for future climate

Findings:
a. RCM data from multiple GCMs required for Caribbean region

Development of 'Change maps' for collective species presence

Findings:
a. Drastic reduction projected for suitable climate space for (i) majority of species modeled and (ii) collective species presence

Effectiveness of PAN

Findings:
a. Most of existing PAN projected to be ineffective in supporting future presence of (i) majority of species modeled and (ii) collective species presence

CHAPTER 6

Conclusions

Findings:
a. Efforts also needed for conservation of forest outside of PAN
b. Lists of important species for conservation needed for both individual islands and for Caribbean region
c. Establishment of regional database for species needed– from conducting RBS surveys within Caribbean SIDS
d. Regional approach to conservation of species needed – assessment of effectiveness of PAN to harbor important species at both island and regional scales
e. Development of 'Novel Community Arks' to allow for translocation of species to islands with projected suitable climate space
f. Collective regional approach required: inter-island co-operation and capacity building

Figure 1.1: Theoretical framework

Chapter 2

Forest cover change across Trinidad from 1969 to 2007

2.1 Introduction

The Caribbean archipelago is a global biodiversity hotspot which contains high concentrations of endemic species, and has been identified as a global priority for conservation (Brooks et al. 2006; Maunder et al. 2008; Mittermeier et al. 2005; Myers et al. 2000). However, the limited geographic space of these islands, within which terrain often restricts human habitation and use, places acute population pressure on the remaining habitable areas of land (Lugo et al. 1981; Pulwarty et al. 2010). As such, deforestation, forest fragmentation and habitat loss have been, and continue to be, one of the consequences of such pressure. For example, estimations of forest removal and fragmentation within Jamaica during the 1980s to the early part of the 2000s were consistently amongst the highest within the tropics (Eyre 1987; Rudel 2005; Tole 2002). Indeed, this continued high rate of habitat loss over the past decades has led to this archipelago, at the turn of the century, being identified by authors such as Brooks et al. (2002) as the region which is expected to lose the most endemics.

An area of land is usually deforested if the benefits of deforestation are perceived to outweigh the cost. Studies that document past and present deforestation, as well as predict future trends, stress socio-cultural, bio-geophysical and ecological perspectives as keys to understanding deforestation, especially at the local scale. Such key determinants often pervade conservation policies and the values placed on forests in different places and countries (Laurance 2007; Rompré et al. 2008; Rudel 2006; Strömquist and Backéus 2009; Veldkamp and Lambin 2001). Furthermore, others argue that deforestation in developing countries is a legacy of historical socio-economic activity, combined with present day events (Armesto et al. 2010; MA 2003; Sala et al. 2000; Vitousek 1994).

The remainder of this introduction describes some of the issues connected to deforestation as well as the establishment and effectiveness of PAs, especially within Caribbean islands.

2.1.1 Past deforestation in the Caribbean

Deforestation in many Caribbean SIDS has been documented to the first establishment of Amerindian settlements. Amerindian cultures deforested land for the establishment of settlements and for several types of agriculture, including sedentary, labour intensive crop farming as well as slash-and-burn shifting agriculture (Honychurch 1997). Recent evidence suggests that Amerindian activities contributed to substantial areas of deforestation until their populations were almost annihilated by colonising Europeans (Strömquist and Backéus 2009). European colonists subsequently cleared forests to establish villages, towns and, eventually, sugarcane, cocoa and coffee plantations (Brothers 1997; Honychurch 1997).

Details of Caribbean vegetation from the start of the 20^{th} century vary from non-existent to detailed inventories carried out during colonial times. Even when inventory data are available, there is often a paucity of accurate maps for comparison with modern forest cover maps (Helmer et al. 2008). In some cases, details can be derived from aerial photographs taken in the 1940s and satellite imagery from the 1960s.

2.1.2 Recent deforestation trends in the Caribbean

Until the 1990s, agriculture was a major source of livelihood, and hence of deforestation, in many parts of the insular Caribbean. Deforestation was promoted by factors such as international credit initiatives aimed at boosting export earnings, increasing populations and the debt crisis (Eyre 1987; Helmer et al. 2008; Tole 2001; Weis 2000). Additionally, large areas of Caribbean islands were occupied by sugarcane, banana, cocoa and coffee plantations established in colonial times, as well as large and small scale cash crop farming (Evelyn and Camirand 2003; Parés-Ramos et al. 2008). Furthermore, since the majority of flat, inhabitable land was located along coastlines, coastal forests, mangroves and wetlands were cleared for the establishment of major settlements, and tourism infrastructure (Parés-Ramos et al. 2008). On islands such as Trinidad and Puerto Rico, urban sprawl and, to a lesser extent, industry, propagated by road networks, have contributed to deforestation within traditionally remote areas (Kenny 2000; Martinuzzi et al. 2007).

2.1.3 Drivers of deforestation

As in many other developing countries, Caribbean deforestation is reduced in areas with low agricultural value, steep slopes, high elevations and areas distant from market centres (Parés-Ramos et al. 2008). Cropper et al. (2001) has argued such areas are likely to be designated as PAs in order to avoid political conflict. Other studies have shown that both urbanisation and agriculture are negatively correlated with elevation and topographic complexity (Evelyn and Camirand 2003; Fuller 2006; Helmer et al. 2008; Lugo 2000; Parés-Ramos et al. 2008). It is therefore unsurprising that on almost all Caribbean islands higher elevation forests are generally protected by formal or informal reserves. For example, the prohibition of land development above 305 m altitude on Nevis has resulted in 98% to 100% of existing evergreen and cloud forests within the island being located above this elevation (Helmer et al. 2008); while in contrast, the proportion of ecological zones and remaining forests that are protected at lower elevations is small and under-represented (Helmer 2004). Additionally, high poverty levels in areas, such as rural Jamaica, have been associated with opportunistic deforestation within National Parks (Evelyn and Camirand 2003). Such activities continue unregulated in many areas because the laws which prohibit deforestation within the boundaries of PAs are generally unenforced. While, there is evidence that law enforcement can be quite effective in reducing deforestation within PAs (Gaveau et al. 2009); such enforcement is not simple and requires the support of socio-economic and political initiatives, hence it is still a cause that remains to be championed by many Caribbean governments.

2.1.4 Forest regrowth patterns

In several Caribbean countries, land cover analyses based on satellite imagery, have revealed a decrease in areas of deforestation and a subsequent increase in forest patch size despite increasing human population densities and urban sprawl (Helmer et al. 2008; Lugo 2002). Over the last decade, increases in forest cover, by more than 50%, have been reported in islands such as Puerto Rico, Jamaica, St. Kitts, Nevis, Grenada and Barbados (Helmer et al. 2008).

This trend is a result of decreasing agricultural activity within the insular Caribbean. Sugar cane cultivation which previously occupied substantial amounts of undulating lowlands within the region has long been declining, and continues to do so. For example, in 2003, sugar production declined significantly in Jamaica, Trinidad and Tobago, Barbados, and St. Kitts and Nevis compared to production levels in the 1980s and the first half of the 1990s. This was due to increased competition from more highly mechanised operations in Brazil and the United States (McDonald 2004). Additionally, the European Union ended its import quotas and price subsidies that gave banana and sugar farmers in former colonies preferential access to European markets. As a consequence, state-run sugar companies have closed in Trinidad and Tobago (2003) and in St. Kitts and Nevis (2005).

Land-cover changes on islands such as St. Kitts and Nevis, Barbados and Puerto Rico are very similar; increases in forest and urban/built-up lands are the result of an economic shift from agriculture to industry, manufacturing and services (Helmer 2004; Kennaway and Helmer 2007; Mar López et al. 2001; Rudel et al. 2000). The resulting shift of rural populations to urban areas in search of wage labour is viewed as the critical element in the regeneration of forests on abandoned pastures and agricultural lands (Grau et al. 2003; Rivera and Aide 1998; Rudel et al. 2000). However, it remains to be seen whether decreases in land under cultivation will result in the allocation of more land for conservation at low altitudes within islands such as Puerto Rico, St. Kitts and Nevis, Barbados and Grenada. Competition of often irreversible land use changes such as housing, industry and commercial centres for these newly available areas may require legislation to protect and restore (i) drier forests on formerly cultivated lands and (ii) mangroves – both of which were poorly represented and protected during the pre-agricultural decline era (Lugo 2002; Parés-Ramos et al. 2008).

Additionally, there are indications that recent socioeconomic trends have begun to induce suburban growth, urban population decline as well as the development of rural areas (Munroe et al. 2005). For example, in islands such as Puerto Rico, urban cover in some areas only increased by 7%, while forest cover increased by 41%, indicating the underutilization of urban areas in preference for open, less densely populated, and even rural spaces for housing and development. Moreover, spatial analysis of population growth, based on elevation range within Puerto Rico, showed rapidly growing suburban populations in all elevation regions, although the largest increase was in the coastal plains (Lambin and Geist 2003).

2.1.5 Protected areas

Protected areas (PAs) are currently one of the main instruments that conservation planners across the world use for the conservation of species and other natural features; they are also used to facilitate recreational activities and scientific research (McNeely and Ness 1995). A paradigm shift occurred within recent decades in which the ‘flux of nature’ replaced the ‘balance of nature’ model (i.e., that because of variation and complexity within natural systems, equilibrium is not always reached) as the prevailing dogma within conservation ecology (Barrett and Barrett 1997; Fiedler et al. 1997) which has resulted in increased sophistication in PA design and management.

While the first PAs were based upon restricted access, today a variety of conservation models exist. These range from stringent restricted access to community-based management designs. Many PAs are now developed in terms of ecosystem management, where conservation objectives focus upon sustaining spatial and temporal heterogeneity in order to promote resilience and variability; rather than specific fixed vegetation assemblages or specific landscapes (Grumbine 1997; Gunderson and Holling 2001).

PA designation in several parts of the developing world has however not evolved in this manner. In order to stem tropical forest decline it became common practice for governments to designate the last remaining tropical forest fragments as PAs (Naughton-Treves et al. 2005). The success of these PAs depends on factors such as size, location, management strategy as well as exogenous factors. Furthermore, many PAs have been designed without formal buffer zones (Cropper et al. 2001). Indeed, many boundaries become *de facto* buffer zones, and the risk of encroachment of these areas is high due to pressure from exogenous factors, such as urbanisation and agriculture (Evelyn and Camirand 2003).

In the Caribbean, isolated examples of the establishment of PAs in the form of Forest Reserves date back as early as 1776 when 2,430 ha of forest within the Main Forest Ridge Reserve in Tobago were set aside for “protection of the rains” (Beard 1944b; Ramdial 1980). However, the majority of Forest Reserves in the English-speaking Caribbean became established in the early 20th century; the primary interest was in controlling the harvest of a few economic tree species rather than conservation (Kenny 2000). In due course, the focus of some of these Forest Reserves shifted towards forest preservation for environmental reasons, such as watershed protection (Kenny 2000). During most of the 20th century, there was weak support for the PA infrastructure, principally due to conflict with developmental land use as well as the reluctance of governments to make long-term funding commitments (Leach 2008). Indeed, the detailed surveys necessary for the recognition and demarcation of National Parks or Wildlife Sanctuaries have been mainly financed by international agencies (Leach 2008). However, during the last three decades, a combination of international attention given to deforestation, the increasing involvement of powerful local and international Non-Governmental Organisations (NGOs), as well as the establishment of

Natural Heritage sites, has resulted in a substantial increase in the number of PAs in the Caribbean.

2.1.6 The effectiveness of PAs within developing countries

Most PAs are usually considered successful based on having a lower deforestation rate inside compared to outside their boundaries (DeFries et al. 2005; Joppa et al. 2008). However, this is based upon the assumption that both the inside and outside of PAs (and buffers) are exposed to the same environmental conditions and threats (Mas 2005). This has prompted calls by some researchers for comparative studies which investigate levels of degradation both before and after the establishment of PAs (Gaveau et al. 2007; Liu et al. 2001). This is particularly pertinent for PAs that have been established in mountainous areas, as the forests in these regions are known to survive because of inaccessibility. Thus, comparisons of deforestation rates inside versus outside PA boundaries overestimate PA effectiveness as they do not incorporate the natural or *de facto* (Joppa et al. 2008) protection that is provided by complex terrain and accessibility.

Few studies have assessed the success of PAs in halting deforestation within their boundaries (Mas 2005; Oliveira et al. 2007; Southworth et al. 2004; Sánchez-Azofeifa et al. 2003) with an increasing number of calls from conservationists for such evaluation (Ferraro and Pattanayak 2006; Liu et al. 2001; McDonald-Madden et al. 2009). Separate temporal gap analyses of PAs conducted in Guatemala, China, Sumatra and Jamaica have indicated varying degrees of success of PAs due to decreases in areas of net deforestation. However, these studies also indicate that such success is limited as forest clearance and fragmentation within the PA boundaries have resulted in species range shifts and biodiversity loss equal to or below pre-PA levels. This situation may not be peculiar to these locations alone, as it is still unclear whether PAs are effectively protected, especially within developing countries.

2.1.7 Problems associated with deforestation assessment within the Caribbean

Generally, few studies have sought to assess historical as well as present-day deforestation drivers in the Caribbean (Evelyn and Camirand 2003; Helmer 2004; Helmer et al. 2008; Parés-Ramos et al. 2008). This is linked to several obstacles, central among which are basic problems related to the quality of institutional data. For example, the documentation of changes in forest cover and deforestation within most Caribbean islands has been carried out by the Food and Agriculture Organization of the United Nations (FAO) since 1972. However, over the last decade it became clear that the FAO statistics published for several of these islands were flawed due to a variety of basic discrepancies; for example, areas of forest cover reported for individual islands could not be easily compared as they were not all based on the same definition of ‘forest cover’ (Evelyn and Camirand 2003; Fuller 2006).

Additionally, there is a paucity of field inventory data in most countries. Apart from being sparse and inconsistent, field inventories are expensive and require large amounts of time to update past inventories. The work of John Stanley Beard is an important source of past inventory data for the islands of the Lesser Antilles as well as Trinidad and Tobago during the first half of the twentieth century. As an ecologist, employed by the British Crown during the 1940s (Beard 1946b), Beard extensively surveyed, inventoried and mapped the vegetation on the islands of the Lesser Antilles from 1942 to 1946 (Beard 1944a, 1949). Furthermore, he estimated the areas of different forest types, pasture, woodlands, cultivated lands and “other uncultivated" lands (towns, villages, sand dunes, salt flats). Most modern day studies have used the tabular results from his publications for comparison since (i) the scales of his published maps are generally too coarse for change detection within a geographic information system and (ii) he did not detail his methods for mapping or estimating land cover areas (Helmer et al. 2008). However, Beard's published estimates of land cover and forest areas are still a primary reference since they are the only documents of their kind available from that era (Helmer et al. 2008).

While deforestation studies using satellite images have been carried out (mainly Puerto Rico and Jamaica), these are usually on the impetus of academic research (Lugo 2002; Parés-Ramos et al. 2008). Most authors have reported the use of satellite imagery to conduct detailed mapping and interpretation of deforestation patterns within the small geographical areas of these islands to be challenging. This is due to a combination of factors including highly variable terrain, steep environmental gradients, spectral confusion between land cover classes and almost constant cloud cover (Helmer et al. 2008). Additionally, methods that work well in one landscape may not distinguish classes that are important in another. Furthermore, ground-truthing in landscape which is characteristically complex, inaccessible and fragmented is difficult. Additionally, land cover changes occur within short distances of each other and may inhibit Global Positioning System (GPS) accuracy, especially under forest cover.

This chapter describes and analyses the change in forest cover from 1969 to 2007 within the island of Trinidad. Documentation of changes in forest cover is conducted at the island and PAN scales, and emphasis is placed upon assessing the effectiveness of the PAN in conserving forest cover over this period. Such analyses which explore past to present trends in forest cover change are necessary in order to estimate areas within the island which are likely to contain forests in the future. This understanding is an essential component for achieving the ultimate goal of this thesis which seeks to indicate areas within Trinidad which will be suitable for the survival of selected species within a future changed climate.

2.2 Case Study – the island of Trinidad

Trinidad is the southernmost island of the Caribbean, located between the Caribbean Sea and the North Atlantic Ocean (Figure 2.1)[1]. It is the larger of the islands in the twin-island state of Trinidad and Tobago, and is located about 12 km from the Venezuelan coast, at the edge of the South American continental shelf, approximately between 10° 38′ N latitude and 61° 23′ W longitude (Algar and Pindell 1993). Geologically, Trinidad is part of the mainland, and appears to have separated from northern Venezuela approximately 11,000 years ago at the end of the last glaciation (Joseph 1970).

As a result of its close proximity to the South American mainland, Trinidad's flora is a relic of the immediate delta region from which it separated 11,000 years ago. This period of separation has been insufficient to allow for the evolution of many endemics, however, this relict flora has been augmented by a few colonising species as well as a larger number of exotic species that have been introduced via human colonisation (Kenny 2000; Santiago-Valentin and Olmstead 2004).

Between 44% and 48% of Trinidad is currently covered by forest, of which approximately half is 'protected forest' (EMA 2005; GOTT 2009a). Terrestrial PAs include an estimated thirty-six Forest Reserves, eleven Wildlife Sanctuaries, a National Park (the Chaguaramas Peninsula), nineteen Prohibited Areas and three Environmentally Sensitive Areas (ESAs) (GOTT 2009b). There are also *de facto*

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[1] All figures are placed in a block at the end of each chapter.

PAs including about eight unproclaimed Forest Reserves managed by the Forestry Division, a National Landmark and several Historic Sites and Recreational Parks (GOTT 2009b).

However many of these figures are considered to be 'transient' in nature since there is to date, no official map of the PAN within Trinidad (Ali, pers. comm. 2012; Ragoonanan, pers. comm. 2012). Reasons for the absence of such a map include unresolved boundary issues for some PAs, as well as some PAs being presently classified under multiple categories. For example, some Forest Reserves have been simultaneously designated as other categories of PAs such as: Wildlife Sanctuaries, Prohibited Areas and ESAs (Ragoonanan, pers. comm. 2012; Ramnath, pers. comm. 2012). This creates further management challenges due to administrative and legislative overlap (GOTT 2009a). Moreover, many of these areas are located immediately adjacent to each other – forming contiguous blocks which are referred to as 'protected areas'. The contiguous blocks (and the individual reserves of which they are comprised) which feature prominently within these analyses are illustrated in Figure 2.2.

Furthermore, the Draft National Forestry Policy (GOTT 2009a) of Trinidad and Tobago considers there are no recent official data on: (i) the forest cover; (ii) the rate of land use change; and (iii) the rate loss of forests within Trinidad. However, recent unofficial estimates indicate there has been a loss of up to 6% in total forest area (for Trinidad and Tobago) between 1969 and 2000. Also, forests may be degraded through poor management and opportunistic exploitation (GOTT 2009a).

The World Bank estimated Trinidad and Tobago's population (2009) to be approximately 1.33 million during 2009 with an annual growth rate of 0.4%, and a population density close to 250 persons per square kilometre; one of the highest in the Western Hemisphere (WBG 2011). The economy and prosperity of Trinidad and Tobago has been, and continues to be, strongly associated with the development of natural gas and petrochemical industries (Coppin and Olsen 2007; Hosein 2007). Industrial development has been encouraged by government subsidies of resource exploitation (Dillon Consulting 2004). These factors in combination with the inadequate valuation of the natural resources, goods and services associated with the island's biodiversity and a general public and political apathy towards environmental issues continue to exert tremendous pressure upon the remaining natural areas within the country (Fairhead and Leach 2003; Kenny 2000). Symptomatic of this situation is a continued loss of forest cover within the island (including within PAs) and a consequent decrease in wildlife populations that inhabit the remaining forests (Dillon Consulting 2004; GOTT 2009b; Kenny 2000).

Intrinsic to the threatened and deteriorating state of remaining forests is that natural resource management and planning in Trinidad and Tobago remains inconsistent, fragmented and chaotic because of out-dated legislation and policy and a lack of a current national land use planning framework (GOTT 2009b). The 1950 'Forest Act', the main legislation that governs forest management in Trinidad and Tobago, is a colonial document designed to regulate the exploitation and sale of timber and non-timber products from State lands; it affords little for the management and protection of natural forests which are not 'production forests'. Under this legislation 'Forest Reserves' may be designated but access to these Reserves is not restricted. This has been a main contributor to a variety of destructive practices occurring within these Forest Reserves, ranging from forest fires to residential and agricultural squatting (Dillon Consulting 2004).

2.3 Methods

Quantification of change in Trinidadian forest cover from the early post-independence era to the present (1969–2007) and the development of Forest Disturbance and Forest Quality maps were all undertaken within a GIS created using ArcGIS 9.3.

The initial steps consisted of constructing Forest Cover polygon themes for the island from Land Use polygon shape files obtained from the Department of Geomatics Engineering and Land Management (DGLM), University of the West Indies (UWI), for the years 1969, 1994 and 2007. These Forest Cover polygon themes together with supplemental polygon themes (the PAN of Trinidad and the outline of Trinidad's coastline) were used to construct, quantify and analyse changes in forest cover, Forest Disturbance and Forest Quality data at varying spatial scales during the above mentioned years. These spatial scales included: (a) the island, (b) the PAN and (c) the buffer zones, constructed at varying distances from the PAN boundaries (internal and external).

2.3.1 Source Data and associated map accuracy

2.3.1.1 Positional errors

Land use data polygon shape files for 1969, 1994 and 2007, were all created within the World Geodetic System (WGS) 1984 datum, Universal Transverse Mercator (UTM) projection. However, they varied with respect to their source, scale and accuracy. The 1969 land use shape file was originally derived from Sheets 3 to 76 of the Trinidad and Tobago Topographic map series 1:25,000 (GOTT 1972b). Based on 1969 aerial photography, the positional error associated with this shape file is given as ±10 m. The 1994 land use shape file was derived from a 1:25,000 orthophoto mosaic of aerial photography conducted in 1994. The associated positional error of this shape file is given as ±2 m. The 2007 shape file was created from IKONOS[2] satellite imagery with a resolution of 1m. The associated positional error of this shape file is given as ±3 m.

The PAN was supplied by the National Forestry Division of Trinidad and Tobago, and has an associated positional error of ±30 m. Protected Areas (PAs) and Forest Reserves were demarcated by surveying technicians, not licensed surveyors, consequently no official or legal PAN map exists. The PAN used in these analyses however represents a combination of the Forest Reserves and PAs (excluding the Chaguaramas National Park) that are acknowledged on a practicing basis.

2.3.1.2 Classification accuracy

The thematic accuracy of each land use epoch (1969, 1994 and 2007) was also provided by the UWI's DGLM. 'Classification errors' were used to derive a measure of accuracy (classification accuracy) for indicating the degree of confidence associated with each mapped land use theme within a given epoch. These errors were calculated using a confusion matrix to compare and quantify the thematic agreement between selected points and (i) ground-truthed data and/or (ii) fine resolution remote sensor data for each land use theme within a given epoch (Jehu 2011; Veregin 1989).

The classification accuracy for the land use epochs are as follows:

(i) 1969 = 95%

(ii) 1994 = 90%

(iii) 2007 = 91.3%

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[2] IKONOS is a commercial earth observation satellite from India.

These classification accuracies apply to all quantifications of forest cover change in the analyses to follow.

2.3.2 Creation of Forest Cover themes for 1969, 1994 and 2007

The land use polygon layers for 1969, 1994 and 2007 were originally classified into land use categories based on two different systems. The land use categories for 1969 were based on criteria developed by the Ministry of Agriculture, Land and Marine Resources, Lands and Surveys Division during 1972. These were different to the categories used in the development of the 1994 and 2007 land use layers, which were based on the Anderson's Classification System (Anderson et al. 1976). In order to overcome the problem of data compatibility due to differences in classification of land use and to keep with the primary objective of this study, quantification and analyses in this chapter were limited to forest cover. Other proximate causes of deforestation such as agriculture and settlement were ignored. Forest Cover polygon themes (1969, 1994 and 2007) were created by re-classifying original land use categories into either 'Forest' or 'Non-Forest' (Table 2.1)[3]. All polygons labelled as 'Forest' within each Forest Cover theme were then aggregated into a single, continuous polygon layer (Figures 2.3 to 2.5).

2.3.3 Creation of internal and external buffer zones from the PAN boundaries

Construction of buffer zones involved using both PAN and Trinidadian coastline shape files. Concentric buffer zones at 250 m, 500 m, 1,000 m and 2,000 m distances from the boundaries of the PAN were constructed, using the 'Multiple Ring Buffer' function within the Analysis Tools, on both the internal and external

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[3] All tables are placed in a block at the end of each chapter.

sides of the PAN boundaries. The external buffer zones were then clipped onto the Trinidadian coastline polygon theme in order to ensure that no buffer zones extended beyond the coastal boundary limits of the island (Figures 2.6 and 2.7).

2.3.4 Quantification of forest cover at the buffer, PAN and island scales

Understanding change in forest cover within Trinidad from early post-independence era to present (1969–2007), requires the area (%) of forest cover at differing scales to be determined. The area of forest cover within each buffer zone (for each year) was calculated by merging each of the individual buffer polygons with each of the Dissolved Forest Cover polygons (1969, 1994 and 2007) using the 'Clip' function within the Analysis Tools. This enabled the geometric intersection of both polygon themes within the boundary limits of the given buffer polygon. These clipped buffer themes showed the spatial delineation of forest cover exclusively within buffer boundaries (Figures 2.8 and 2.9). The Field Calculator was used to quantify the total area of each buffer polygon and its area of forest cover. The same process was repeated for the PAN (Figures 2.10 to 2.12) with the Field Calculator being used to calculate forest cover at the island scale from the Dissolved Forest Cover polygons and Trinidad's Coastline polygon (Figures 2.3 to 2.5).

2.3.5 Quantification of deforestation and reforestation during Periods A and B at the island, PAN and buffer (zone) scales

The Dissolved Forest Cover polygons were used to define regions of deforestation and reforestation between 1969 and 1994 (Period A) and 1994 and 2007 (Period B; Figures 2.13 and 2.14). The deforestation and reforestation areas outlined for Period B were those which were new (occurred after Period A), and are not cumulative areas of deforestation or reforestation between 1969 and 2007. The resulting areas of deforestation and reforestation were saved as unique polygon themes, and clipped with the buffer (Figures 2.15 and 2.16) and PAN polygons (Figures 2.17, 2.18, 2.19 and 2.20). The Field Calculator was used to calculate areas of deforestation and reforestation for each period at the buffer (internal and external), PAN and island scales.

2.3.6 Rate for forest cover change during Period A (1969 to 1994) and Period B (1994 to 2007)

The magnitude and direction of change in forest cover between successive years at the island, PAN and buffer (internal and external) scales were calculated according to Puyravaud (2003):

$$\text{Rate of change in forest cover} = \frac{\ln F(t_2) - \ln F(t_1)}{t_2 - t_1} \times 100 \tag{2.1}$$

where F is the area under forest (ha), t_1 is time 1 (base year) and t_2 is time 2 (current year). These results (Table 2.2) were expressed as 'Annual rate of change in forest cover' for each period.

In order to investigate the effectiveness of the PAN during Period A and B, simple statistical comparisons of these rates of forest cover change inside and outside the PAN boundary (at the PAN and buffer scales [2000 m, 1000 m, 500 m and 250 m]) were done using chi-square tests of independence .

2.3.7 Forest disturbance and forest quality

‘Forest Disturbance’ is defined as the chronological frequency of deforestation across the forested areas of Trinidad which is a coarse indicator of ‘Forest Quality’. To map Forest Disturbance (1969, 1994 and 2007), the respective Dissolved Forest Cover polygons were first converted from polygon to raster format. Each pixel within the Dissolved Forest Cover raster grids represented an area of 1 km^2.

A pixel-to-pixel comparison of the three Dissolved Forest Cover maps was used to map different patterns of change from forest to non-forest and vice-versa. In the raster grids, each given pixel, arranged in the chronological sequence 1969 to 1994 to 2007, was scored as either ‘Forest’ (F) or ‘Non-Forest’ (N). A total of eight sequence combinations were derived (Table 2.3) and the ‘Times’ function within the Spatial Analyst Tool was used to multiply the binary 1969 Dissolved Forest Cover raster grid by 4 (where $4 = 2^2$ in Table 2.3), and the binary 1994 Dissolved Forest Cover raster grid by 2 (where $2 = 2^1$ in Table 2.3). These products were added to each other, and the sum added to the unchanged 2007 Dissolved Forest Cover raster grid (Table 2.3). The final result, for each year, was a raster grid which reflected the distribution of Forest Disturbance within the island. These raster grids were converted into polygon format (Figure 2.21) and these Disturbance Index polygon layers were then clipped with the PAN and buffer polygons to allow for the quantification of Forest Disturbance at the island, PAN and buffer scales.

Forest Quality categories (Figure 2.22) were derived for all chronological sequences within which ‘Forest’ was the final stage of the sequence (Table 2.3). These consisted of three coarse categories which ranged from Grade 1 (undisturbed forest cover throughout the entire period) to Grade 3 (alternating ‘Forest’ and ‘Non-Forest’ states and/or recently forested areas). These categories were quantified at the island, PAN and buffer scales.

2.4 Results

These results describe changes in forest cover that occurred during Periods A and B at the buffer (to the PAN) scales. These changes are described with respect to: (i) total forest cover, (ii) deforestation and reforestation and (iii) forest disturbance and forest quality.

2.4.1 Total Forest Cover

2.4.1.1 Island scale

The total area of forest cover within the island of Trinidad has not been constant during 1969, 1994 and 2007 (Figure 2.23). Forest cover increased from approximately 59% of the island's total area in 1969 to 63% in 1994, which was followed by an almost equal decrease to 58% between 1994 and 2007. This trend is mirrored in Figures 2.3 to 2.5, which revealed changes in the degree and placement of pockets of forest cover loss that occurred within both the island and the PAN.

When compared to island-wide forest cover data available from the FAO (FAO 2010) for 1969, 1994 and 2005 (time period closest to 2007), this study's forest cover totals for 1969 and 2007 were approximately 10,000 ha less than the FAO data, while its forest cover figure for 1994 was about 5,000 ha greater than the FAO's forest cover estimate (Figure 2.23). This discrepancy may have arisen as a result of two reasons, firstly, the FAO's definition of forest cover considers a canopy cover of 10% or more as forest, however this study defined forest cover as areas which contained closed, continuous canopy cover. Hence, it is unsurprising that FAO forest cover figures would be greater than those of this study. The exception to this trend was for 1994 - for which the the FAO data was based on estimates of forest cover across the island and not on detailed quantification of forest cover from aerial photography.

During Period A (1969 to 1994) an overall coalescing of forest cover was observed at both the island and PAN scale which resulted in the major forested regions within the island appearing almost continuous and non-fragmented (Figures 2.3 and 2.4). An exception to this trend was observed within the south-western part of the island, where large portions of forest were removed from areas both inside and outside of the PAN.

However, during Period B (1994 to 2007) a reversal of this coalescence was seen, with the Dissolved Forest Cover for 2007 (Figure 2.5) appearing more fragmented and less continuous on an island-wide basis compared to that of 1994 (Figure 2.4). Additionally, encroachment into PAs within the North, Central and Southern parts of the island was observed for this period.

Finally, compared to 1969 the forest cover of the present day (2007) is less within the south-central and south-western parts of the island (including within the PAN) (Figures 2.3 and 2.5). Additionally, there is now much less connectivity of the forests within the eastern part of the Northern Range with the forests located within the central and southern parts of the island (Area A).

2.4.1.2 PAN scale

The total area of forest cover within Trinidad's PAN fluctuated between 1969 and 2007, with an initial increase of approximately 1% during Period A – from approximately 145,000 ha in 1969 to about 146,200 ha in 1994. There was a subsequent decrease of approximately 4% during Period B – leading to a forest cover of 139,400 ha in 2007. Hence a decrease of approximately 5,600 ha of forest cover occurred within the PAN from 1969 to 2007 (Figure 2.24).

Closer inspection at the PAN scale (Figures 2.10 to 2.12) showed that during Period A, there was a reversal of the majority of small deforestation pockets within most of the island's PAs which resulted in an increase in the total area of forest cover within the PAN. Exceptions to this trend were observed for PA within (i) the south-western part of the island (PA-sw) and (ii) Area A – the southern part of PA-ne in conjunction with the series of smaller connecting PAs immediately south of this area.

During Period B, there was continued erosion of forested areas within Area A and the PA-sw. Additionally, with the exception of the northern part of PA-ne, loss of forest cover occurred within all other PAs of the PAN, most noticeable of which was the large area of deforestation within the south-central Protected Area (PA-sc).

2.4.1.3 Buffer scales

Total forest cover at the buffer scales, varied with distance from the PAN boundary – with the proportion of forest cover within the buffers inside the PAN being greater than in those outside the PAN at all scales during 1969, 1994 and 2007 (Figure 2.25). Within the external buffers, the percentage of total forest cover decreased consistently as distance from the PAN boundary increased; while the reverse trend was observed within the internal buffers. However, as observed in Section 2.4.1.2 above, the PAN was not effective in maintaining and increasing forest cover with time. This was also reflected at the buffer scale with the percentage of forest cover within the internal buffers for 1994 being consistently greater than that of 1969 at all scales; while during 2007, there was a decrease of total forest cover to below the 1969 levels at all buffer scales.

2.4.2 Deforestation and reforestation

2.4.2.1 Island scale

During Period A, the total reforested area exceeded deforested areas by approximately 17,000 ha at the island scale (Figure 2.26). However, this trend was reversed during Period B, with deforestation exceeding reforestation by approximately 25,400 ha. During Period A both deforestation and reforestation occurred across much of the island, although mainly within areas of land which were not part of the PAN (Figures 2.13, 2.17 and 2.18). This was dramatically different during Period B when, apart from very little new areas of reforestation occurring, new areas of deforestation developed further eastwards, and nearer to the PAN boundaries (Figures 2.14, 2.19 and 2.20).

During Period A the largest network of reforestation patches was located at Area C, located south of Area A (Figure 2.13). Other areas included the central portion of the south-facing slopes of the Northern Range, as well as along the north-eastern and north-central coastlines. Elsewhere on the island, reforestation occurred in small scattered patches – mainly outside of the PAN. Noticeably large areas of deforestation, (apart from the above-mentioned Area A) occurred within Area B (to the west of Area A) as well as within PA-sw and its northern, eastern and southern external peripheries (Figures 2.13, 2.17 and 2.18).

Unlike Period A, reforestation occurred only in a few small pockets within the island during Period B, very little of which were located inside the PAN (Figure 2.14). Additionally, the majority of deforestation occurring during Period B was located outside the PAN, within a network of mainly of small pockets. Apart from these, large areas of deforestation also occurred in Area C and within the PA-sc and its northern exterior (Figures 2.14, 2.19 and 2.20). Most noticeable was the network of deforestation patches that occurred in Area C, which, during Period A, was recognised as the largest network of reforestation. During Period B, this region was subsequently degraded with a high density of deforestation pockets of varying size, most of which occurred outside of the PAN.

2.4.2.2 PAN scale

During Period A, reforestation surpassed deforestation both inside and outside the PAN, while the inverse occurred for Period B (Figures 2.27 and 2.28). During Period A, the total reforested area exceeded deforested areas by approximately 1,200 ha inside and 15,800 ha outside the PAN. During Period B deforestation instead surpassed reforestation both inside and outside the PAN by approximately 6,800 ha and 18,600 ha respectively (Figures 2.27 and 2.28).

During Period A, small pockets of reforestation occurred within several PAs of the PAN – but no large areas were observed. However, deforestation occurred in large areas of the PA-sw and the southern part of the PA-ne. Additionally, very small veins of deforestation were observed within a few other PAs across the island (Figures 2.13 and 2.17).

During Period B reforestation also occurred in a few small pockets within the island, of which very few were located in Protected Areas. Additionally, noticeably large areas of deforestation were observed within the PA-sc as well as to its exterior. Small pockets of deforestation were also observed within the majority of the PAs of the PAN (Figures 2.14 and 2.19).

2.4.2.3 Buffer scale

Analysis of the buffer zones for Period A showed a decrease in the total area (%) of reforestation and deforestation as the internal distance from the PAN boundary increased. The opposite trend occurred within the external buffers, with an observed increase in both reforested and deforested areas as distance from the PAN boundary increased (Figure 2.29).

For the internal buffers, the lowest level of reforestation (9%) was recorded at the 2,000 m buffer while the highest proportion (≈14%) occurred within the 250 m buffer. Deforestation levels ranged from approximately 8% within the 2,000 m buffer to 10% within the 250 m buffer. The opposite trend was noticed for the external buffers with the smallest area of reforestation (≈16%) being recorded within the 250 m buffer, whilst the largest (≈18%) occurred within the 1,000 m buffer. Deforestation proportions ranged from approximately 10% at the 250 m buffer to 11% at the 2,000 m buffer (Figure 2.29).

During Period B, areas of reforestation within both internal and external buffer sets were observed to steadily decrease with increasing distance from the PAN boundary. In a similar manner, deforestation areas within the internal buffers decreased with increasing distance from the PAN, while the opposite trend occurred within the external buffers (Figure 2.30).

During this period, low levels (<1% total area) of reforestation were observed at all buffer scales. However, areas of deforestation were greater with areas of deforestation ranging between approximately 6% and 7% within the internal buffers, and approximately 7% and 8% within the external buffers.

Finally, it should be noted that when compared to Figure 2.29, the percentage area that was deforested during Period B was less than Period A. However when combined with the very low levels of reforestation during Period B, the cumulative area of non-forest cover within the PAN turned out to be greater in 2007 than in 1969. Additionally the low levels of reforestation within the PAN boundary during Period B imply sustained anthropogenic activity within the areas that were deforested during Period A.

2.4.3 Annual Rate of Change in Forest cover (RCF)

As has been echoed in the results above, the positive values of the annual RCF (Puyravaud 2003) in Table 2.2 during Period A denotes increases in total forest cover across all scales, while the negative RCF values for Period B refers to decreases in overall Forest Cover – which also occurred across all scales.

RCF magnitudes during Period B were greater than corresponding Period A magnitudes at all scales – indicating that the rate at which the change in forest cover occurred during Period B was faster than during Period A. The RCF were consistently lower inside the PAN (including buffers) than outside. RCF magnitudes within the external buffers increased with increasing distance from the PAN boundary, while the opposite trend was observed for the internal buffers (Section 2.3.6).

Additionally, the following results were obtained for the Chi-square tests of independence carried out with these RCF values for Periods A and B:

- Period A: $\chi^2(1) = 2.0,\ p = 0.157$
- Period B: $\chi^2(1) = 3.54,\ p = 0.253$

The large ($p \geq 0.05$) Chi-square significance values obtained for Period A ($p = 0.157$) and Period B ($p = 0.253$) both indicated that there was no statistical significance between the rates of forest cover change inside and outside the PAN during both these periods.

2.4.4 Forest Disturbance and Forest Quality

The maps of Forest Disturbance and Forest Quality (Figures 2.21 and 2.22) produced by these analyses represent a merging of the general trends that have been described by the reforestation/deforestation results of Periods A and B (Figures 2.13 and 2.14).

2.4.4.1 Island scale

Over half of Trinidad's area has been forested since 1969 (Grade 1 forests), this is considerably more than the area of land that has been categorised as Historic Non-Forest (27.7%) (Figures 2.22, 2.31 and 2.32). When combined with areas that have been under forest since 1994 (Grade 2 forests) this amounts to 58.5% of the island; which is more than twice the combined areas of Historic Non-Forest and Early Deforestation (Figures 2.21 and 2.32). This combination of Grade 1 and Grade 2 forests dominate the northern and eastern parts of the island and also line its southern edge. However, Early Deforestation, Recent Deforestation and Unstable Deforestation together constitute 13.3% of the island's area; this exceeds the combined areas of Early Forest, Recent Forest and Unstable Forest which together account for 9.6% of the island. Finally, zones of forest removal (Unstable - Deforestation, Unstable - Forest, Recent Deforestation and Early Deforestation) have occurred mainly along the periphery of the PAN, with large areas of forest removal detected at Area A, Area B, and along the southern edge of the island (PA-sw, and PA-sc) (Figure 2.21). Of these, a noticeable band of Recent and Unstable Deforestation has occurred around the northern periphery of the PA-se, as well as inside and around the PA-ce.

2.4.4.2 PAN scale

Within the PAN, it is clear that a combination of Grade 1 and Grade 2 forests constitute the vast majority of the PAN's area (87.3%) (Figures 2.33 and 2.34). However it was also observed that apart from Early and Recent Deforestation accounting for almost 9% of the PAN; 1.2% of the PAN is also categorised as Unstable Deforestation (Figure 2.33). This contrasts with the situation observed outside of the PAN, where the majority of this area is categorised as Historic Non-Forest, which, in addition to Early Deforestation and Recent Deforestation, constitute 52.8% of the available land. However, outside of the PAN, Grade 1 forests constitute the second largest category, which together with Grade 2 forests comprise 44.1% of land outside the PAN (Figures 2.35 and 2.36).

2.4.4.3 Buffer scale

At the buffer scales, Grade 1 forest was observed to be the dominant category within both internal and external buffers (Figure 2.37). Historic Non-Forest increases with distance from the PAN boundary within the external buffers, while the reverse is true for internal buffers. Additionally, the area of Grade 2 forests was found to increase with distance from the PAN boundary within the external buffers while the reverse occurs within the internal buffers. The Unstable areas (Unstable Forest and Unstable Deforestation) are, like at the other scales, minimal; however, Recent Deforestation was observed to occur at almost constant proportions within all buffer scales (Figure 2.38).

2.5 Discussion

The overall increase in forest cover across Trinidad between 1969 and 1994, as well as the reversal of this trend between 1994 and 2007, can be attributed to different proximate causes (activities that directly result in the conversion of land use). These stem from a combination of several drivers (the underlying processes which give rise to proximate causes) which are, by nature dynamic and the effects of which, are difficult to distinguish on an individual basis.

There is also, an acute paucity of published material on these proximate causes and drivers which could be cited for this chapter. Hence there is frequent qualification of information under the category of 'personal communication' within this discussion. Indeed, a wealth of local, unpublished knowledge exists about the history and management of forests in Trinidad as well as the consequences of such management. However this information is lodged only in the minds of several individuals who have been involved in forest related activity over many years. Unless an effort to record and publish this information is made, this knowledge is in peril of disappearing once these individuals are no longer alive.

2.5.1 Effectiveness of the PAN

It is unsurprising that the Chi-square analyses in Section 2.4.3 indicated that there was no statistical significance between the rates of forest cover change inside and outside the PAN during both Periods A and B. Firstly, Trinidad's PAN is distributed across both flat (and hence accessible) and difficult (to access) terrain; with the latter being associated mainly with PAs located within Northern Range. Because there is no bias towards difficult to access locations for the placement of PAs, there is no automatic protection from anthropogenic activity across the majority of the PAs that comprise the PAN. Additionally as discussed within Sections 2.5.2 to 2.5.4, there are a multitude of proximate causes (and associated drivers) of reforestation and deforestation both inside and outside of the PAN – which may not necessarily be connected to each other. For example, the harvesting of teak by the Forestry Division within the PAN is in no way influenced by the neighbouring anthropogenic activity occurring along the outer borders of these PAs. Additionally, within private lands, reforestation or alternatively deforestation for agriculture or settlement are not believed to directly influence deforestation (or reforestation) within the PAN.

2.5.2 Reforestation

The importance of primary forests remains a cornerstone of biodiversity conservation, as these areas are known to be more biologically diverse than secondary (regenerating) forests. However, comparative studies investigating biodiversity levels within primary and secondary forest report that while primary forests are characterised by greater species richness, secondary forests may also contain relatively positive levels of species richness. Further, compared to recent regeneration, older areas of regeneration are known to have (i) higher levels of species richness (Dunn 2004) and (ii) higher levels of community similarity to adjacent primary forest (e.g., Sodhi et al. 2005).

Hence, while efforts to preserve remaining bodies of primary forest are imperative, areas of regenerating forest are also important for the conservation of biodiversity – as apart from maintaining greater levels of species richness than agricultural and other human-dominated land uses (Wright and Muller-Landau 2006); they also provide ecosystem goods and services (Myers 1997) and feature prominently within carbon sequestration initiatives (Yu 2004). These characteristics are complementary to PAs (Barlow et al. 2007), and hence planned (and natural) reforestation can be used as a valuable instrument for increasing landscape connectivity (Fischer et al. 2006) by linking forest fragments to each other or to other bodies of extensive forest both inside and outside of PAs (Stouffer et al. 2006).

During Period A, reforestation within Area C, as well as along the north-central and north-eastern coastlines of Trinidad (Figure 2.13), has been attributed to the abandonment of agricultural lands, mainly cocoa and coffee estates during the 1960s (Ali, pers. comm. 2010; Maharaj, pers. comm. 2010). Collapse of the local cocoa and coffee industry resulted in an abandonment of the majority of these plantations during the 1960s and 1970s; as these industries, already plagued with problems of disease, suffered from a plummet of global cocoa and coffee prices as well as a shortage of labour (Bekele 2003; Griffith 1987). This shortage of labour for agricultural activity increased dramatically between 1973 and 1983 following decades of strong economic, industrial and infrastructural growth. During this ‘Oil Boom’ era much agricultural land was abandoned in preference to more lucrative employment within industry and commerce (Fairhead and Leach 2003). These abandoned cocoa and coffee estates as well as other abandoned agricultural lands eventually developed into secondary forest.

Another contributor to the high level of reforestation during Period A was the ‘Northern Range Reforestation Project’ which was initiated by government funding during the 1970s, and continued into the 1980s with aid from the United Nations Development Programme (UNDP) and the FAO (Fairhead and Leach 2003). It involved the replanting of denuded or semi-denuded state-owned watersheds primarily with Caribbean Pine (*Pinus caribaea*) (Lackhan 1980, 1984). The choice of the non-native Caribbean pine for reafforestation was questioned by many and it led to a noticeable change in the structure and composition of many areas of adjacent forests. Additionally, these forests suffered from increased incidence of fires as well as acidification of their soils due to the large scale introduction of this species (Ali, pers. comm. 2010; Maharaj, pers. comm. 2010; Mohammed, pers. comm. 2010).

Additionally, small pockets of reforestation, scattered throughout the island, were initiated by community groups and NGOs. The 1980s and mid 1990s also saw an increase in environmental concern within the public and ultimately the political domains. This process was boosted by public concern generated from a number of isolated events such as the extended dry season of 1987 – and the forest fires that ensued. The result was a noticeable increase in environmental activism as well as an organised network NGOs, community based groups and organisations, many of which actively engaged in community conservation projects (Fairhead and Leach 2003; Kenny 2000). Additionally, according to Maharaj (pers. comm. 2010), there was an increase in the development of private timber plantations of species such as the Columbian Cedar (*Cedrela odorata*) during Period A. This was seen as a lucrative investment without unwanted risks, such as praedial larceny.

One of the most striking observations derived from the study of Figures 2.26, 2.27, 2.28 and 2.29 was the dramatic reduction in the areas of reforestation at all scales from Period A to Period B (Figures 2.13 and 2.14). While it is difficult to discern proximate causes for this drastic reduction of new areas of reforestation during Period B; it is clear that during this period (B) there was a continued spread of residential settlement, commerce and agriculture eastwards across the island.

2.5.3 Deforestation

Consultation with local personnel of the National Forestry Division indicated that the majority of the large areas of deforestation occurring during Period A were caused by isolated fire events. According to Ali (pers. comm. 2010) the deforestation within Area A occurred as a result of two major fires occurring within the Aripo Savannas and the Melajo Forest Reserve during the 1980s (Figure 2.13). The destructive effects of these fires were later compounded by a combination of legal and illegal quarrying, illegal logging and squatting for settlement and shifting agriculture (Kenny 2000). Deforestation within Area B occurred mostly due to the spread of residential settlement further east, this was also mixed with a combination of small scale industry such as quarrying activities and residential squatting. Similarly, deforestation within the PA-sw and its northern, eastern and southern periphery is attributed to the encroachment of agriculture and the influence of settlement and industry which expanded south-eastwards from Point Fortin and other neighbouring towns. Finally, the small scattered pockets of deforestation observed across the island stemmed mainly from the development of private lands for isolated settlements, agriculture as well as illegal slash and burn agriculture (Ali, pers. comm. 2010; Maharaj, pers. comm. 2010).

Despite deforestation exceeding reforestation during Period B, the gross area of deforestation occurring at all scales during Period B was less than that which occurred during Period A (Figures 2.26, 2.27, 2.28 and 2.29). During Period B, Area C, which was reforested during Period A, was subsequently infiltrated by road networks stemming from Sangre Grande. This eventually gave rise to small, scattered pockets of agriculture and to a lesser extent, the establishment of settlement. Settlement within this area is also reported to have given rise to a number of forest fires which contributed further to the scattered pockets of deforestation within this area (Maharaj, pers. comm. 2010).

According to Ali (pers. comm. 2010), during Period B, the large area of new deforestation located to the north of PA-ce as well as the small pockets within the PA-ce (Figure 2.14) occurred as a result of the harvesting of teak (*Tectona grandis*) by the Forestry Division. Likewise, the two large areas of deforestation within and to the north of the PA-sc were also due to *T. grandis* harvesting by the Forestry Division.

Apart from larger pockets of deforestation discussed above, the buffer analyses for both Periods A and B indicate that small pockets of deforestation continued to occur within the PAN. These were mainly attributed to illegal squatting for agriculture and marijuana (Ali, pers. comm. 2010; Mohammed, pers. comm. 2010). During vegetation sampling trips, I have on several occasions encountered areas of forest that have been cleared and replaced by cash crops some several hundred metres within the PAN boundaries, while marijuana plantations were always encountered much further into the PAN – usually (but not always) within difficult terrain. These activities appeared to be the direct result of a lack of enforcement of the PAN boundaries.

During Period B the patterns of (i) increasing areas of deforestation as the external buffer radius increased, (ii) the accompanying opposite trend within increasing internal buffer radii (Figures 2.29 and 2.30) together with the observation that (iii) most of the major PAs (apart from those within Area A and the PA-sw) did not experience increased deforestation (relative to Period A) (Figure 2.27) can be explained by several factors. Firstly, the majority of the PAs on the island are located within the eastern half of the island – away from major centres of settlement and development. Both the PA-sw and those that were affected by deforestation within Area A were either directly adjacent to population centres and/or were in the direct path of development trajectories. Secondly, the PA-ce, most of PA-ne (unaffected by deforestation) as well as smaller PAs located within the north-western regions of the island are characterised by difficult terrain – which is a well documented natural deterrent to settlement, agriculture and development of population centres. The PA-se is protected by the operations of the local petroleum industry located within it – which actively secures the perimeter of this PA, thus preventing unauthorised encroachment of any kind. The small pockets of deforestation within the PA-se were due to activities of the petroleum industry as well as the granting of permission to small-scale farmers to cultivate limited areas along the periphery. Finally, many parts of the periphery PA-sc consist of state-owned teak plantations – which serve as an effective deterrent to encroachment of agriculture and settlement.

During Period B, a combination of (i) the decrease of gross areas of new deforestation at all scales (versus Period A), (ii) a general shift in the proximity of new deforestation pockets nearer or adjacent to the PAN boundary (compared to Period A) and (iii) the occurrence of very little new reforestation infer the possibility that anthropogenic activity is beginning to exhaust the amount of land that is available outside of the PAN. This is especially significant when combined with the facts that: (i) the rate of forest cover change for Period B was much faster at all scales than during Period A, (ii) the cumulative area of forest loss within the PAN was greater during 2007 than during 1969 (Figure 2.24) and (iii) there appears to be sustained anthropogenic activity within the areas that have been deforested within the PAN during Period A.

2.5.4 Persistent proximate causes

The loss of forest cover due to fires is an annual cause for concern. It is estimated that an average of approximately 4,600 ha of forest was destroyed by fires each year between 1987 and 1996 – with anthropogenic activity listed as the primary cause (Dillon Consulting 2004). These forest fires vary each year in location and area; however, with the almost non-existent enforcement of the PAN boundaries, little has been done to address and prevent potential fires (Ali, pers. comm. 2010).

Quarrying is also a know contributor to the erosion of forest cover, especially since its effects are almost impossible to reverse. According to Dillon Consulting (2004), during 1993 there were an estimated fifty-seven registered quarries – of which 77% were operated on state land. Since then there has been a perceived increase in the amount of forested land that has been converted to quarries – fuelled by increased demand for gravel and sand from a booming construction industry. There is growing public concern at this increase since little or no remediation is done after an area has been quarried (Maharaj, pers. comm. 2010).

Additionally illegal logging on both private and State lands remains a common and widespread problem. Discussions with personnel from the National Forestry Division and several NGOs indicated that possible solutions to this problem may involve (i) active enforcement of the PAN boundaries as well as (ii) a change in legislation which allows forest officers based in the field to be trained in the carrying fire-arms for self-protection during the execution of these enforcement duties.

Furthermore during 2004, agricultural cultivation (including slash and burn agriculture) was estimated to occupy 35% of the island; in addition to which, there has been consistent expansion of areas under irreversible land use such as settlement, transport networks, industry and commerce (Dillon Consulting 2004). This in combination with a population increasing at a rate of 1.2% and a population density of about 261 persons per square kilometre (WBG 2011) has led to land use conflicts which have not been resolved and which continue to increase with time (Dillon Consulting 2004; Hosein 2007).

2.5.5 Final comments

As mentioned in Section 2.1.4, increases in forest cover as a result of declining agriculture over the last decade has been reported in several Caribbean nations such as Puerto Rico, St. Kitts and Nevis (Grau et al. 2003; Helmer et al. 2008; Rudel et al. 2000). However, as shown in this study's comparison between Periods A and B, land abandonment does not guarantee forest recovery. The direction of economic activity and resulting allocation of land as well as the distributions of populations are key elements that determine the fate of forest recovery. For example, the island of Puerto Rico experienced increased reforestation during the 1980s and 1990s due to a declining agricultural industry. This regrowth of forest was initiated by this change in economic activity from agrarian to manufacturing and services in conjunction with population migration towards urban centres. Forest regrowth was however sustained by the shifting of the population centre to the coastal zones (away from the geographic centre of the island) – which contains centres of industry, transport and commerce (Lugo 2002). This is not the case in Trinidad – where as shown above, it seems that remaining areas of non-protected, flat lands are being encroached by settlement, agriculture and industry and other forms of irreversible development at an increasing rate.

Human population densities of the Caribbean SIDS have long been known to be higher than their continental neighbours within the tropics (Lugo 2002; Lugo et al. 1981). The management and protection of forest cover in the face of increasing populations within these small, fixed geographic areas will require foresight and land use planning. This study illustrates the failure of Trinidad to (i) sustain forest regrowth between Periods A and B and (ii) maintain or increase the area of forest cover within its PAN. Additionally it highlights an increasing threat of encroachment into the PAN within the southern edge of the island by showing that the peripheries of major PAs such as the PA-sw, PA-sc, PA-se and PA-ce are being lined with Recent Deforestation (Figure 2.21) and Grade 2 Forests (Figure 2.22). Case studies such as this should serve as sentinels which herald the need for careful management and planning of existing forest resources within small islands if conservation of biodiversity is to be attempted. The ad-hoc 'crisis management by prohibition' approach which is the main strategy of the Forestry Division for the conservation and management of its forest resources may not be adequate or effective in conserving remaining areas of forest which are under increasing pressure from alternative and often irreversible forms of development.

The introduction of proactive management strategies is required for state owned forests– as these have been identified as better representations of natural areas than private forests (which have been converted in varying degrees to other uses) (Dillon Consulting 2004). Examples of more proactive management include (i) the establishment of an effective mechanism for the enforcement of the PAN boundaries; (ii) regulation of activities both within the PAN and designated external buffer zones and (iii) the development of management plans based on both scientific data and community consultation (GOTT 2009b). Additionally, independent studies have suggested the need for implementation of conservation strategies that are sustainable and holistic in nature and which also include (i) the protection of endemic and other species of high conservation value as well as (ii) the identification of areas of high biological significance for the conservation of biodiversity during the present-day and into the future (Dillon Consulting 2004; EMA 2005).

There is to date, no established, legal system of national parks and protected areas for Trinidad and Tobago, indeed there are not even existing officially surveyed maps of the PAN. The absence of this legal system of National Parks is directly linked to the absence of an effective and legal structure to facilitate such a system (Dillon Consulting 2004; EMA 1999; Thelen and Faizool 1980). Examples from other Caribbean SIDS such as Jamaica and Dominica have shown that a National Parks and Protected Areas agency or administrative body is required to administer management and conservation of the remaining forest resources – however, such a body can only be established via effective legislation (Dillon Consulting 2004).

The first step in this direction was taken in early 2011 when drafts of the 'National Protected Areas Policy' and the 'National Forest Policy' were approved by the cabinet of the government of Trinidad and Tobago. The former works toward 'the selection, legal designation and management of a national system of PAs' while the latter aims to update archaic legislation and a list of other pre-requisites which are necessary for "the maintenance of forest ecosystems in light of competing demands for land". The success of implementing these policies will ultimately play a large part in determining the fate of the remaining forest resources and the terrestrial biodiversity of Trinidad.

2.6 Tables

Forest	**Non-Forest**
Forest plantation	Mangrove
Forest Land	Swamp
Evergreen Forest	Mixed Rangeland
	Herbaceous Rangeland
	Shrub and Brush Rangeland
	Forested Wetland

Table 2.1: Noteworthy land use categories included in the 'Forest' and 'Non-Forest' themes of the Forest cover polygons.

	Annual Rate of Forest Cover Change (per year)	
Scale	**Period A (1969–1994)**	**Period B (1994–2007)**
Island	0.23	-0.67
Inside PAs	0.03	-0.37
Outside PAs	0.42	-0.95
250 m outside PAs	0.30	-0.60
500 m outside PAs	0.30	-0.63
1,000 m outside PAs	0.36	-0.70
2,000 m outside PAs	0.38	-0.82
250 m inside PAs	0.27	-0.56
500 m inside PAs	0.19	-0.54
1,000 m inside PAs	0.10	-0.54
2,000 m inside PAs	0.04	-0.50

Table 2.2: Annual Rate of Forest Cover Change at all scales during Periods A and B.

Forest (F) or Non-Forest (N)							
1969	**1994**	**2007**	**Binomial Code**	**Conversion to Decimal value**	**Decimal Value**	**Forest Disturbance Status**	**Coarse Forest Quality**
N	N	N	0 0 0	$0 \cdot 2^2 + 0 \cdot 2^1 + 0 \cdot 2^0$	0	Historic Non-Forest	–
F	N	N	1 0 0	$1 \cdot 2^2 + 0 \cdot 2^1 + 0 \cdot 2^0$	4	Early deforestation	–
F	F	N	1 1 0	$1 \cdot 2^2 + 1 \cdot 2^1 + 0 \cdot 2^0$	6	Recent Deforestation	–
N	F	N	0 1 0	$0 \cdot 2^2 + 1 \cdot 2^1 + 0 \cdot 2^0$	2	Unstable with Deforestation	–
F	F	F	1 1 1	$1 \cdot 2^2 + 1 \cdot 2^1 + 1 \cdot 2^0$	7	Historic Forest	Grade 1
F	N	F	1 0 1	$1 \cdot 2^2 + 0 \cdot 2^1 + 1 \cdot 2^0$	5	Unstable with Forest	Grade 3
N	F	F	0 1 1	$0 \cdot 2^2 + 1 \cdot 2^1 + 1 \cdot 2^0$	3	Early Forest	Grade 2
N	N	F	0 0 1	$0 \cdot 2^2 + 0 \cdot 2^1 + 1 \cdot 2^0$	1	Recent Forest	Grade 3

Table 2.3: Derivation of Forest Disturbance status and Forest Quality between 1969 and 2007.

2.7 Figures

(Generated by Department of Geomatics Engineering and Land Management, 2009)

Figure 2.1: Location of Trinidad within the Caribbean.

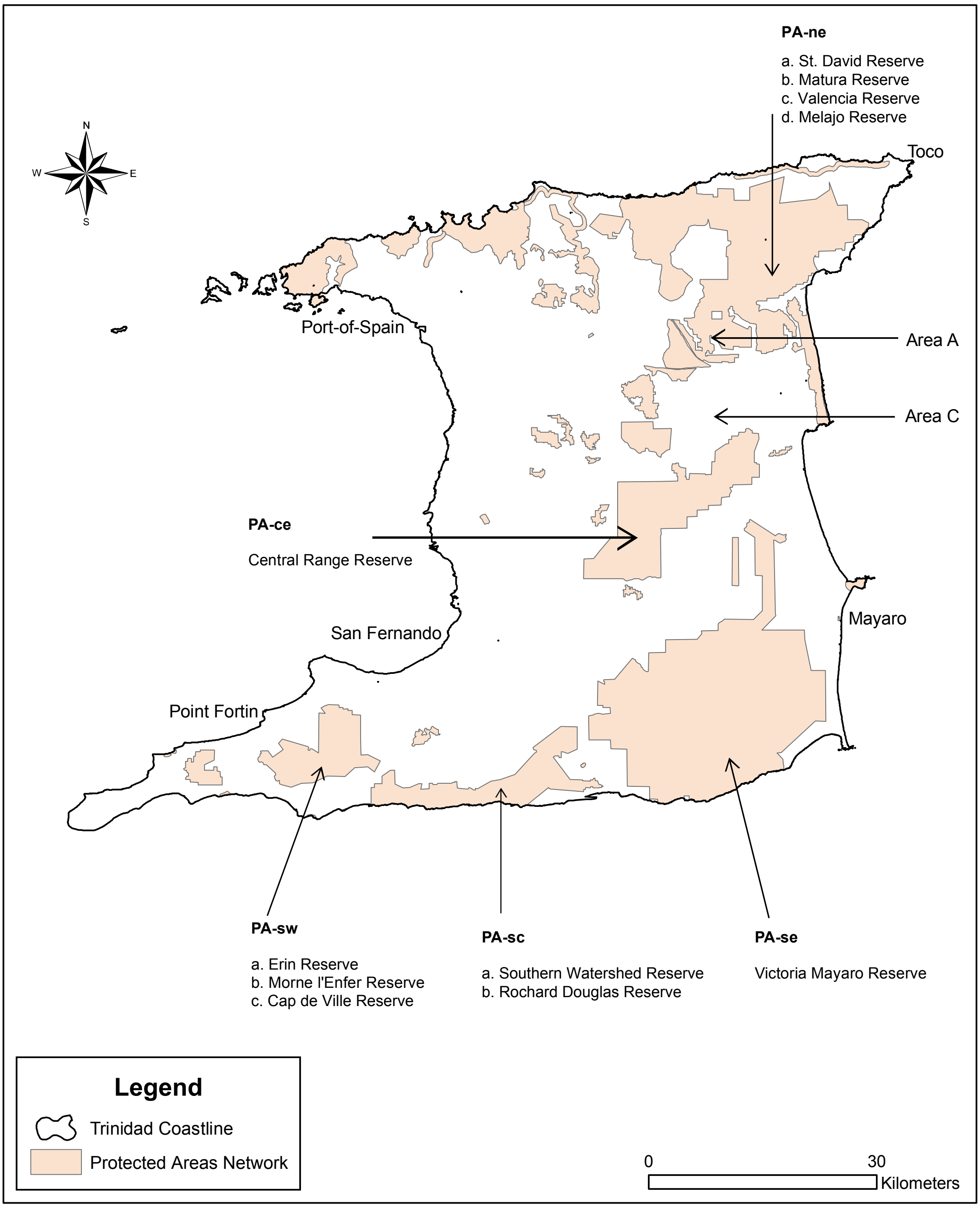


Figure 2.2: The Protected Areas Network (PAN) of Trinidad.

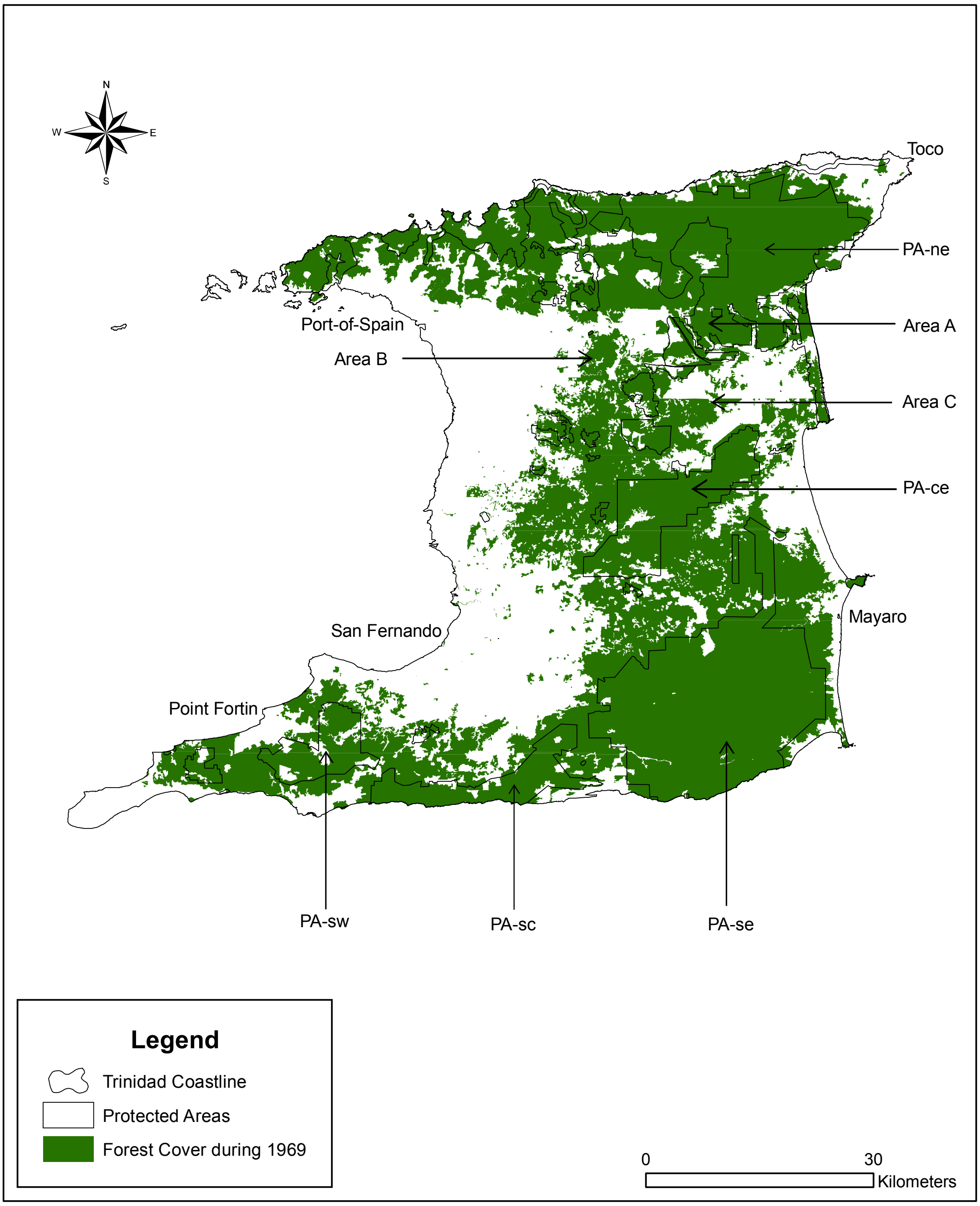


Figure 2.3: Dissolved Forest Cover during 1969.

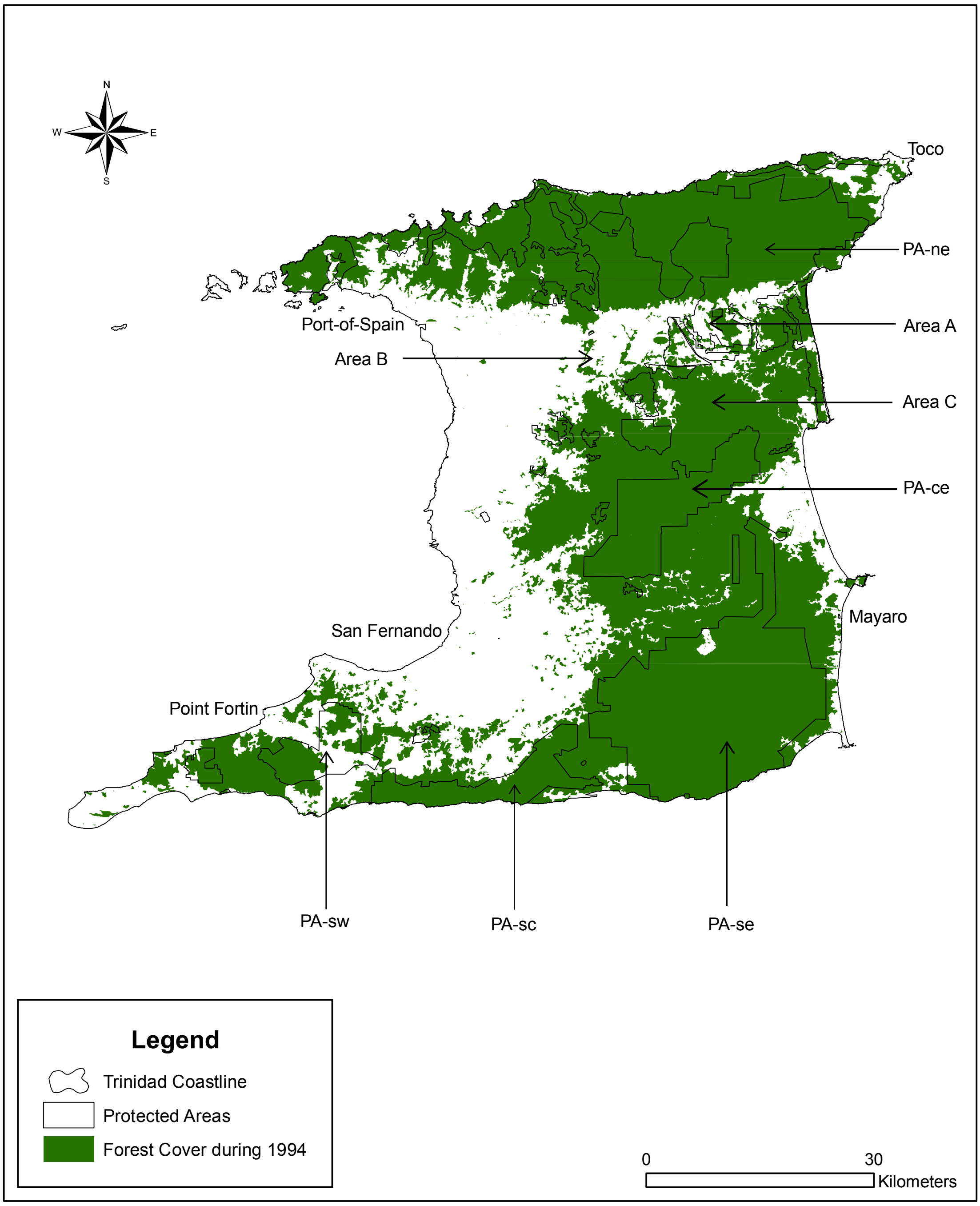


Figure 2.4: Dissolved Forest Cover 1994.

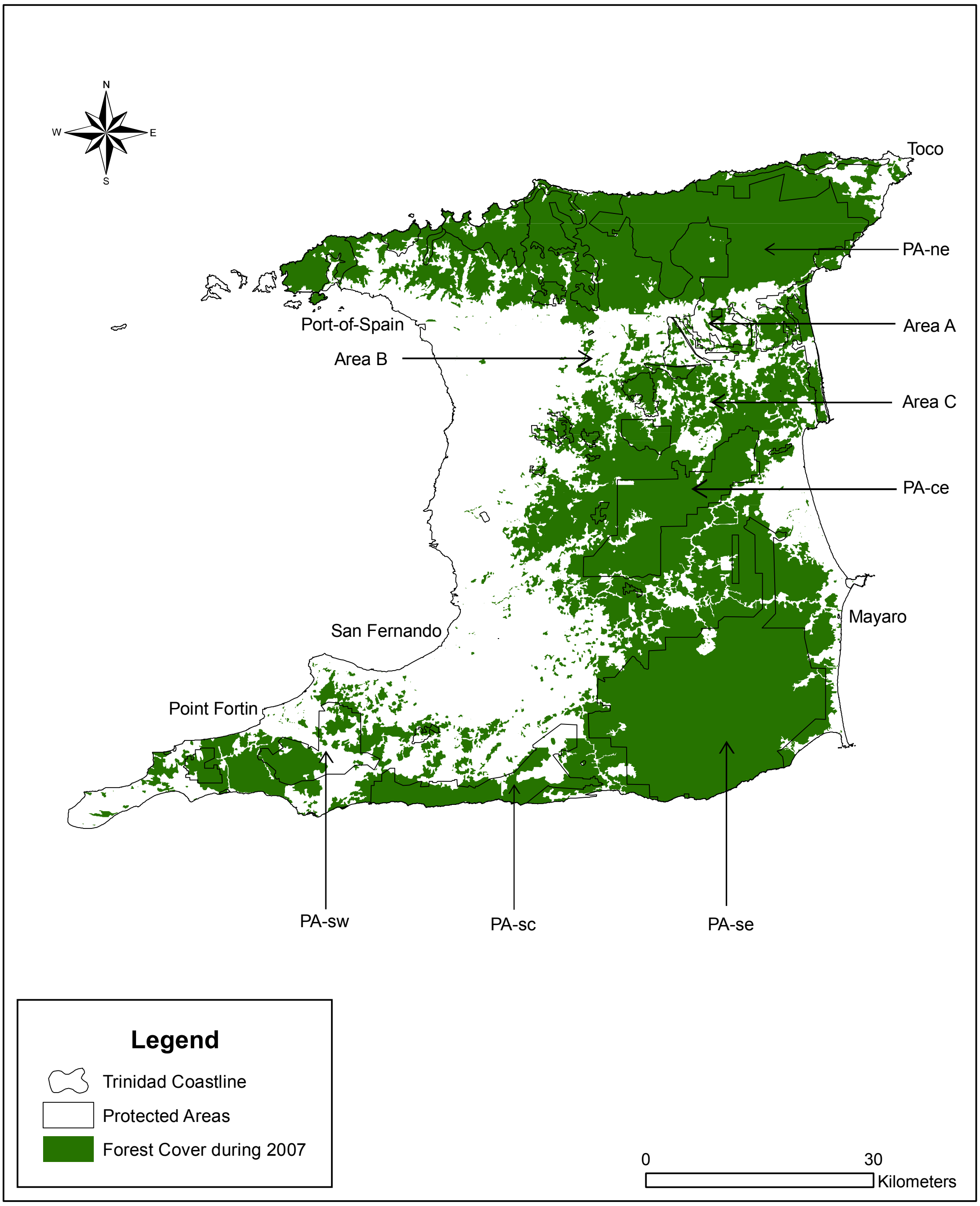


Figure 2.5: Dissolved Forest Cover 2007.

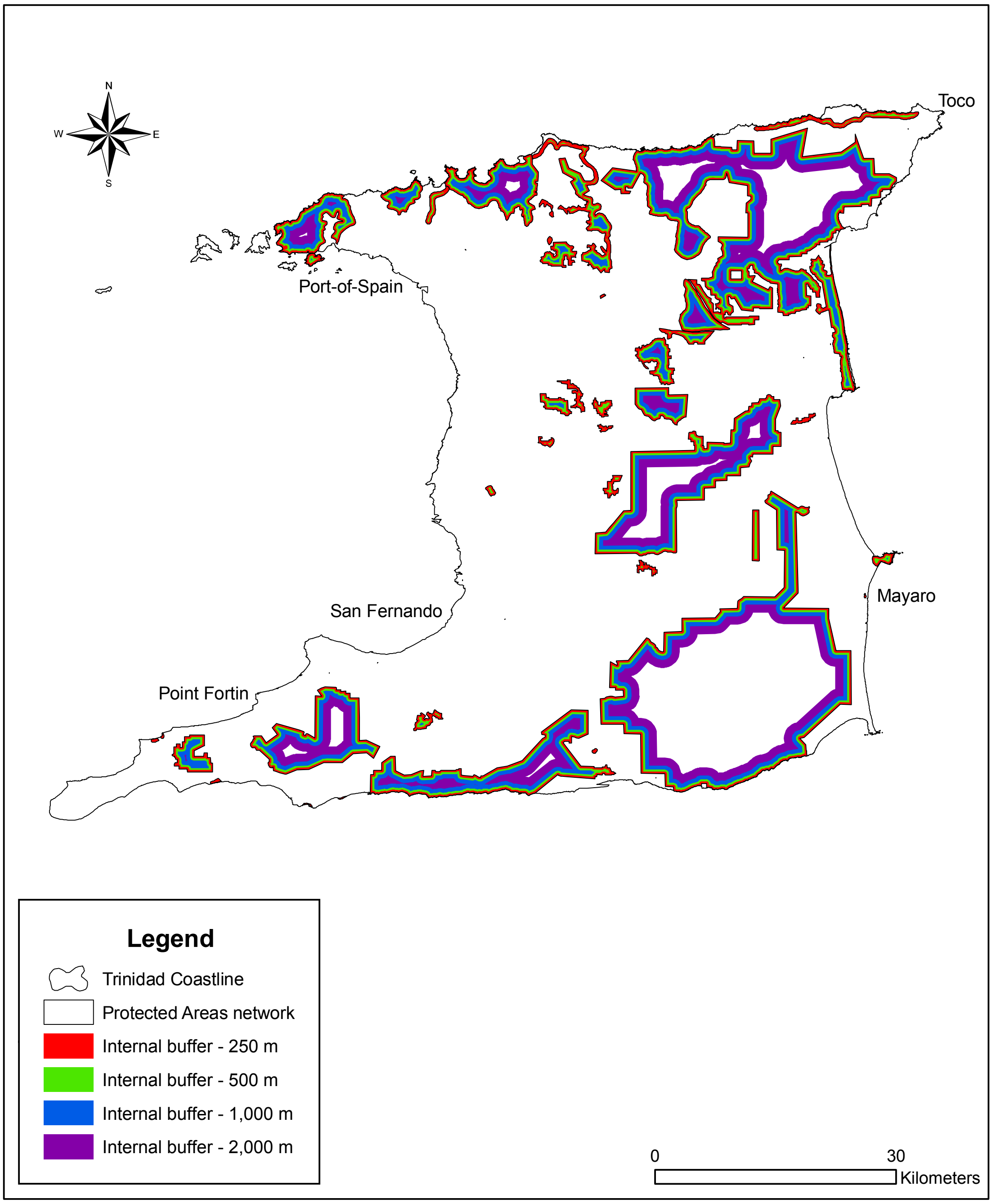


Figure 2.6: Overlay of buffer zones constructed within the boundaries of the Protected Areas Network.

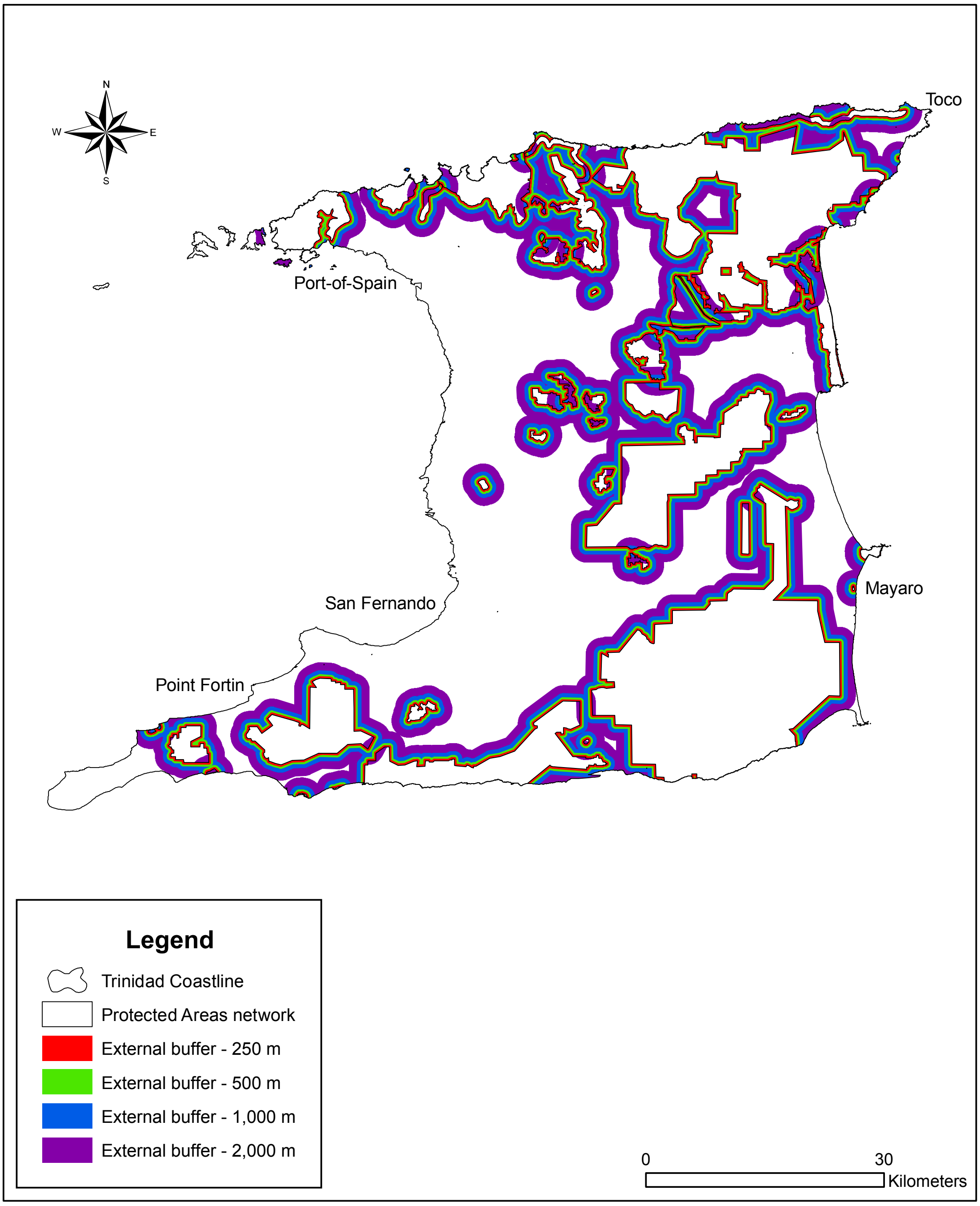


Figure 2.7: Overlay of buffer zones constructed outside the boundaries of the Protected Areas Network.

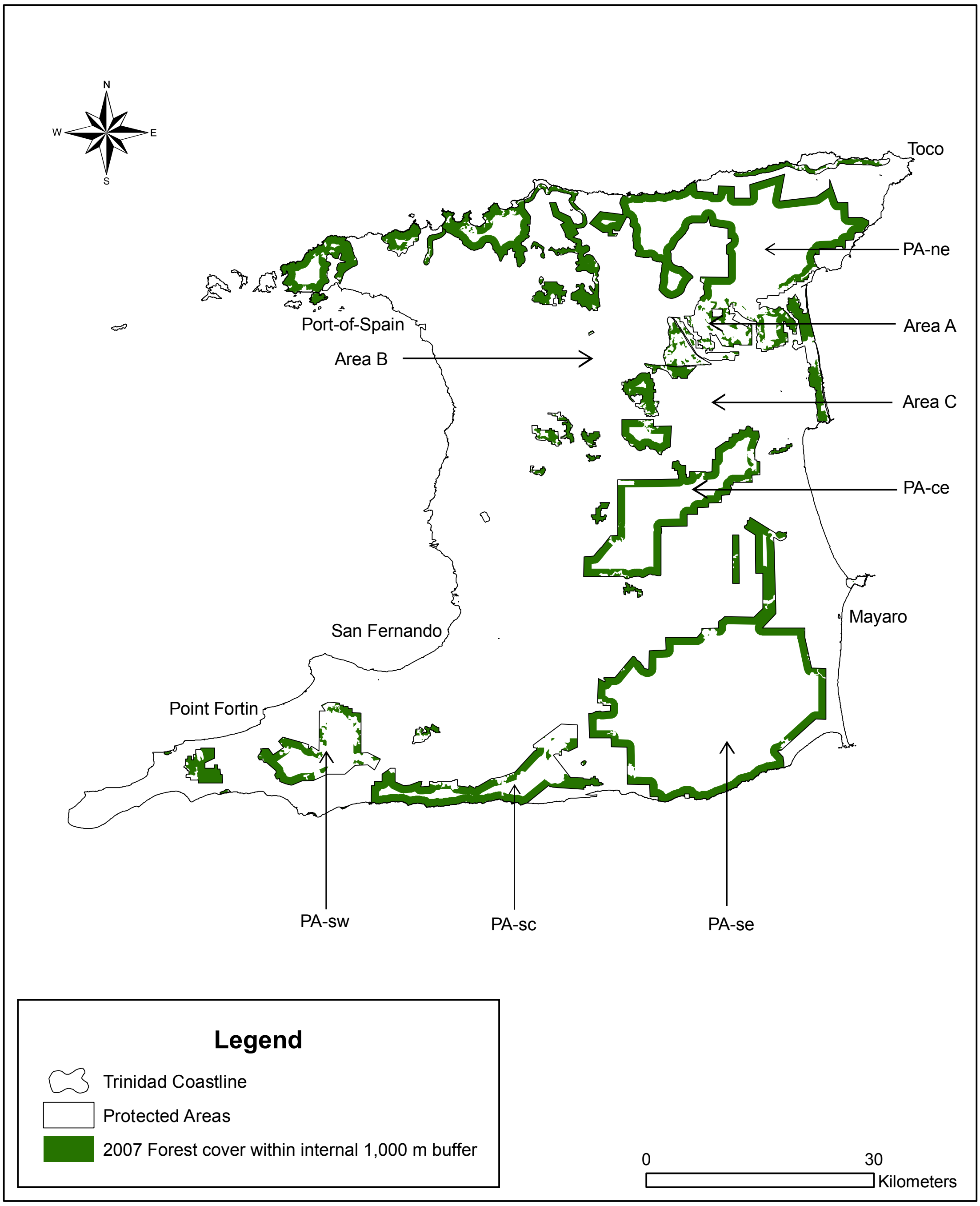


Figure 2.8: Forest Cover within the internal 1,000 m buffer during 2007.

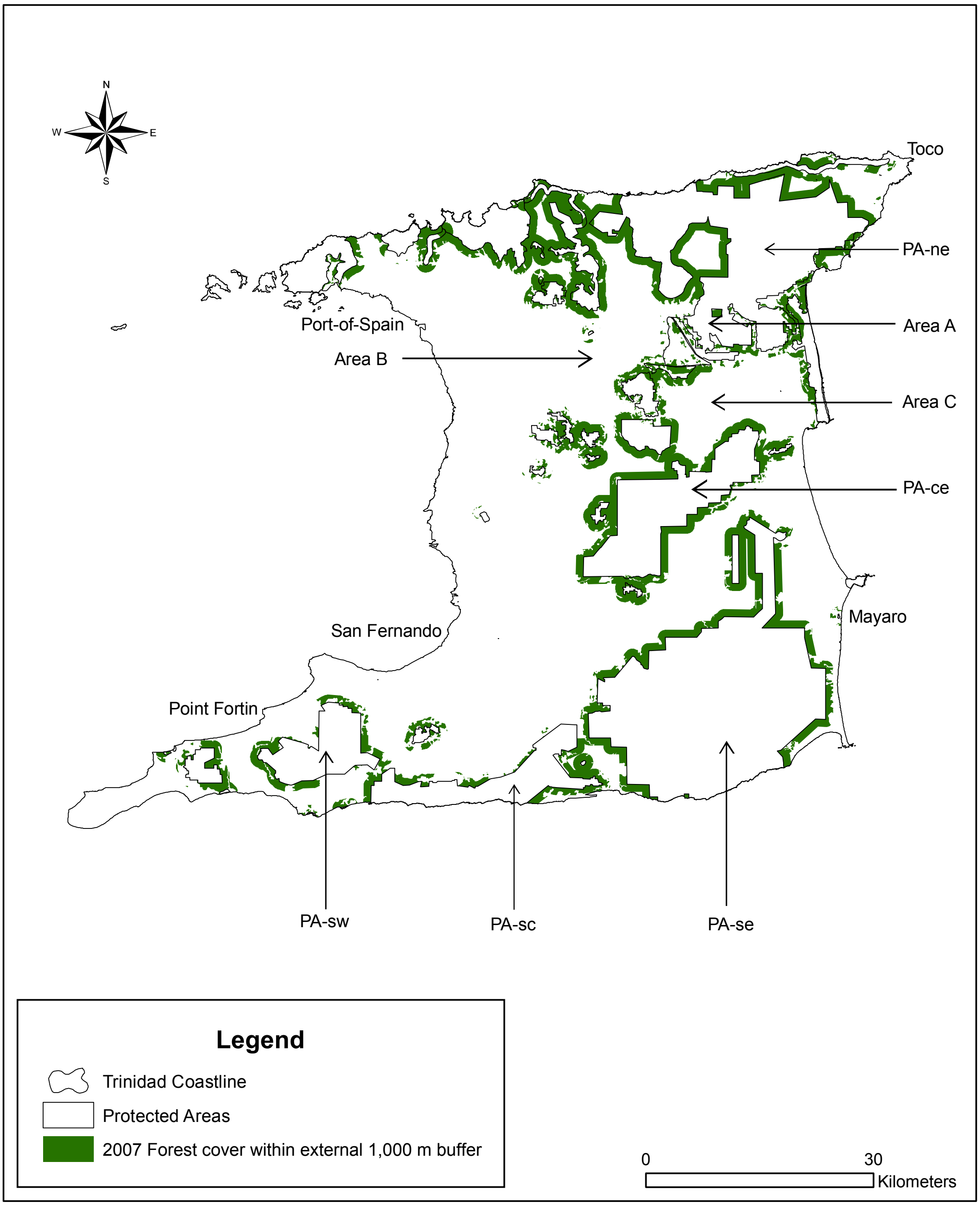


Figure 2.9: Forest Cover within the external 1,000 m buffer during 2007.

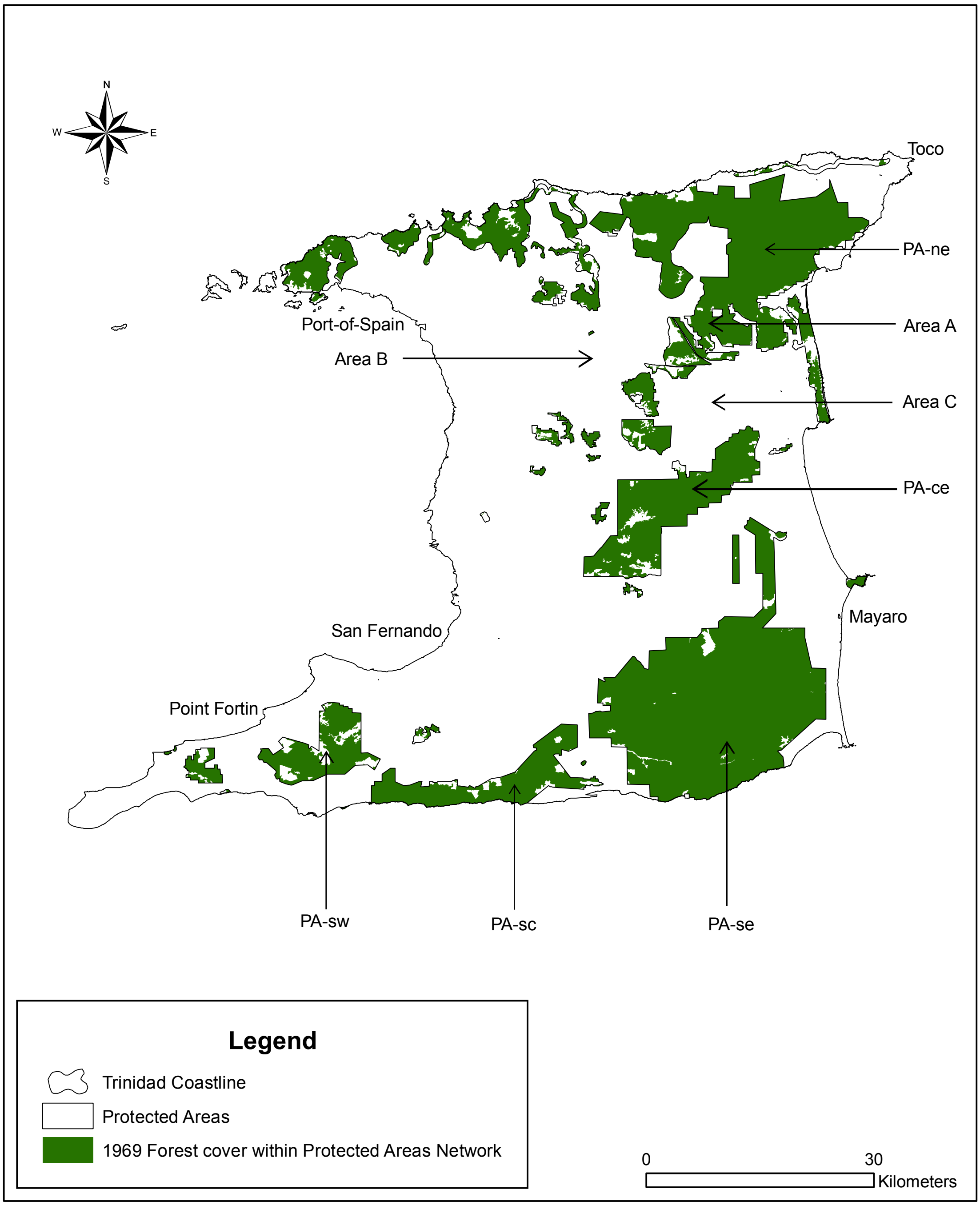


Figure 2.10: Forest Cover within the Protected Areas Network during 1969.

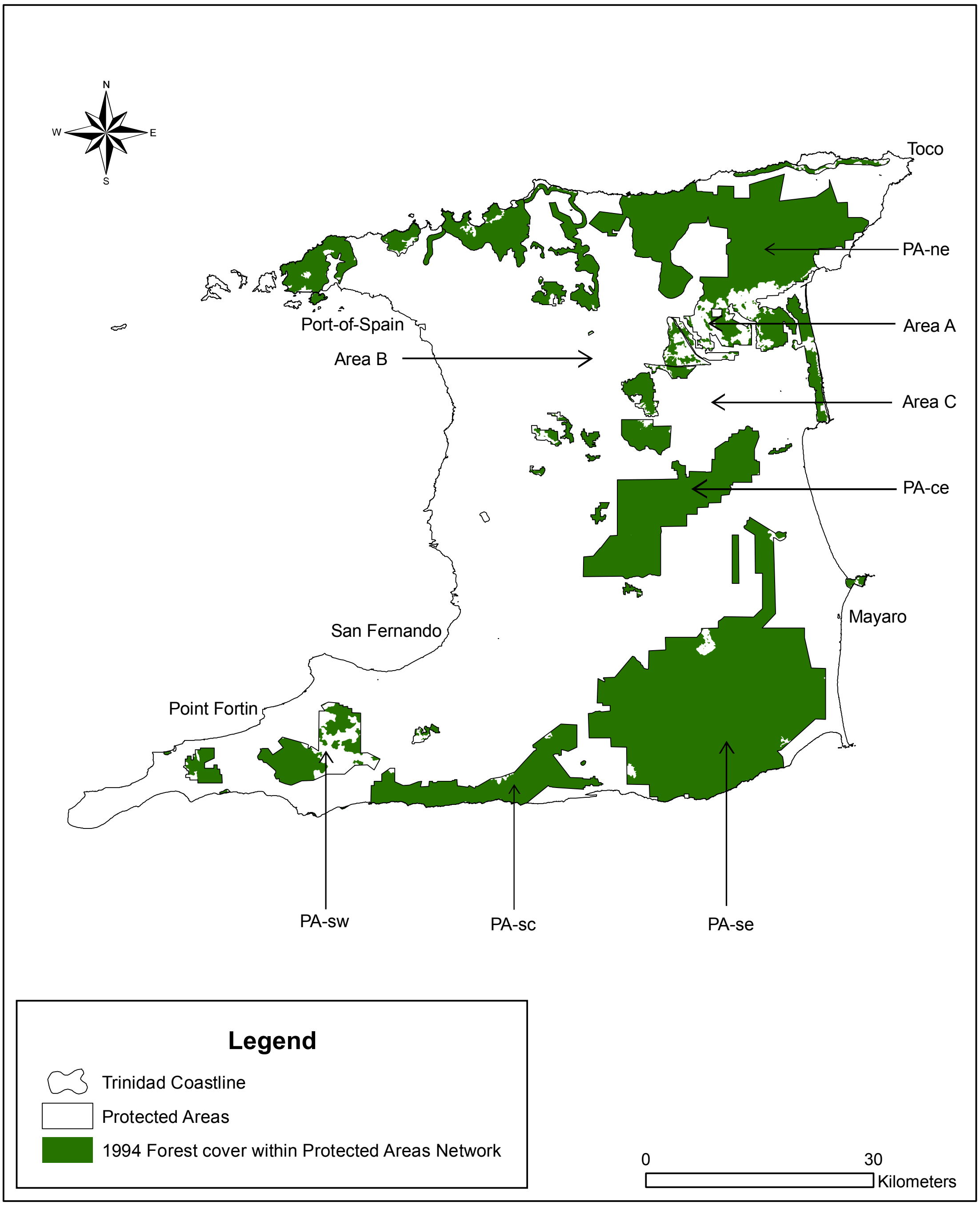


Figure 2.11: Forest Cover within the Protected Areas Network during 1994.

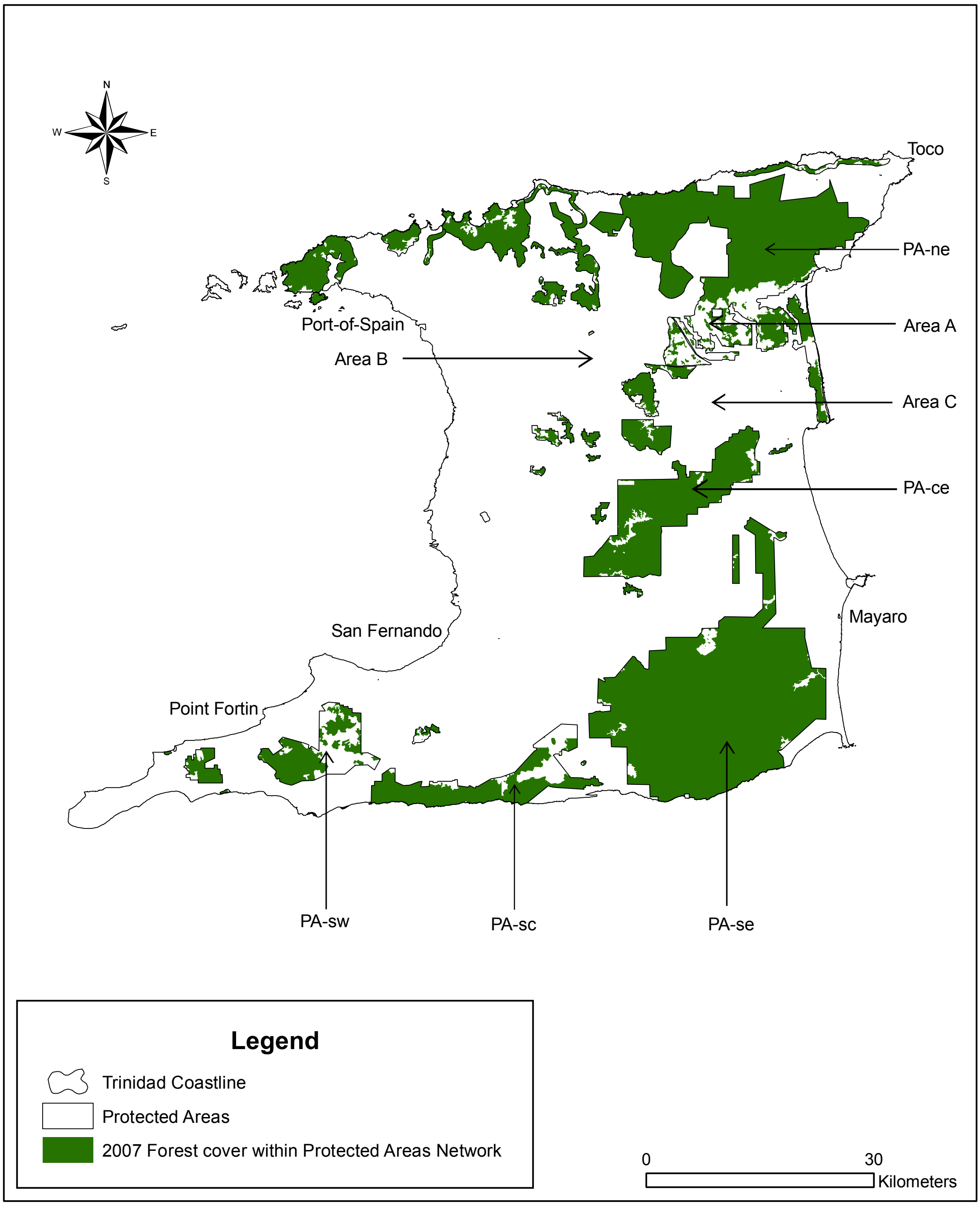


Figure 2.12: Forest Cover within the Protected Areas Network during 2007.

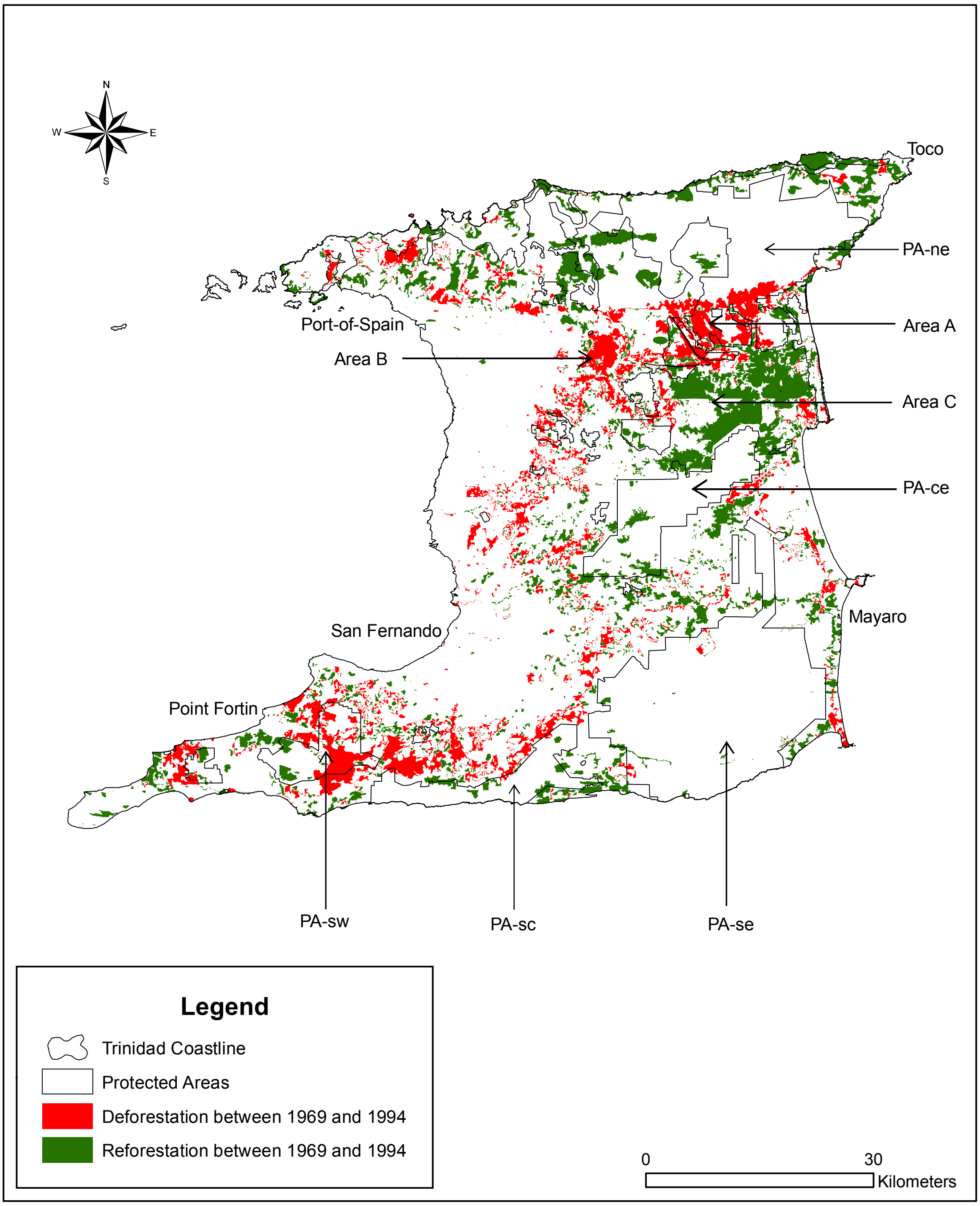


Figure 2.13: Areas of deforestation and reforestation between 1969 and 1994.

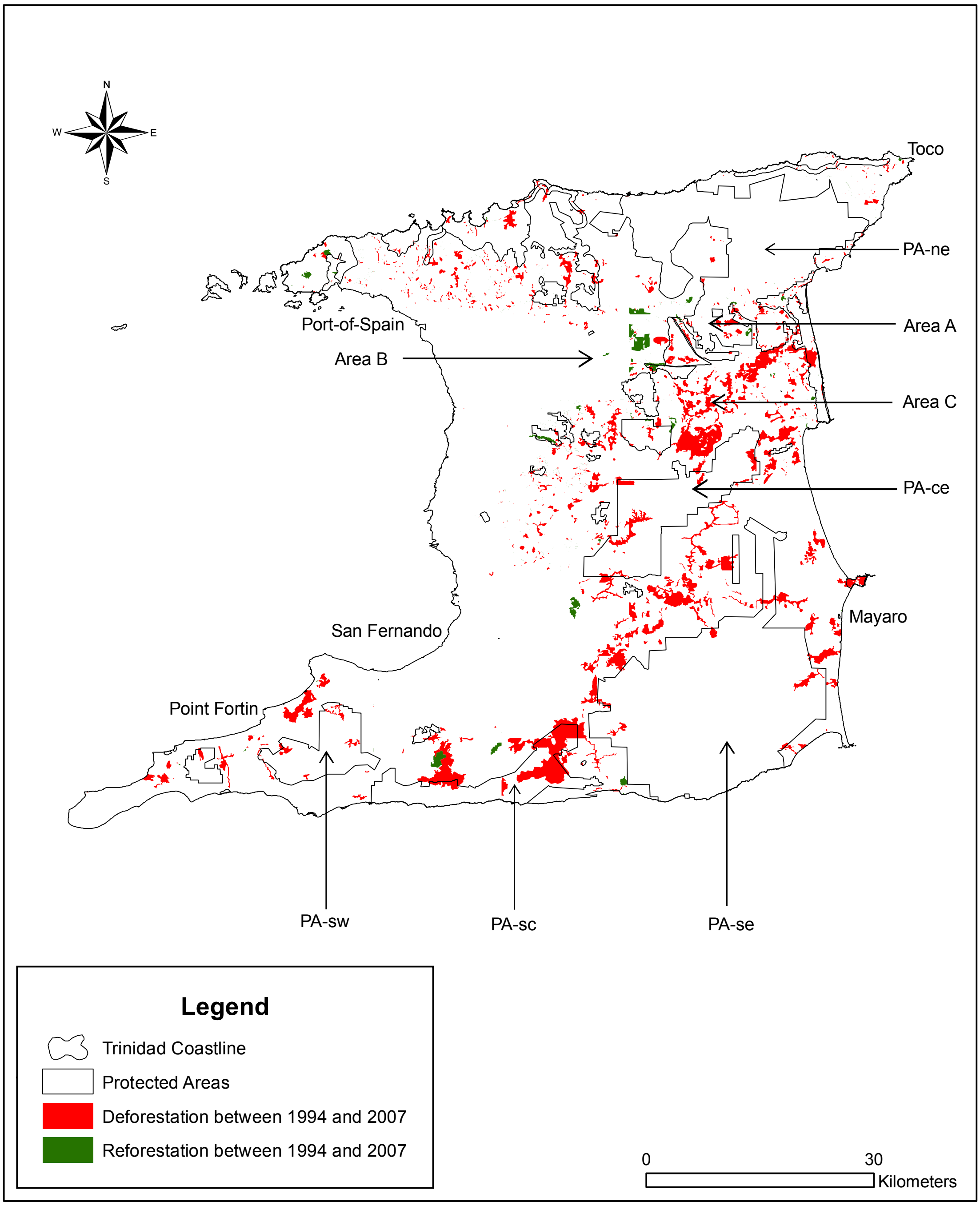


Figure 2.14: Areas of deforestation and reforestation between 1994 and 2007.

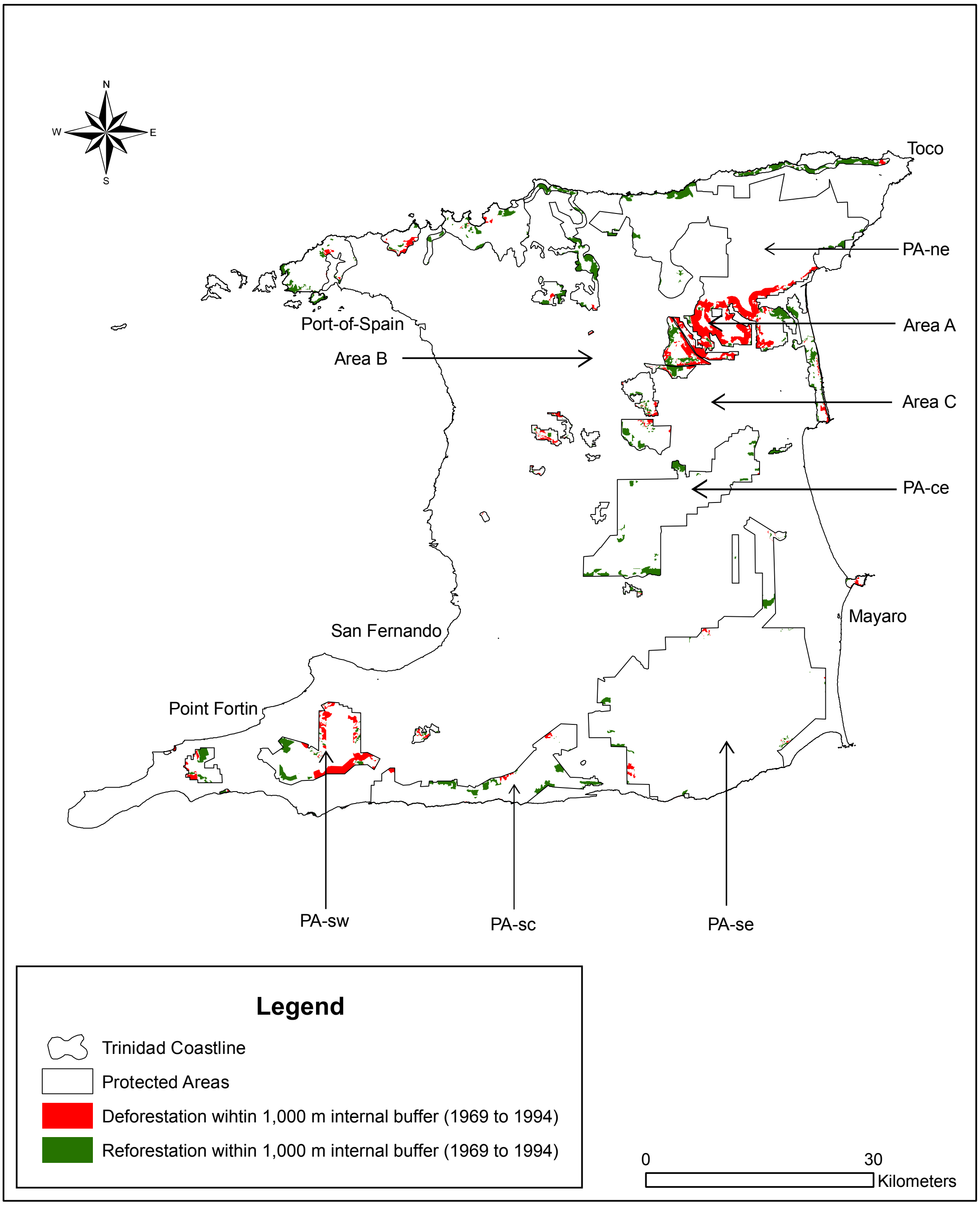


Figure 2.15: Deforestation and reforestation within the internal 1,000 m buffer during Period A (1969 to 1994).

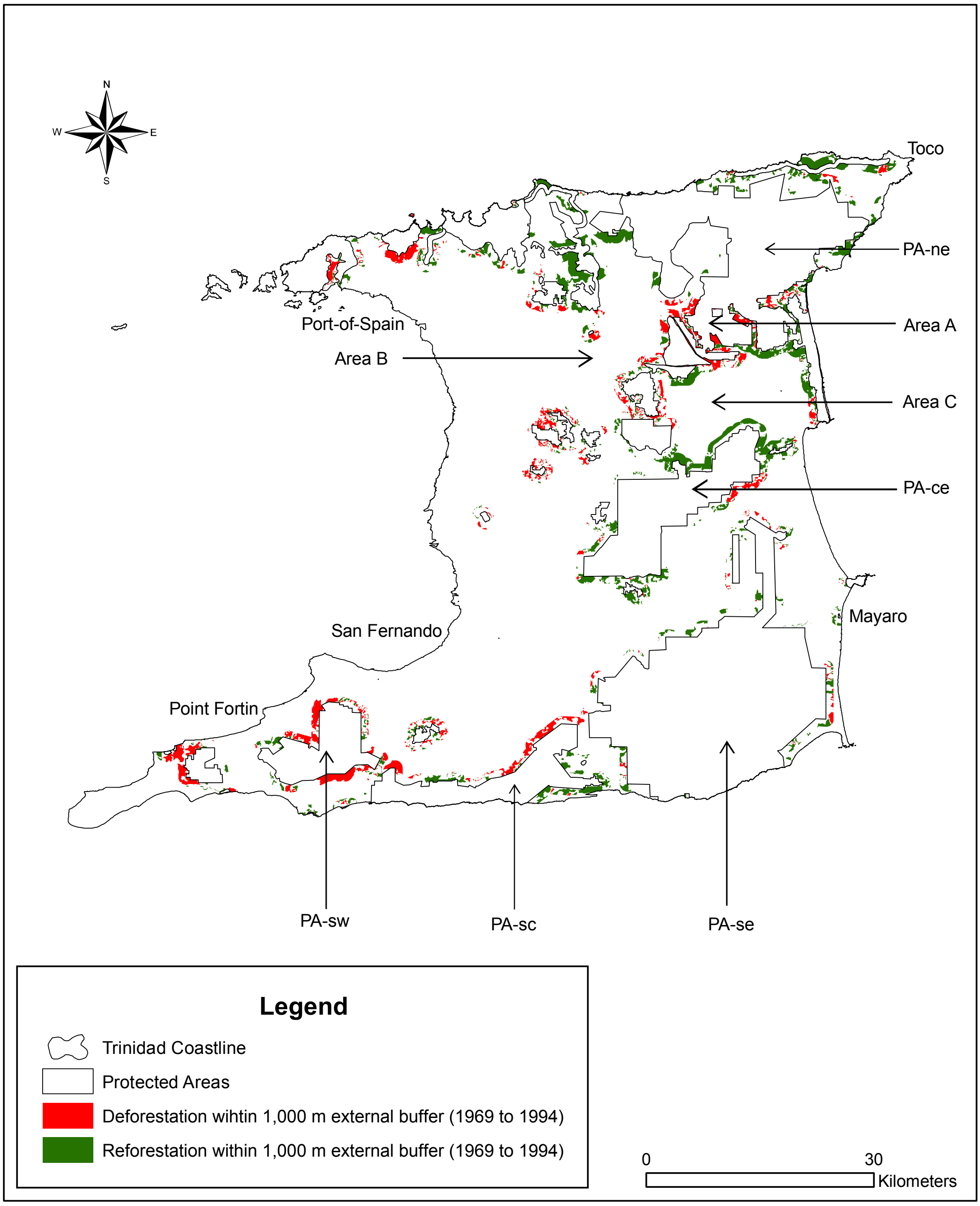


Figure 2.16: Deforestation and reforestation within the external 1,000 m buffer during Period A (1969 to 1994).

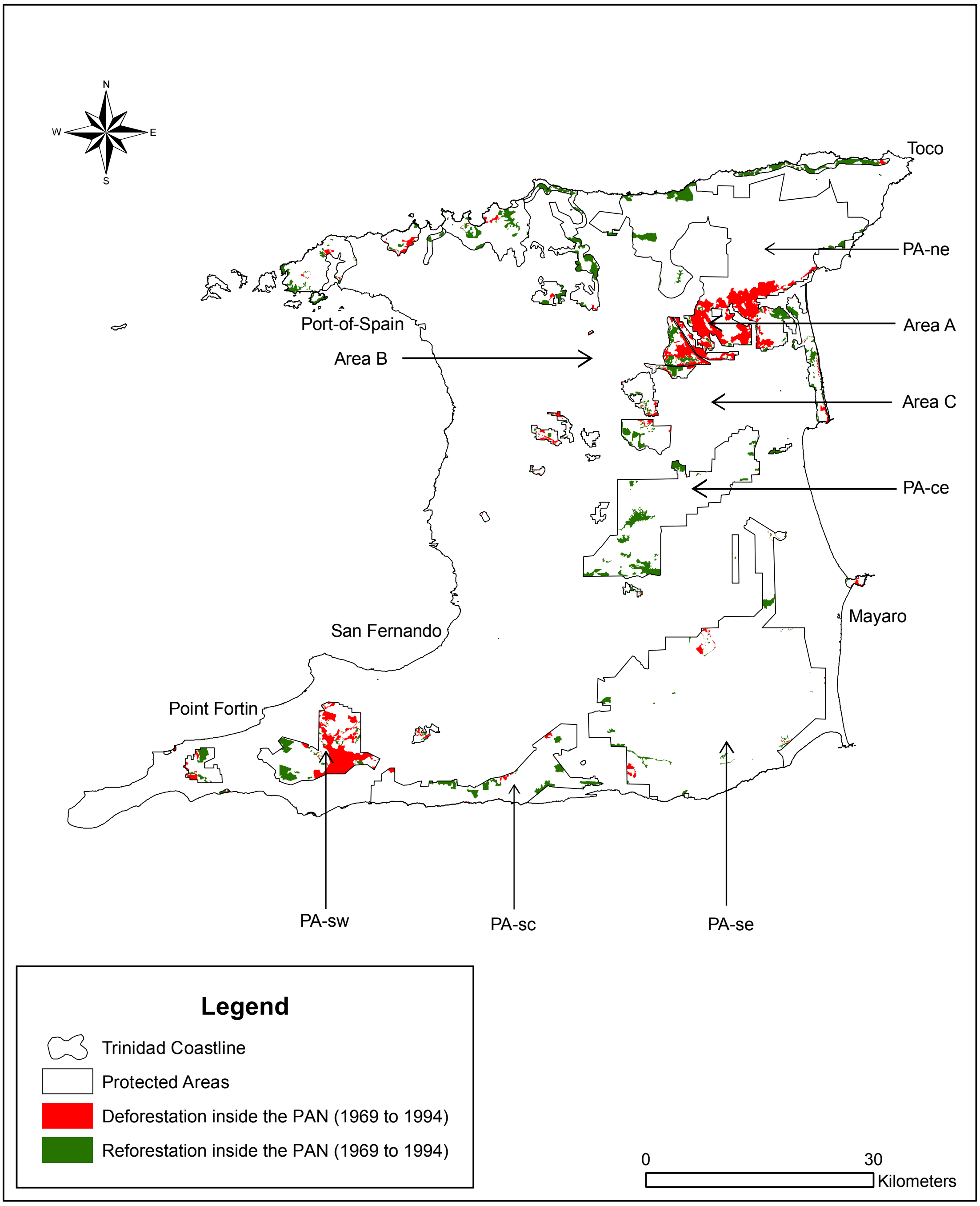


Figure 2.17: Areas of deforestation and reforestation inside the Protected Areas Network during the period 1969 to 1994.

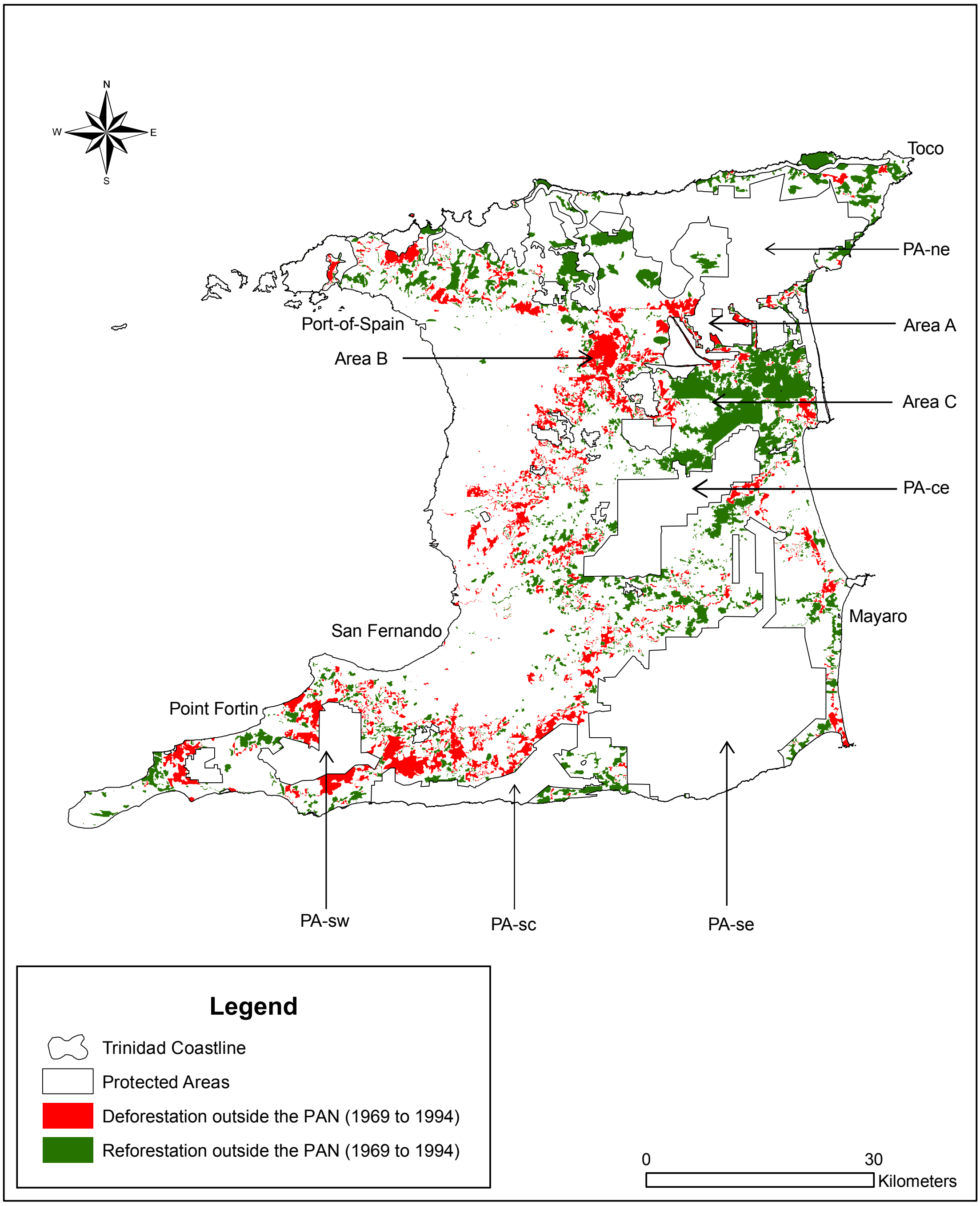


Figure 2.18: Areas of deforestation and reforestation outside the Protected Areas Network during the period 1969 to 1994.

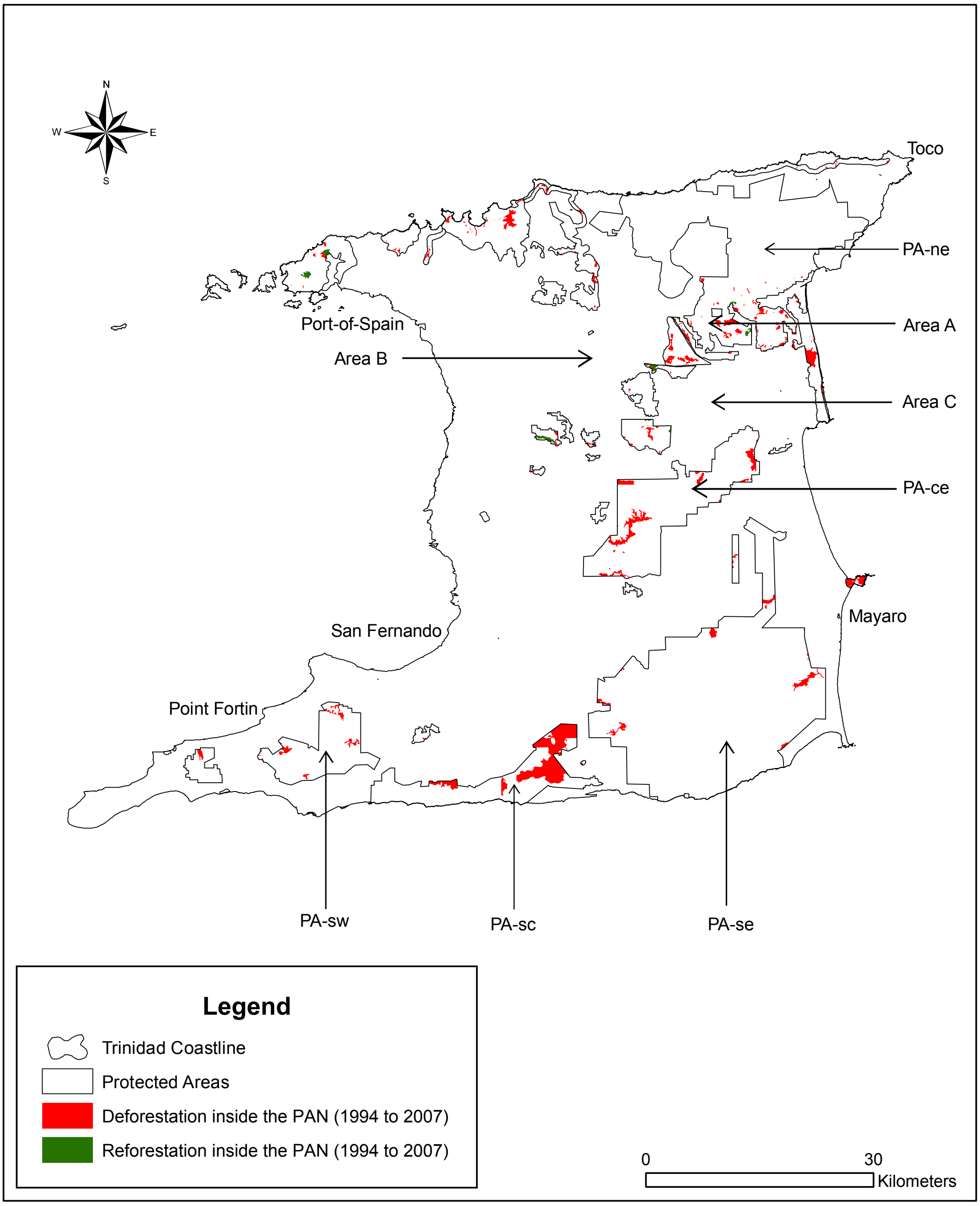


Figure 2.19: Areas of deforestation and reforestation inside the Protected Areas Network during the period 1994 to 2007.

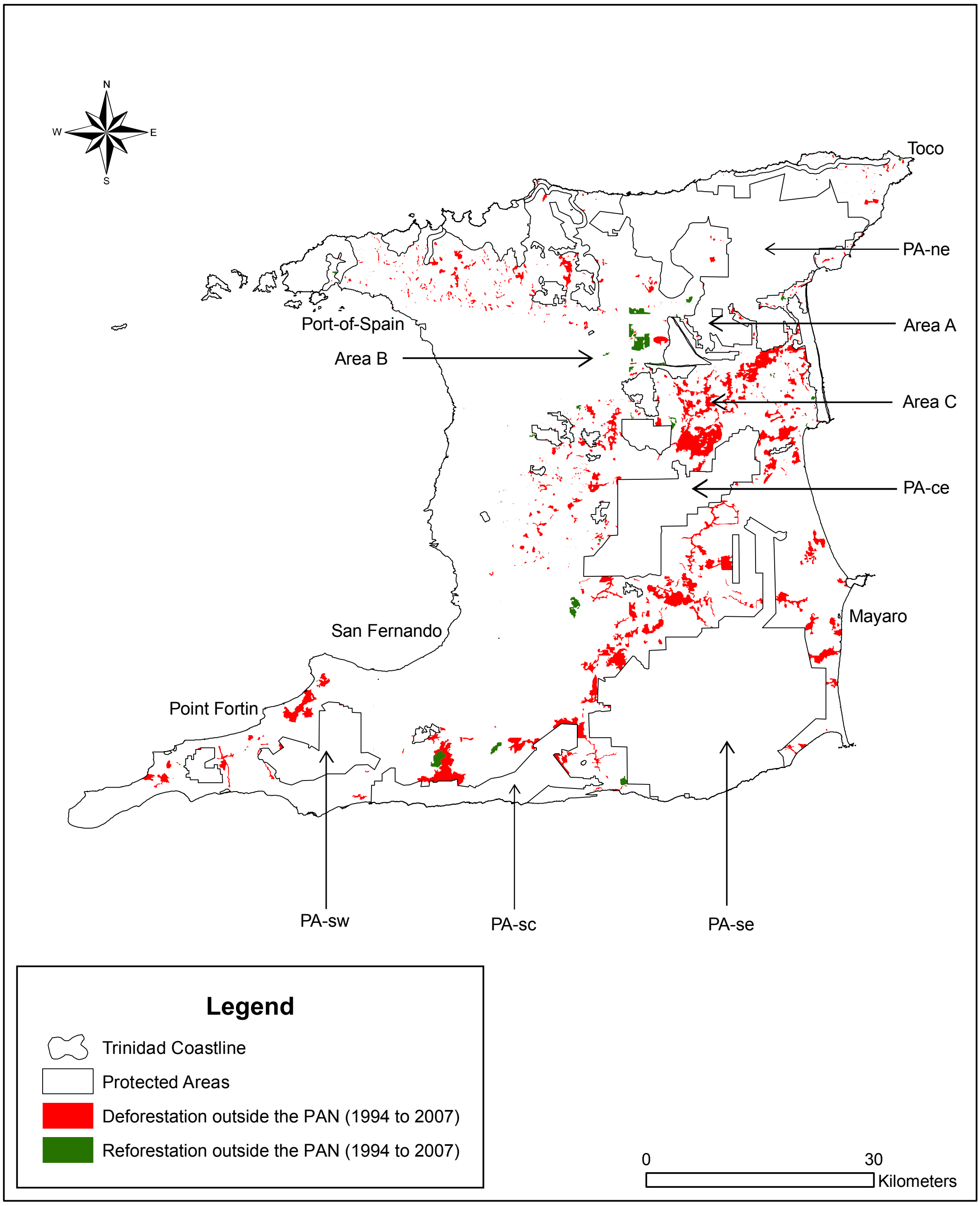


Figure 2.20: Areas of deforestation and reforestation outside the Protected Areas Network during the period 1994 to 2007.

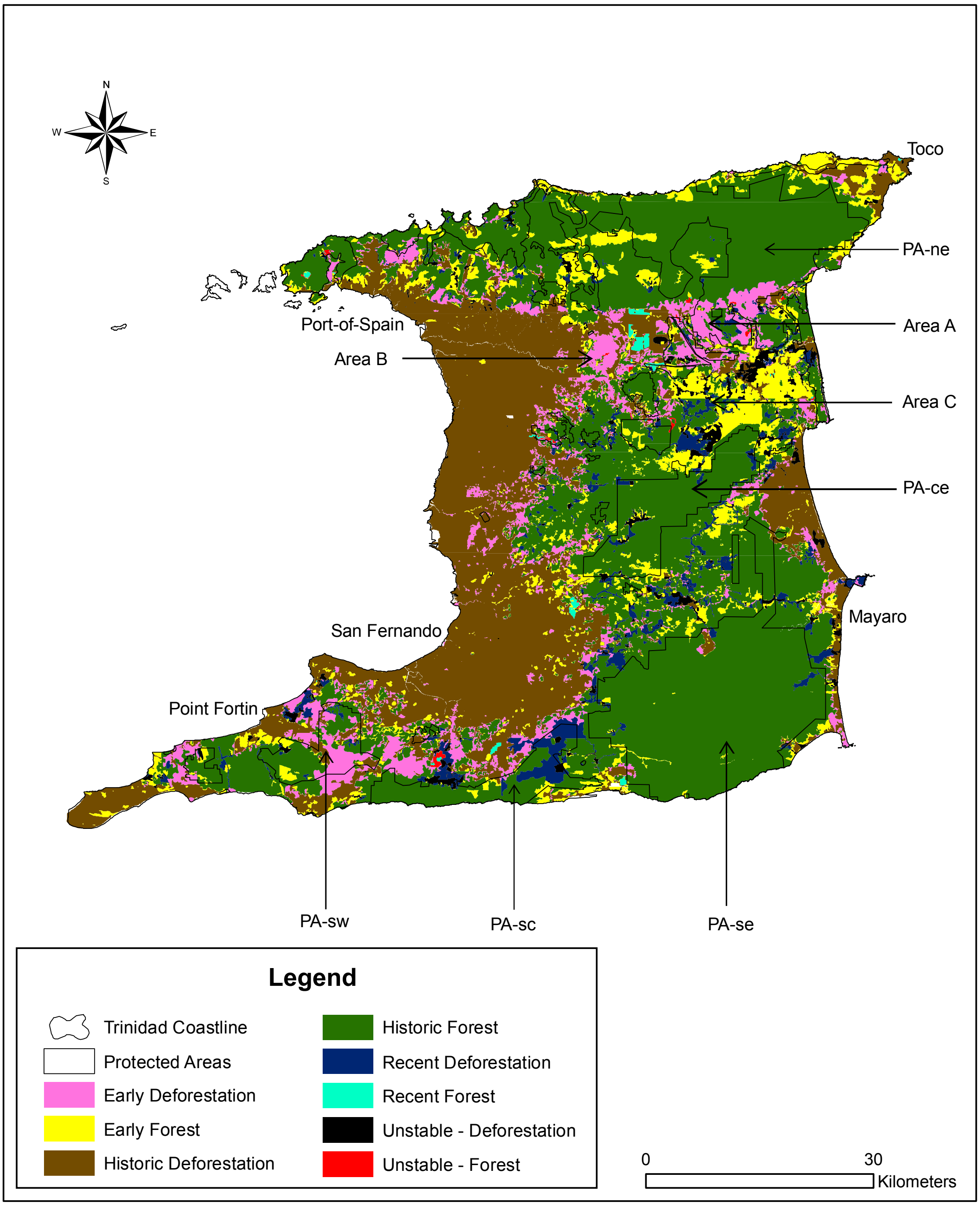


Figure 2.21: Forest Disturbance within Trinidad between 1969 and 2007.

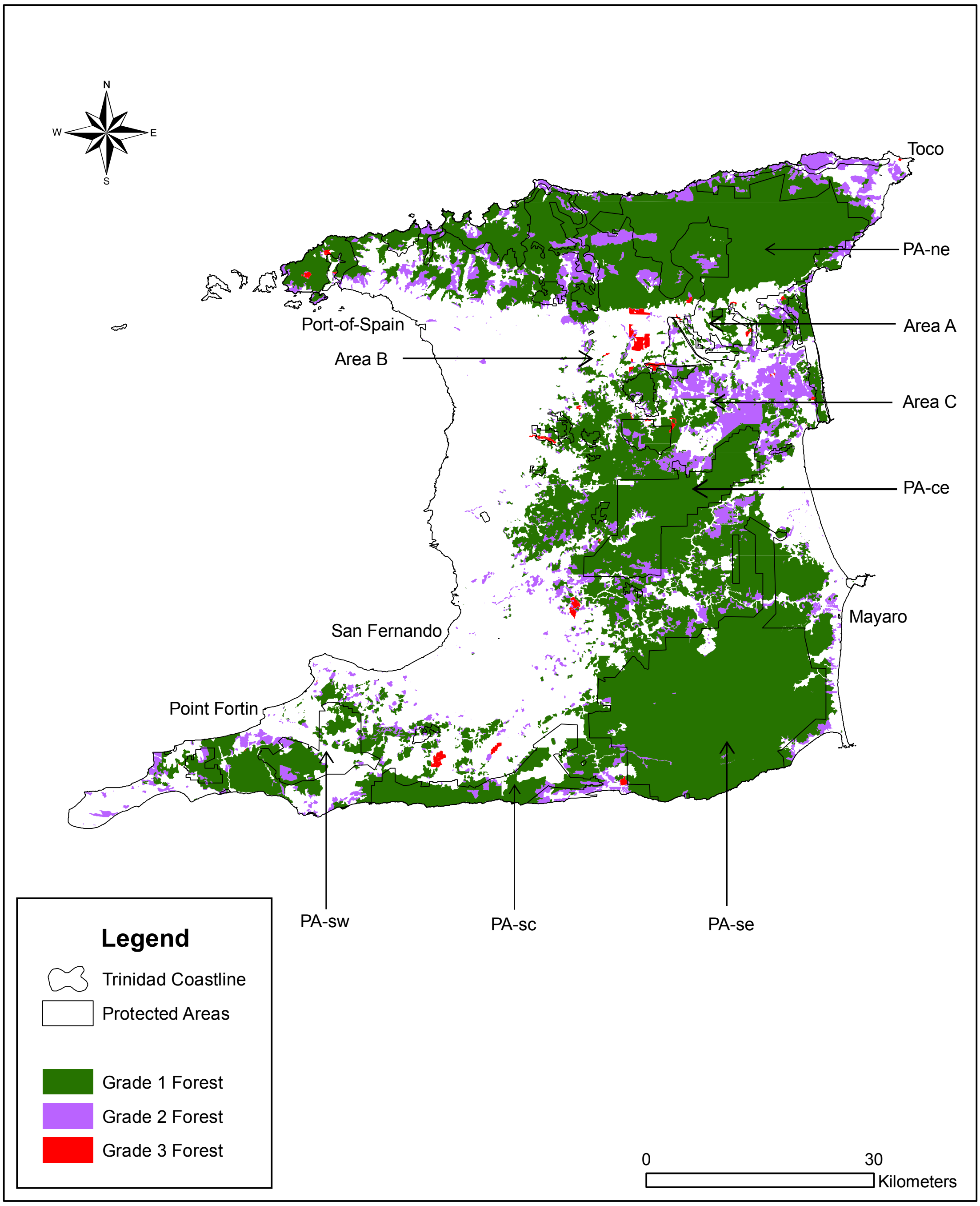


Figure 2.22: Forest Quality within Trinidad between 1969 and 2007.

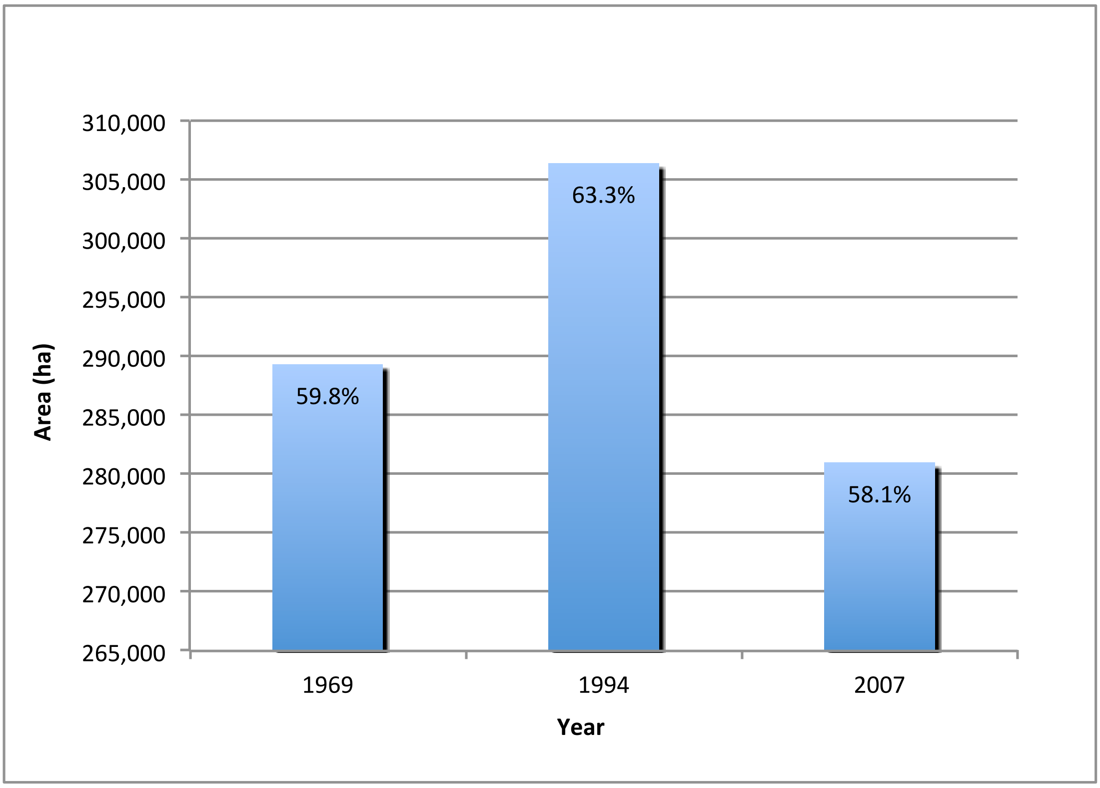


Figure 2.23: Total forest cover within Trinidad during 1969, 1994 and 2007.

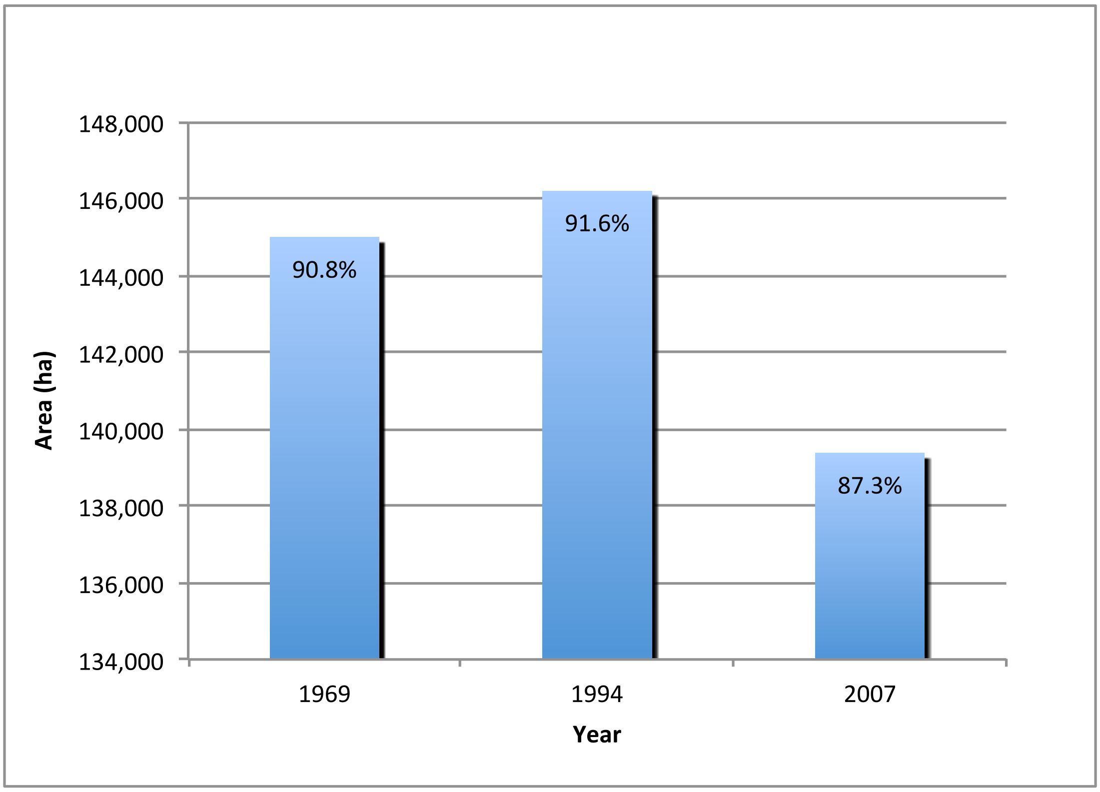


Figure 2.24: Total forest cover within the Protected Areas Network during 1969, 1994 and 2007.

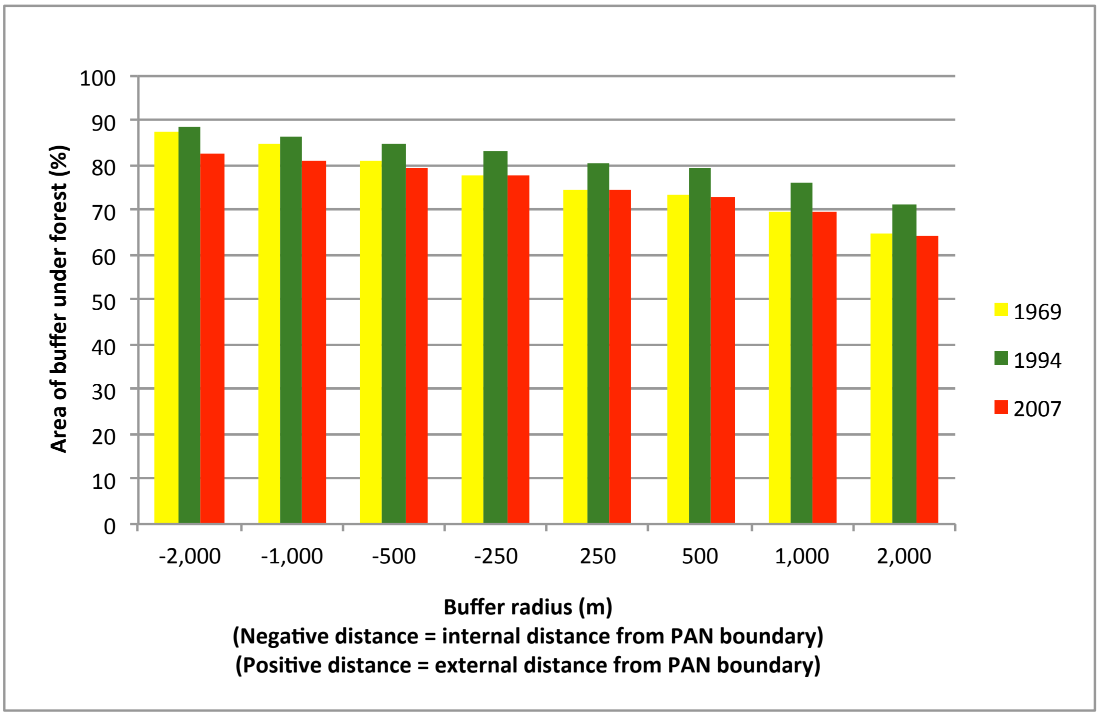


Figure 2.25: Total forest cover within buffer zones during 1969, 1994 and 2007.

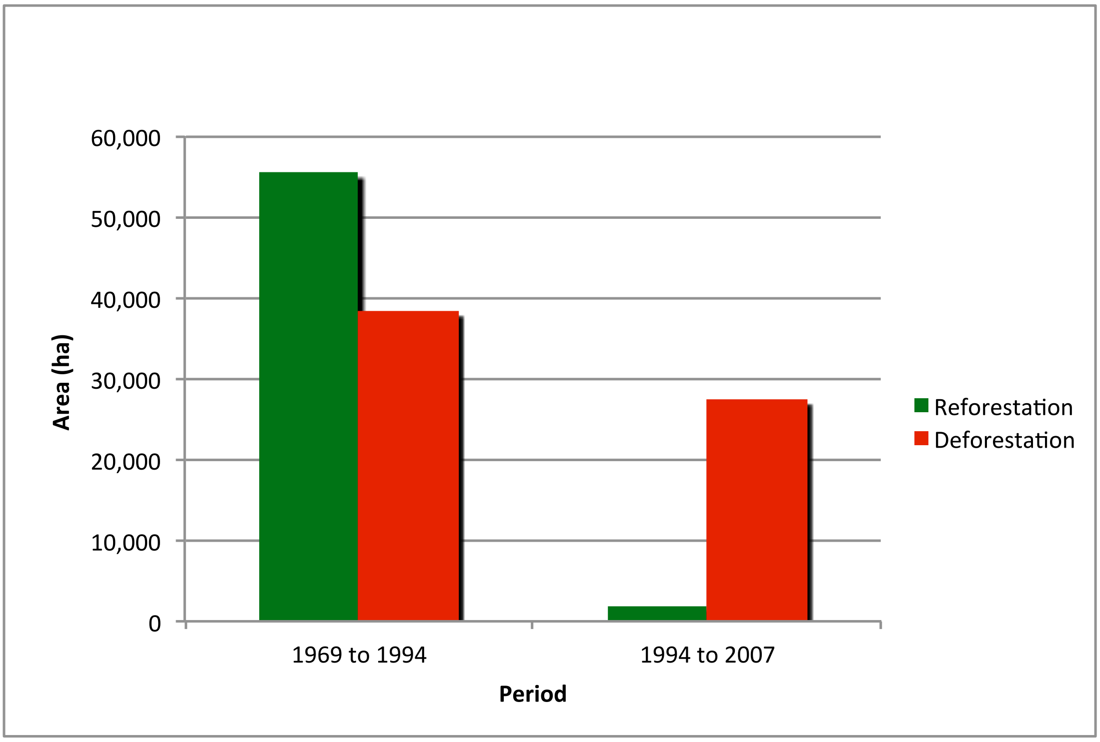


Figure 2.26: Areas of deforestation and reforestation during Periods A and B at the island scale.

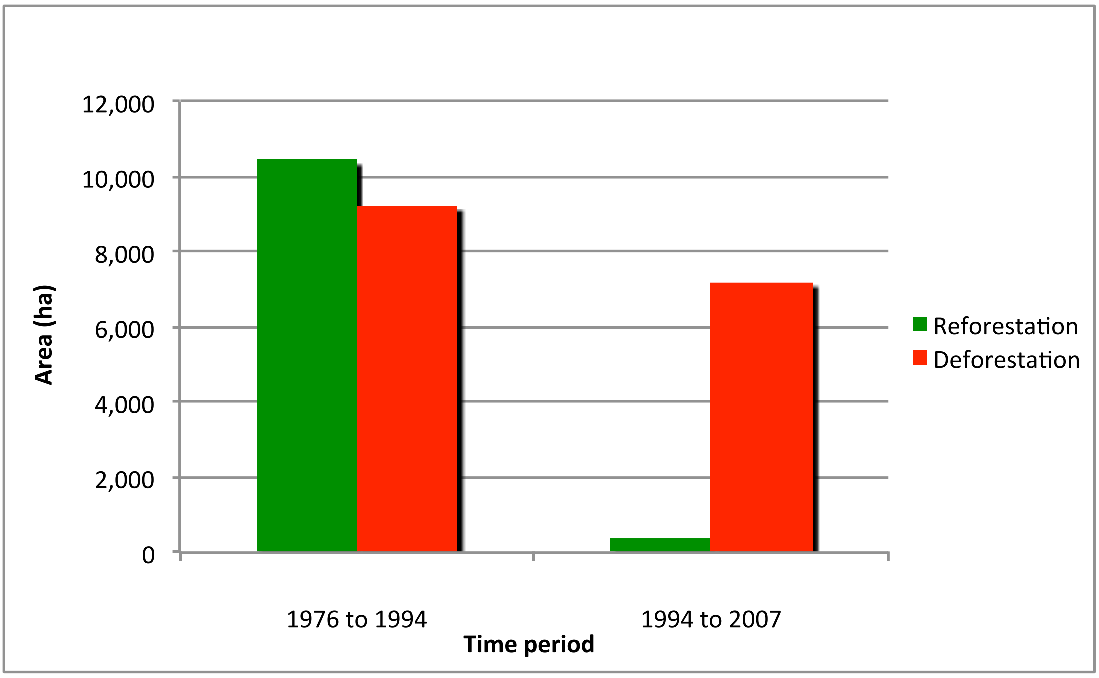


Figure 2.27: Areas of deforestation and reforestation inside the Protected Areas Network during Periods A and B.

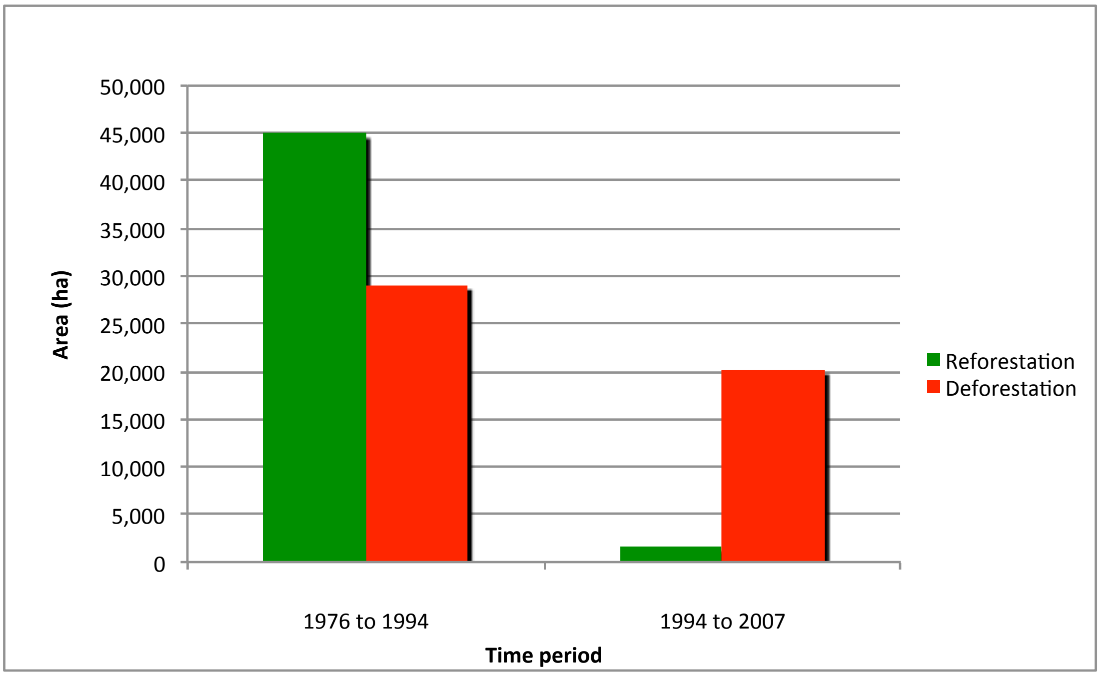


Figure 2.28: Areas of reforestation and deforestation outside the Protected Areas Network during Periods A and B.

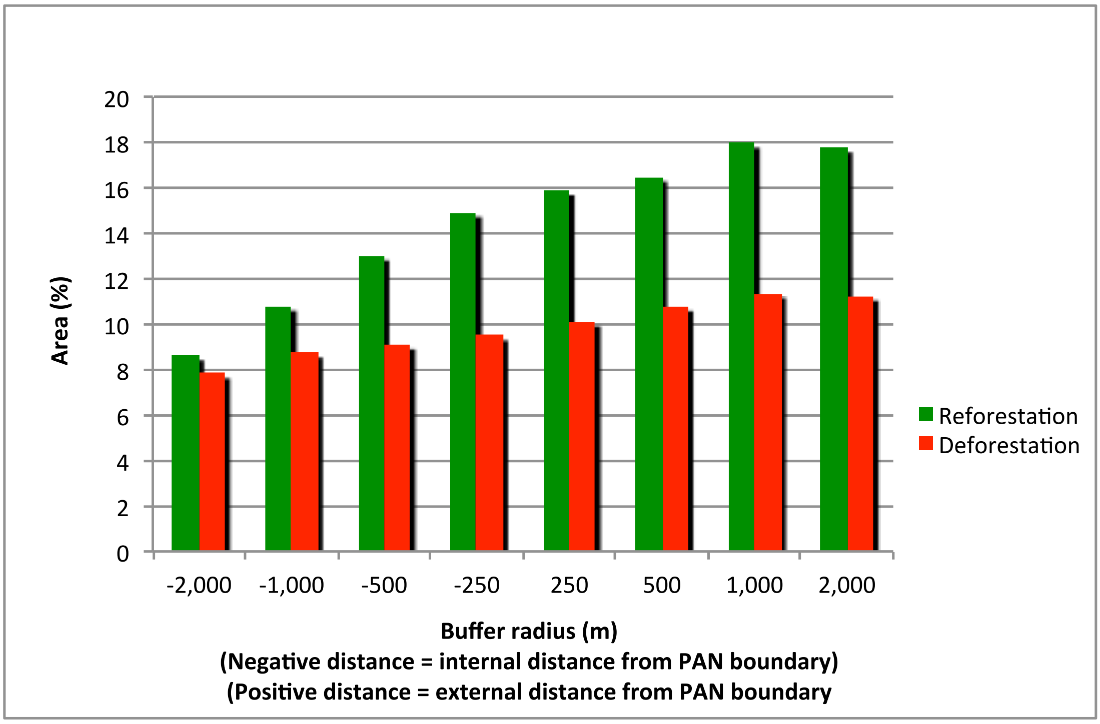


Figure 2.29: Deforestation and reforestation within internal and external buffer zones for Period A.

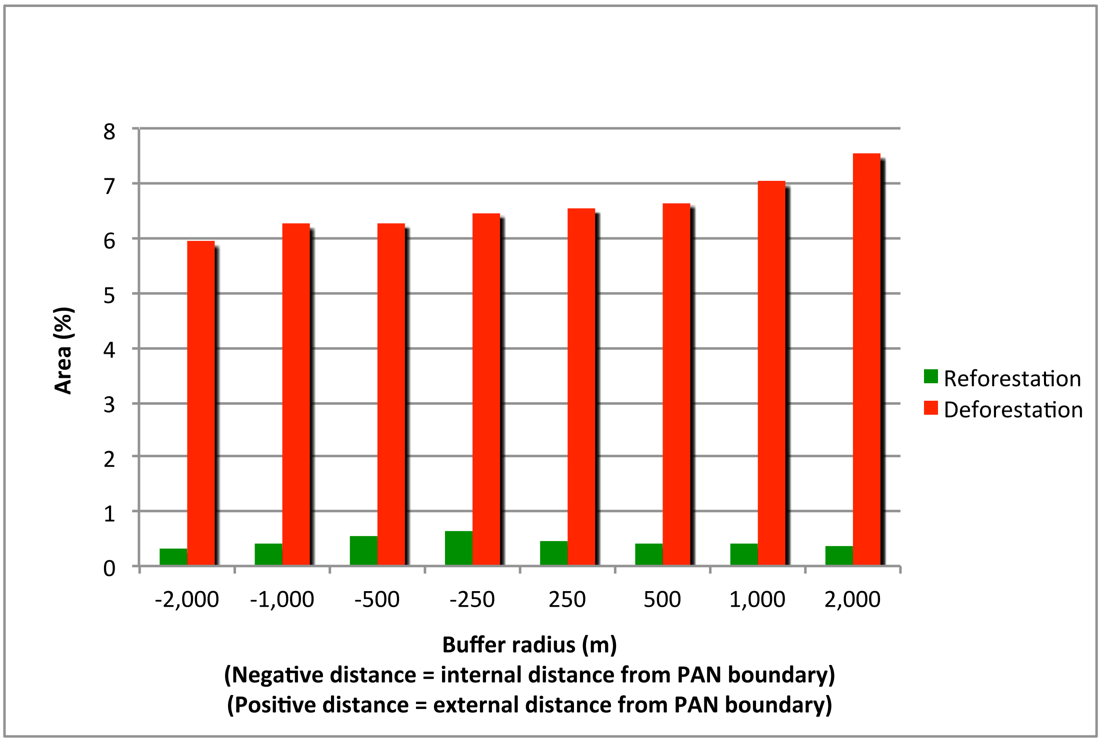


Figure 2.30: Deforestation and reforestation within internal and external buffer zones for Period B.

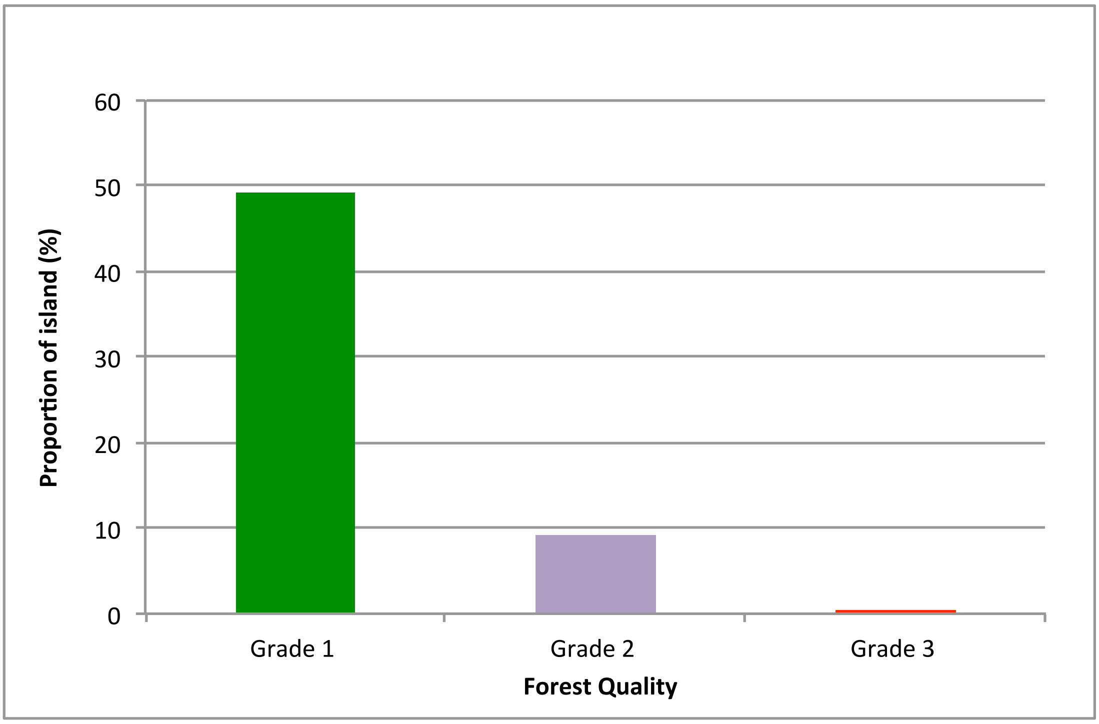


Figure 2.31: Forest Quality at the island scale.

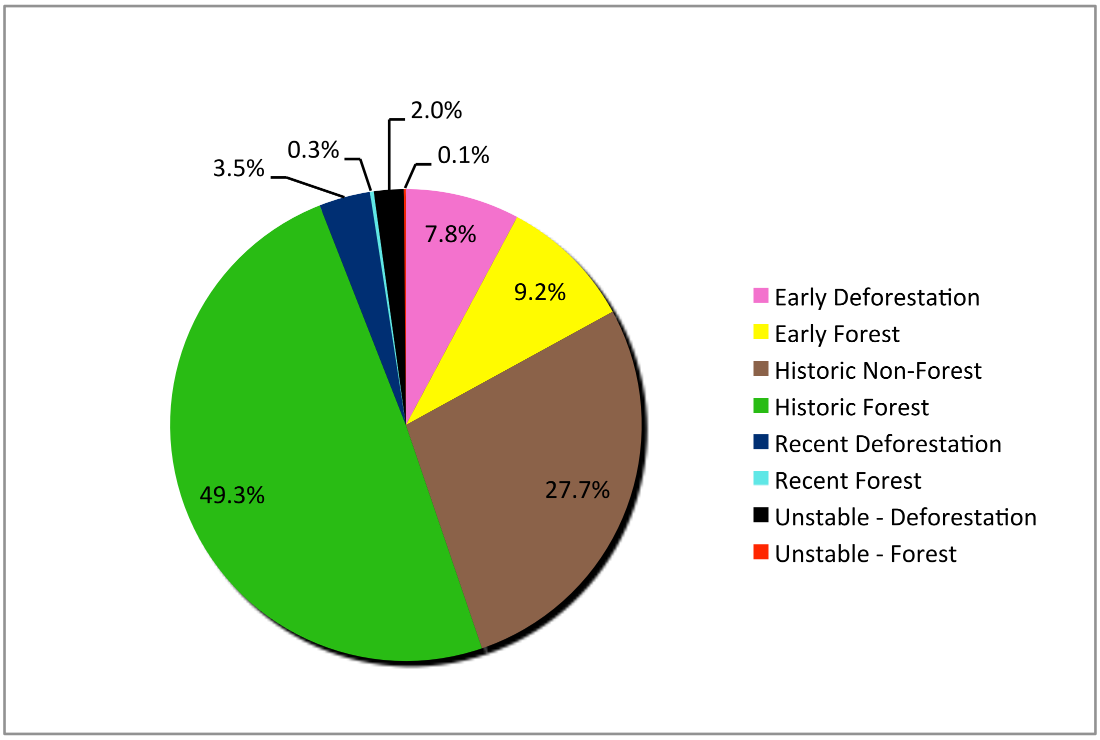


Figure 2.32: Forest disturbance status at the island scale.

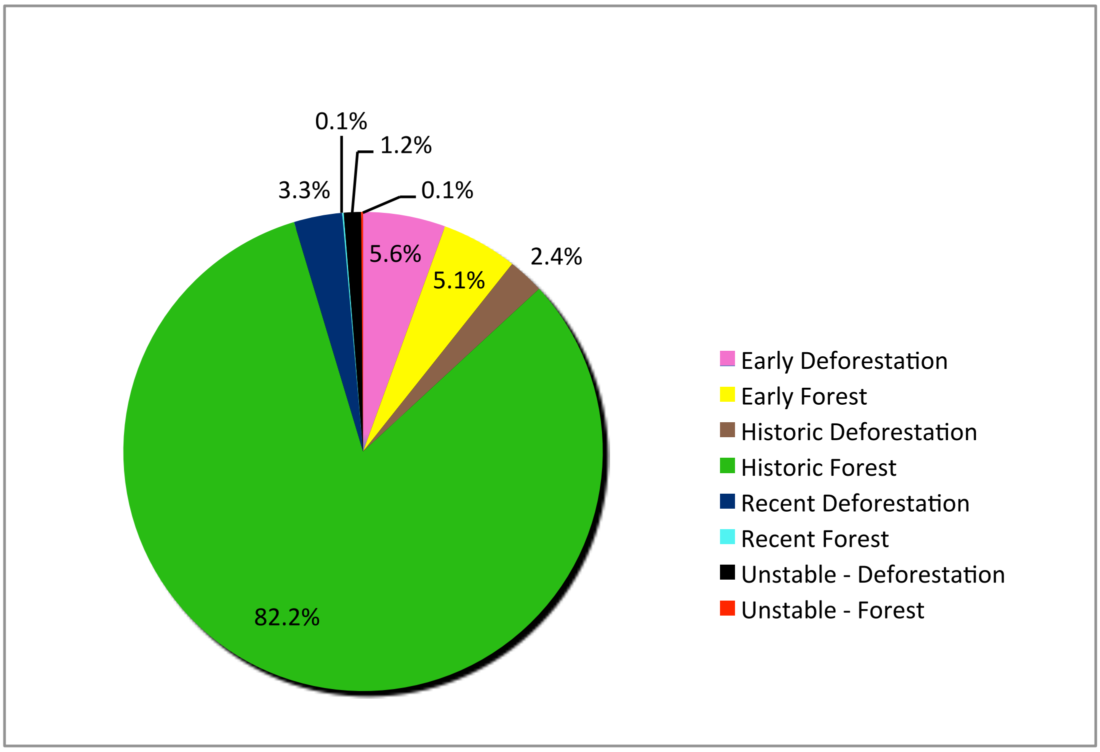


Figure 2.33: Forest disturbance inside the Protected Areas Network.

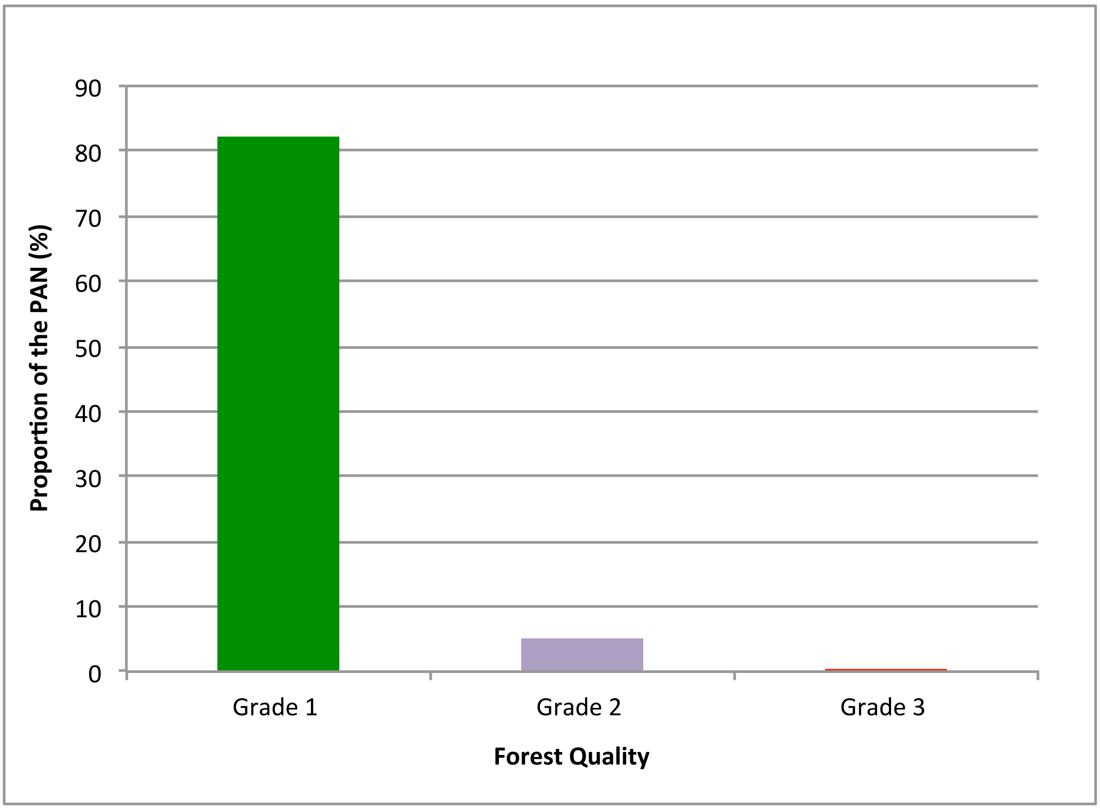


Figure 2.34: Forest Quality within the Protected Areas Network.

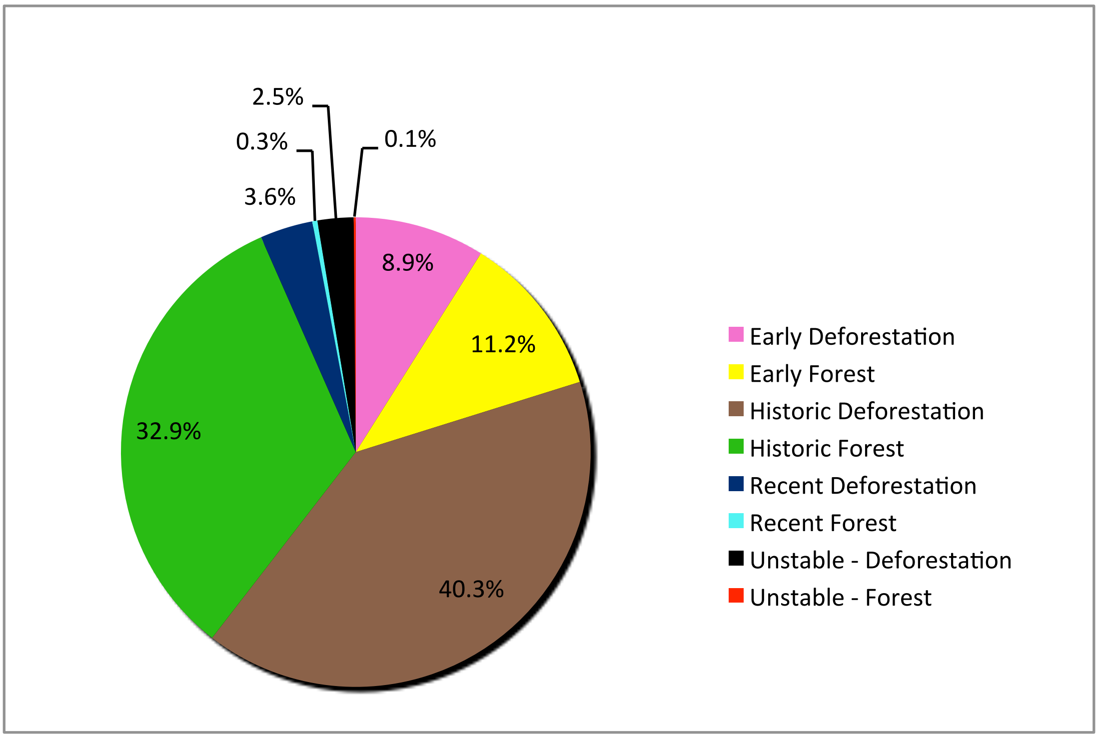


Figure 2.35: Forest disturbance outside the Protected Areas Network.

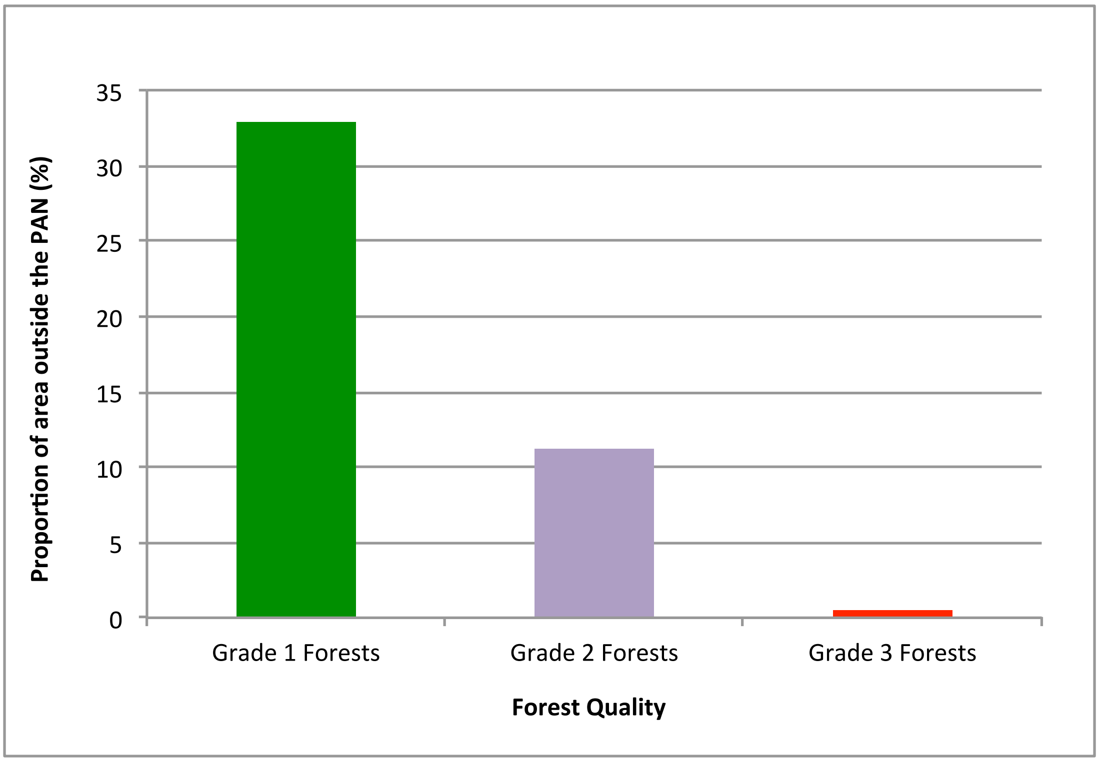


Figure 2.36: Forest Quality outside the Protected Areas Network.

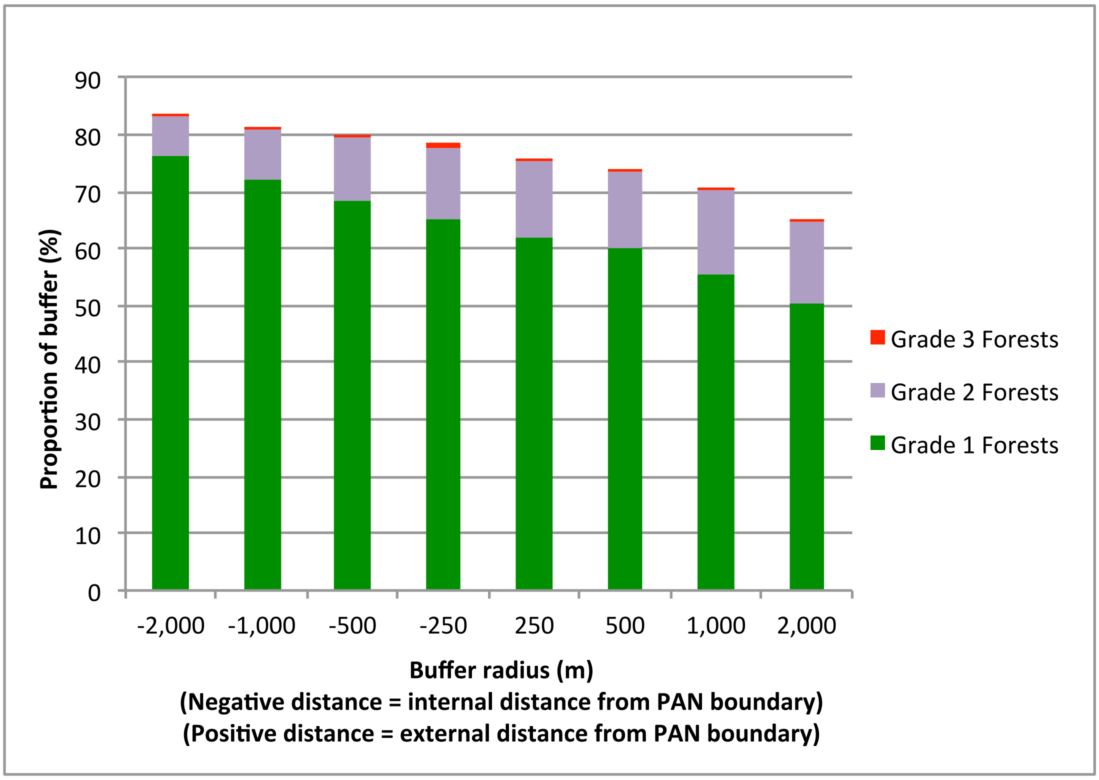


Figure 2.37: Forest Quality within internal and external buffer zones.

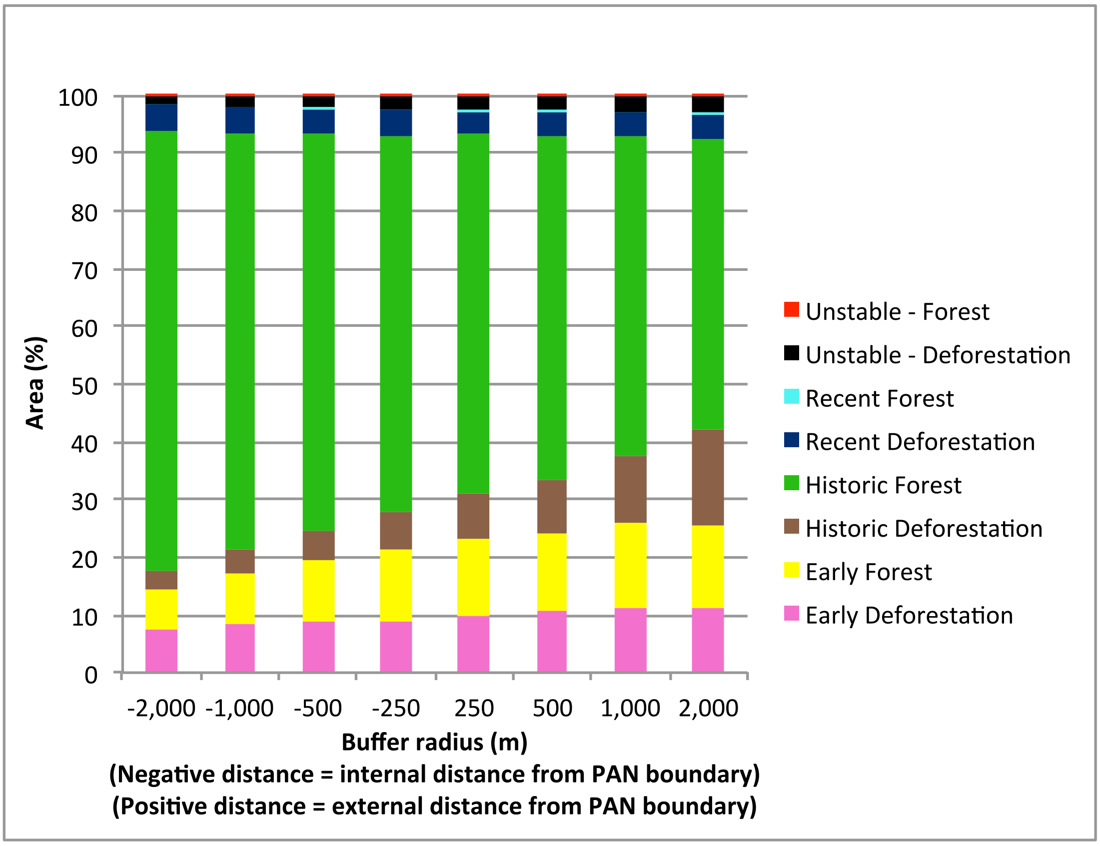


Figure 2.38: Forest disturbance within the internal and external buffer zones.

Chapter 3

Ecological Perspectives of the Vegetation within Trinidadian Forests

3.1 Introduction

3.1.1 Past ecological perspectives of Trinidadian forests

Trinidad has a long history of plant collection and description which can be traced back to the early sixteenth century to the work of Spanish historian and writer Gonzalo Fernández de Oviedo y Valdés (1478–1557) (Baksh-Comeau et al. 2011). During the 20^{th} century, floristic and taxonomic studies gave way to national forest-based vegetation and synecological studies geared towards trees and timber production. The first detailed forest inventories and analyses of the then British colony began during the 1920s, under the Forest Conservator, Captain Reginald Charles Marshall. Marshall (1925, 1926, 1928) was concerned that there was only 'a vague general idea' of the island's forest resources and a self-supporting timber industry was needed (Marshall 1925, 1926). Consequently, the Forestry Department embarked upon a detailed enumeration survey of the type and amount of timber on the island in 1927.

Marshall's survey consisted of a one percent sampling of the forests within the Crown Lands of Trinidad using strip transects (spaced five kilometres apart), along which all trees above 30 cm Diameter at Breast Height (DBH) were recorded and identified. Soil, topographic and ecological details which, based on long-term observations, were believed to affect the distributions of the trees were also measured. *Physiography and Vegetation of Trinidad and Tobago* (Beard 1946b; Marshall 1934) was based on data collected from surveys across the bulk of lowland Crown forest between 1927 and 1933. Inspired by the work of Arthur Tansley (1871–1955), then Professor of Botany at Oxford, Marshall distinguished twenty-one different vegetation associations, based on habitat, structure and floristic composition, and named according to the most plentiful of the valuable timber dominants found within each forest. Additionally, Marshall noted transition zones between different forest types and surmised that moisture availability was the main controlling factor responsible for the distribution of different vegetation types.

Today, the most universally applied description of Trinidadian forests, with respect to forest management, is the work of John Stanley Beard (1916–2011), an ecologist employed by the Forestry Department in the 1940s. *The Natural Vegetation of Trinidad* (Beard 1946b), described by many as the most comprehensive vegetation classification for the island, was the result of ecological research carried out to provide data for the formulation of a land policy by the Lands Advisory Committee of the Government. While based on Marshall's (1934) publication, Beard's study had the advantages of additional data from the enumeration surveys, which continued until 1941, and data from the Northern Range (which was previously not surveyed due to its difficult terrain).

Unlike Marshall (1934), Beard's definition and description of forest structure was based upon a hierarchy of ‘associations’ and ‘formations’. The ‘association’, referring to floristic units (based on dominant timber species), was the more basic unit. ‘Formations’ were climax associations, grouped according to their structure and physiognomy, and were independent of the plants they comprised. Following strict hierarchy, formations could have one or more associations, but an association could only belong to one formation.

Furthermore, he was of the opinion that in the tropics, it was the moisture-supplying ability of the soil which was the important consideration and that this was not necessarily at all closely concerned with climate. While he maintained that ‘the ecosystem, in fact, is one and indivisible,’ he classified his formations based entirely on moisture relations which he believed result from the interplay of climate, topography and soil. With this as a basis, he classified the forest communities within Trinidad into formations, and proposed four climatic and two edaphic climax formations – from which he identified a total of seventeen different associations and fourteen sub-associations within the island.

This classification system was based upon his collection of data on physiognomy, inspiration from the works of Richards, Tansley and Watt (Richards et al. 1940) and the development of well-illustrated forest profile diagrams inspired by Richards' work in Sarawak (Richards 1936). In the process, Beard went against the prevailing wisdom at the time which maintained that there could only be one type of climax vegetation (namely a climatic climax, and that communities influenced by edaphic factors were sub-ordinate) (Clements 1928, 1936). This was perhaps not surprising, given Beard's ‘support’ of Tansley, who was very much against Clements' views on this matter.

3.1.2 Vegetation research in the 21st century

In the 21st century, two studies inventoried and sought to describe island-wide vegetation patterns within Trinidadian forests. Howard Paul Nelson (2004), in his doctoral thesis, conducted a vegetation inventory using 43 modified-Whittaker plots sampled between 1998 and 2001. All woody stems above 10 cm DBH were measured and identified in each plot (0.1 ha). Nelson developed a conceptual model, strongly influenced by the Holdridge's Life Zones concept (Holdridge 1964), that showed how vegetation varied with climate. Nelson's model comprised a three-tiered hierarchical system of: (i) ecoregions; (ii) life zones; and (iii) landscapes in decreasing spatial extent. It was concluded that the island's forest ecosystems were biogeographically part of a transitional zone between the moist tropical forests of Guyana (south and east Trinidad) and the savannahs and dry forests of Venezuela (south and west Trinidad). Furthermore, he postulated the Northern Range was biogeographically-associated with Venezuelan coastal montane forests.

Nelson pointed out that a fundamental weakness of Beard's (1946b) forest classification system was that it was based only on dominant trees. Additionally, he criticised Beard's underlying assumption that Trinidad's forest communities are relatively stable in composition and ecology and which tend towards a 'climax' condition. In contrast, Nelson's study assumed Trinidadian tropical forest systems were not at equilibrium and showed forest composition could shift in response to periodic, irregular and stochastic climatic processes, as well as human activities. Nelson's study also questioned the 'uniqueness' of some of the forest associations described by Beard, suggesting that these communities existed on a precipitation/moisture availability continuum and not necessarily as discrete units.

The second Trinidadian vegetation inventory (2005 to 2008) was a collaboration among the UWI, Trinidad, the National Forestry Division of Trinidad and Tobago and the University of Oxford. This inventory was the first Trinidadian vegetation inventory to include all terrestrial, vascular plants; not just tree species. All terrestrial vascular plants at one hundred and ninety-five sites across the island were sampled using the Rapid Botanical Survey (RBS) method (Hawthorne and Abu-Juam 1995). The results of this survey were used to produce *The vascular flora of Trinidad and Tobago: A checklist with conservation status* (Baksh-Comeau et al. 2011), although no assessment of the vegetation structure or ecology based on these data has been published.

Today, the Forestry Division of Trinidad and Tobago continues to manage most of the country's forest resources based on Beard's work (1946b). It continues to produce annual reports of forest composition based on timber stocks. Timber species composition and size data have been regularly sampled within at least one hundred and seventy-four Permanent Sample Plots (PSPs), established in 1983, but these data have not been analysed in detail (Fairhead and Leach 2002). Furthermore, neither the annual forest composition reports nor the PSP data includes information on non-timber species and thus continue to lack a holistic account of vegetation biodiversity or structure.

This chapter makes use of the above RBS inventory's species abundance data collected for both trees and non-tree species to assess the distribution and ecology of the island's vegetation 'communities'. This is in order to generate a list of species to be used in the analyses of Chapters 4 and 5 which investigate the use of SDM as potential tool for informing conservation planning in the face of a changing climate. Limited to already existing knowledge and information that will be generated by this chapter's analyses, this list will be based solely on (i) the ecological importance, (ii) commercial importance and (iii) global/regional rarity status of dominant tree species within the island. Moreover, the choice of species will be limited only to tree species, as this is the only group that has been adequately sampled within the island to have ample distribution data that is necessary to develop sound species distribution models (discussed further in Chapter 4). Finally, it is emphasised that this chapter neither seeks to develop another vegetation classification scheme nor suggest a conservation strategy for the forests of Trinidad.

3.2 Methods

3.2.1 Sampling of vegetation data

3.2.1.1 Rapid Botanical Surveys

A high resolution inventory of Trinidadian terrestrial vascular plants was conducted using the plotless RBS method (Hawthorne and Abu-Juam 1995) between 2005 and 2008. As described in detail by Baksh-Comeau et al. (2011) the RBS technique is a hybrid of synecological and purely floristic methods, and is designed to describe details of a flora for the purposes of biodiversity management; it does not include data on tree size, volume and growth rates.

The distribution of RBS sites (Figure 3.1) was designed to maximise the coverage of the terrestrial vascular indigenous flora of Trinidad. The majority of the 195 sites sampled within the island were located within areas of natural vegetation (mainly forests), with a bias against sites which were likely to be of very low conservation value, for example, plantations, ruderal, urban and temporary communities. However, some presumed low conservation value communities were included to ensure a uniform spatial distribution of RBS sites within the island. Non-forest locations included savannahs, swamps, coastal vegetation, plantations (cocoa, coffee, teak), rice fields, abandoned sugar-cane plantations and partially-settled regions.

3.2.1.2 Sampling procedure

Plotless RBS samples were conducted within vegetation landscapes across the island; with 'plotless', meaning that they could be of any shape, and were usually limited by the physical features within a given landscape. For example, a sample area would be linear in shape if situated along the top of a narrow mountain ridge.

Samples were based around a focal point, from which all taxa were collected within 10–100 m (depending on physical limitations). Collection of vegetation was divided into three main groups: trees, shrubs and herbs. Due to difficulties in sampling and identification, germinated seedlings and dead trees were excluded, whilst epiphytes were collected only if within easy reach from the ground.

Canopy trees (trees with boles $\geq$30 cm DBH) were identified to species. As a general rule of thumb at least 40 tree stems (not species) were counted for the extent of a sample to be considered adequate (in practise this number was usually easily surpassed). In areas with few large trees such as logged areas, palm marsh forest, swamps and savannahs, a smaller DBH size threshold was used. This was based on the average DBH of an arbitrary 30 trees closest in proximity to the focal point from which the survey was based. RBS sites with few trees, such as rice fields and abandoned sugar-cane plantations, were considered complete when sampled within a radius of 100 m (unless restricted by terrain).

The abundance of tree species with $<$30 cm DBH was ranked according to a

3-point index (based on field observations): 1, rare, few or not many within the entire area; 2, common, occurring frequently within the area sampled; and 3, dominant within the area. Shrubs and herbs were also ranked according to this index. These assessments were done by the same personnel throughout the entire sampling effort, and were based on visual rather than measured quantities of individuals. In addition, background site information was also recorded, including the state of the vegetation with respect to management, threats and disturbance levels, soil texture and colour, slope, GPS location co-ordinates and gazetteer information.

Specimens of each plant ‘morpho-species’ were tagged with unique alpha-numeric codes and brief ecological details recorded on a field survey sheet. All specimens were pressed in the field and taken to the National Herbarium of Trinidad and Tobago for later processing and identification.

3.2.1.3 Identification and databasing

Of the 195 RBS sites sampled during the inventory of Trinidad (Figure 3.1), approximately 20,000 specimens were collected, of which about 90% of these were sterile. The identification of these thousands of mainly sterile specimens took place at the National Herbarium of Trinidad and Tobago. The specimens were first sorted according to families from which the species names were further resolved using the reference collection and resources of the National Herbarium. The identified specimens together with their respective field notes were managed within the Botanical Research and Herbarium Management System (BRAHMS) (DPSOX 2004).

3.2.2 Selection and preparation of RBS data

3.2.2.1 Omission of RBS points

As this study sought to find tree species important to vegetation associations within the natural, terrestrial forests of Trinidad; a total of thirty RBS sites from the vegetation survey (Section 3.2.1.1) which were not located within naturally-occurring terrestrial forests were omitted from these analyses. These included: (a) swamp/marsh vegetation; (b) savannahs; (c) xerophytic coastal vegetation; (d) plantation samples – including teak, Caribbean Pine, citrus and coconut; (e) rice fields; (f) abandoned sugar cane plantations; and (g) abandoned and regenerating coconut plantations. The RBS abundance data (trees, shrubs and herbs) for the remaining 165 RBS sites (Figure 3.1) were extracted from the BRAHMS database.

3.2.2.2 Creation of an abundance index for canopy trees

Abundance data were collected in different ways for canopy trees vs non-canopy trees (saplings); the former were count data, while the latter were categorical (0 to 3). The abundance of trees, shrubs and herbs were each collected by the same surveyors within the survey team at all RBS sites. Because the objective of these analyses was to generate a list tree species for SDM in Chapters 4 and 5, it was necessary to combine the sapling abundance data with the 'adult' count data. This combination was necessary because sapling abundance (<30cm DBH) is considered to be an indicator of the regenerative capacity of tree species. It is therefore necessary to integrate sapling abundance with that of 'adult' trees when modelling the distribution of tree species. This is because a list based only on the contribution of count data of usually long-lived 'adult' trees would not necessarily imply that the present climate was still suitable for their continued regeneration.

In order to combine these two data types, it was necessary to convert adult tree count data into an abundance index, with the same limits as the sapling data (0 to 3). For a given canopy tree species the number of individuals was calculated as a percentage of the total number of trees counted for the plot. These percentages were converted to abundance scores as follows:

- 0 = absent
- 1 = up to 33.33%
- 2 = from 33.34% to 66.66%
- 3 = from 66.67% to 100%

3.2.2.3 Combination of tree and sapling abundance indices

Three methods were considered for combining tree and sapling abundance indices for a given species: (i) using the maximum index value, (ii) using the minimum index value; and (iii) using the mean index. Option (iii) was dismissed since both abundance indices were categorically different and could not be averaged. Option (i) potentially over-estimated sapling data since high sapling abundance may not reflect high abundance of mature trees. Option (ii) displayed the opposite problem since low sapling abundance compared to adult abundance may be due to factors such as sampling prior to germination, initial growth of seedlings and human interference. Option (i) was chosen as it was likely to provide the best representation of the potential of a species to occur within a given RBS site, in addition to which, less stochasticity (e.g., human interference) was associated with it than with option (ii). As such, the final ‘modified species abundance’ used for the ordination analyses was then taken as the higher of the two scores (observed non-canopy abundance vs calculated canopy tree abundance scores).

3.2.3 Treatment of data for multivariate analyses

The combined species abundance data were imported as a rectangular matrix into the PRIMER VI software (Clarke and Gorley 2006) for subsequent analysis. All analyses were multivariate and included: (i) calculation of a similarity matrix; (ii) definition of ‘ecological clusters’ consisting of similar sample sites; and (iii) the breakdown of species contribution to within-cluster similarity (Clarke 1993).

3.2.3.1 Transformation

Tropical forests are characterised by higher levels of plant alpha diversity (versus temperate forests); with high numbers of rare and uncommon species within a given unit area (Turner 1996; Wright 2002). Because of this potential for only a small proportion of the species within a given RBS site to be abundant, a mild transformation was needed to provide greater weight to the mid-range and rare species in relation to abundant species within a given site. Square root transformation enabled down-weighting of the importance of the few highly abundant species so similarity analyses would depend not only on these few highly abundant species, but also on the less common mid-range species (Warwick and Clarke 1995).

3.2.3.2 Alternative treatment of abundance data

It is clear that the treatment of the data described in Sections 3.2.2.2 to 3.2.3.1 above was not ideal. However, in order to (i) include sapling abundance and (ii) integrate the effects of abundance within the analyses, the above treatment of the data was considered to be the best possible combination of the options available at each stage of the treatment.

Alternatively, one might argue that the only way to remove most of the potential errors within the above described treatment would be to perform a presence/absence transformation upon the combined abundance data matrix (Section 3.2.3.1). This would certainly remove any concerns pertaining to the use and combination of different abundance indices for the tree and sapling data described in Sections 3.2.2.2 and 3.2.2.3. However, the use of a presence/absence transformation was not considered to be a suitable choice in keeping with the objectives of this chapter. This is because it would remove all of the abundance information altogether from the RBS sites – giving the impression that the abundance levels for all species were uniform to each other. This conflicts with the objective of these analyses, which seeks to identify tree species based on their ecology – of which differences in abundance are thought to play a key role.

However, for comparison, alternative analyses in which the combined abundance matrix was transformed using presence/absence was also carried out. These results are included in Appendix A.

3.2.3.3 Similarity matrix

A triangular similarity matrix, using the using the Bray-Curtis measure (Bray and Curtis 1957), was needed where similarity within groups are higher than between groups. The Bray-Curtis measure was used for four reasons. Firstly, Bray-Curtis takes a value of 100 when two samples A and B are identical, and changes in measurement unit do not affect its value. However, unlike other coefficients, when there are no species in common it takes a value 0. Unlike most other coefficients, it can also maintain an unchanged value (between A and B) in the following scenarios: (i) the inclusion of a species into the array that is mutually absent from both samples A and B or (ii) there is this inclusion or exclusion of a third sample C into the array. Finally, the Bray-Curtis measure does not standardise by sample totals, this flexibility allows it to define differences in total abundance between A and B as a less-than-perfect similarity even when the relative abundance values for all species are categorised as identical (Bray and Curtis 1957; Clarke and Warwick 2001). These features were seen as especially relevant to the application of the RBS dataset given (i) the higher numbers of rare and uncommon species within these samples (Section 3.2.3.1) and (ii) the 'plotless' nature of the RBS samples which yielded variation in total abundance between samples (Section 3.2.1.2).

3.2.4 Ordination analyses

3.2.4.1 Similarity profile test (SIMPROF)

Prior to conducting ordination analyses which seek to define ecologically similar groups within the entire abundance dataset (165 RBS samples), a SIMPROF test was carried out to discern whether internal group structure within the overall dataset existed.

SIMPROF is a permutation test of the null hypothesis that a given set of samples, which are not divided into groups on an *a priori* basis (as is the case with the RBS data), do not differ from each other in multivariate structure. Validation of the null hypothesis would imply a lack of internal group structure, while the opposite result would provide validation for further investigation of internal group structure (Clarke and Gorley 2006). The similarity profile itself consists of the entire collection of resemblances between the given samples (ranked smallest to largest). These resemblances are ordered and plotted against their rank. Departure of this curve from the 'expected' shape of the null hypothesis curve is the basis of this test.

3.2.4.2 Cluster analysis

Cluster analysis, using complete-linkage, was applied to the similarity matrix of the RBS abundance density data. The clustering was carried out in conjunction with the SIMPROF routine in order to generate dendrograms with objectively-defined groups, indicating the statistical strength (set at a 5% significance level) of the branches/sub-structures within the tree.

The complete-linkage technique was chosen instead of the single linkage or group average options for two reasons. Firstly, complete-linkage (as well as single-linkage) are effectively non-metric. This means that Bray-Curtis similarities are replaced by their ranks. The rank-similarity matrix is preferred as it maintains the original Bray-Curtis structure but is unaffected by any non-linear rescaling of the similarities which would otherwise affect the analyses. Secondly, single-linkage produces large groups of linked samples in a chain like structure (resulting from the addition of single samples at each stage of the analyses). In contrast, the complete linkage option creates small clusters at early stages of the analyses – and is easier to relate to for ecological analyses which seek to identify ecologically similar groups of samples (Clarke and Warwick 2001).

3.2.4.3 Mapping of Clusters

RBS sample site locations for each of the ten clusters defined at the 9.17% similarity level were mapped out within the geographic space using ArcGIS 9.3 (ESRI

2009). This enabled determination of the: (i) general ‘location’ of these clusters; and (ii) spatial coherence of RBS sites within each cluster.

3.2.4.4 Non-Metric Multidimensional Scaling (NMDS)

Non-Metric Multidimensional Scaling (NMDS), an unconstrained, non-parametric ordination, was used to illustrate differences in species abundance among the 165 RBS samples. This technique was chosen as it is flexible, non-metric and allows the use of any association measure. Additionally, it can be applied to a wide variety of scenarios, with relatively fewer assumptions about the quality and nature of the data than for most other ordination methods (Clarke and Warwick 2001). This final feature was particularly appropriate as the abundance data for these analyses were ‘modified’ by combining tree count data with an abundance index (sapling abundance) (Section 3.2.2.3).

The Bray-Curtis similarity matrix of modified species abundance densities was used to produce a two-dimensional representation of among site resemblances. Each site within the ordination was coded to represent their respective clusters (Figure 3.7) and sub-clusters (Figure 3.8).

3.2.4.5 Sub-division of RBS dataset for NMDS analyses

Inspection of the arrangement of the RBS sites within Figure 3.8 (Section 3.3.2.1) led to the further sub-division of the RBS dataset into two groups at a 0.5% similarity level (Figure 3.5). Group 1 consisted of sub-clusters 1A to 6A while Group 2 was comprised of sub-clusters 7A to 10A. two-dimensional NMDS plots were then generated for both these Groups.

3.2.4.6 Creation of a 'summary' NMDS plot

A 'summary' two-dimensional NMDS plot of ecological resemblance among all thirteen sub-clusters (without the noise within the data) was then constructed from amongst the entire RBS dataset. This was done by selecting and plotting three of the most centrally-located RBS sites from each sub-cluster within the NMDS plots of Groups 1 and 2.

3.2.4.7 Influence of environmental variables upon sub-cluster arrangement

Moisture/precipitation has been considered a key element in shaping the distribution of vegetation types across the island (Beard 1946b; Marshall 1934; Nelson 2004). Additionally, Beard and Marshall included topography and soils as important factors (albeit to a lesser extent than moisture). The existence of potential gradients within the distribution pattern of the sub-clusters associated with (i) annual precipitation; (ii) altitude; and (iii) soil drainage capacity were investigated.

However, because no replicates were collected at each of the sites sampled within the RBS survey, it was not possible to use a statistical approach – such as the BIOENV procedure – to explore the association between the species composition and abundance within the vegetation sub-clusters and these environmental variables. It was also statistically invalid to treat the individual sites within a vegetation sub-cluster as replicates – as these were situated in different localities which were scattered across the island; and hence were not true replicates representative of species composition and abundance as well as the environmental conditions within a given vicinity of forest (Clarke and Gorley 2006).

Consequently, bubble plots for these parameters were superimposed upon the NMDS plots of Groups 1 and 2 (Section 3.2.4.5) as well as the summary NMDS

(Section 3.2.4.6). The influence of these parameters upon the vegetation within sub-clusters (Table 3.1) was then inferred based on these results in conjunction with Figures 3.21 to 3.23.

3.2.5 Similarity Percentage (SIMPER) analyses

The SIMPER routine was applied to the sub-clusters of the RBS samples derived from the cluster dendrogram at: (i) the 9.17% similarity level for sub-clusters 1A, 2A, 3A, 6A, 7A, 9A and 10A; and (ii) the 13.26% similarity level for clusters 4A, 4B, 5A, 5B, 8A and 8B.

The SIMPER procedure is an exploratory rather than statistical testing framework. Based on Bray-Curtis dissimilarities within a given dataset, it highlights species that are responsible for: (i) defining a sub-cluster; and (ii) discriminating between pairs of sub-clusters. This is done by ordering the contributions of each species to the similarity within groups, as well as the dissimilarity between groups (Appendix B).

For each sub-cluster, all tree species contributing to an arbitrary top 35% of the within group cumulative similarity were determined (Table 3.2). These species were considered the dominant tree species that defined potential vegetation associations (sub-clusters) within the island; they are referred to as ‘ecologically important’ species.

3.2.6 Creation of a list of tree species to be used for species distribution modelling

The Trinidadian tree species used for SDM analyses was derived from those species belonging to two or more of the following categories: (i) ecologically important; (ii) commercially important; and (iii) globally/regionally/locally rare.

Firstly, both ecologically important species and the 25 most commercially important Trinidadian tree species (Table 3.3) (ICL 1980) were given their corresponding Star rankings (Hawthorne and Abu-Juam 1995). The Star system, developed by Hawthorne and Abu-Juam (1995), was designed specifically for the classification of plant species according to global rarity and conservation concern – based on herbarium and inventory data (Baksh-Comeau et al. 2011).

From both these lists [(i) ecologically and (ii) commercially important], species which were also categorised as (a) locally endemic or (b) with distributions limited to local and regional ranges (Black, Gold and Blue Stars) (Section 3.2.6.1, Tables 3.4 and 3.5) were highlighted in Table 3.3. These highlighted species from both (i) and (ii) were then cross-checked – to create a final list which consisted of any species which belonged to 2 or more of the three categories [(i) ecologically important, (ii) commercially important and (iii) globally/locally/regionally rare [Black, Gold and Blue Stars]] (Table 3.6).

Twenty species were identified, of which nineteen were chosen (Table 3.6) for the SDM analyses. This list of 19 species was supplemented with two species. *Sterculia pruriens* var. *glabresens* was the most ubiquitous of all the ecologically-important species (Section 3.2.5), but is neither commercially important nor globally/locally/regionally rare. Secondly, the Black-Star species *Ilex arimensis* was included as an example of an endemic (no Black-Star species featured in the derived list). The final list of SDM species comprised 21 species (Table 3.6).

3.2.6.1 Application of the Star system to the flora of Trinidad and Tobago

Assessment of the conservation status of the RBS survey data considered both the International Union for Conservation of Nature (IUCN) Red List categories as well as the Star system. However, despite the International Union for Conservation of Nature (IUCN) Red List categories being established as a globally accepted standard for the expression of extinction risk, it requires criteria such as global ecology and distribution – which are difficult to collate. As such, many of the plant species collected during the RBS survey have not been classified under this system; for example, prior to 2008, just seven Trinidad and Tobago species had been included within the IUCN database. Of these, one has since been identified as a synonym (and hence cannot be assumed to remain in its original threat category); another species has been classified as 'data deficient', while four of the remaining five species were categorised to be of 'least concern'.

The results of the survey were instead ranked according to the Star system – which was originally developed for the purpose of classifying large numbers of plant species according to global rarity and conservation concern (Table 3.5) within a 'reasonable' period of time. According to (Baksh-Comeau et al. 2011) this system was not meant to be a substitute or replacement of the IUCN Red List system, it is instead designed to emphasise conservation priority based global rarity – which can then be further integrated into systems which assess the 'bioquality' of each RBS site. Further, because it was developed specifically for plants, it allows for ample use of herbarium and inventory data.

Additionally, IUCN Red List status can be short-listed for most species collected within the survey using the Star rankings and global ranges. Table 3.4 provides a rough guideline of categories of the IUCN Red List and the Stars which can be used to short-list them.

3.3 Results

3.3.1 SIMPROF and Cluster results

3.3.1.1 SIMPROF results

The SIMPROF test, based on 165 RBS samples collected from sites scattered across Trinidad's forests, showed statistical evidence for the sub-structures defined by cluster analysis since the similarity profile fell outside the 95% limits of the null curve (Figure 3.2).

3.3.1.2 Cluster and mapping results

The cluster analysis yielded an agglomerative dendrogram of the RBS samples with the statistical strength (via SIMPROF) of the branches and sub-structures being indicated by either solid dark lines (statistically significant) or dashed red lines (statistically insignificant); ten clusters were defined at an arbitrary but statistically significant similarity level of 9.17% (Figure 3.3).

When mapped in geographical space, the RBS components of the ten clusters, defined at a 9.17% similarity level, were, for the most part, located within clearly defined 'zones' (Figure 3.4). However, the RBS sites comprising clusters 4, 5 and 8 were ubiquitous, located in zones which spanned the island's entire north-south length. When these three ubiquitous clusters (4, 5 and 8) were sub-divided (taking SIMPROF significance levels into consideration) at a 13.26% similarity level (Figure 3.5), each separated into two distinct and spatially refined sub-groups (Figure 3.6).

All clusters and sub-groups were subsequently referred to as 'sub-clusters' and were labelled with alpha-numeric ids ending in ‘A’ or ‘B’. Sub-clusters which consisted of an alpha-numeric id ending only in ‘A ’with no counterpart ending in ‘B’ (1A, 2A, 3A, 6A, 7A, 9A and 10A) represented former clusters (1, 2, 3, 6, 7, 9 and 10) which were not further sub-divided at the 13.26% similarity level. However, sub-clusters consisting of alpha-numeric counterparts ending in both ‘A’ and ‘B’ (4A and 4B; 5A and 5B, 8A and 8B) were derived from former clusters (4, 5 and 8) which were further sub-divided at the 13.26% similarity level (Figures 3.4 and 3.6).

Cluster 4 sub-divided into sub-cluster 4A which maintained a distinct north-south distribution; with the RBS sites of this sub-cluster that were located within the Northern Range being restricted to the north-eastern part of the island. Sub-cluster 4B consisted of the remaining RBS sites which existed exclusively within the Northern Range in an east-west zone. Both clusters 5 and 8 subdivided into sub-clusters located either within or outside of the Northern Range. Sub-cluster 5A consisted of RBS sites which were located both within the south-west peninsula and central Trinidad; while sub-cluster 5B was comprised of RBS sites located only within the central part of the Northern Range. Sub-clusters 8A and 8B were both comprised of RBS sites located mainly within the western parts of the island. However, sub-cluster 8A was confined to the south-western peninsula while most of the RBS sites for 8B were located within the north-western peninsula (Figure 3.6).

3.3.2 NMDS ordinations

Despite the stress levels of Figure 3.8 being moderately high (at 0.165), the plot indicated that the sub-clusters were very similar to each other. With the exception of sub-cluster 3A, no distinct pattern or grouping of RBS sites was discerned.

3.3.2.1 Ordination plots of Groups 1 and 2

Further inspection of the arrangement of the RBS sites (Figure 3.8) revealed an 'arc' or 'horse-shoe', i.e., the two-dimensional NMDS space was too small, leading to curvature in the arrangement of points within the plot (Clarke and Warwick 2001; Wildi 2010). This phenomenon is known to occur with large datasets, and according to Clarke and Warwick (2001), its solution lies in the *a priori* sub-division of the dataset or sub-division with respect to well-defined subsets from a cluster analysis (see Section 3.2.4.5).

However, despite the 165 RBS plots being split into two groups based on well-defined subsets of clusters (Section 3.2.4.5), the stress levels of both these NMDS plots remained high. The high stress levels of 0.19 for both NMDS ordinations of Group 1 and Group 2 (Figures 3.9 and 3.10) implied that, while useful at the 'big-picture' scale, little emphasis should be placed on within plot details (Clarke and Gorley 2006).

Sub-cluster 3A was the only distinct sub-cluster, its RBS sites located close to each other and collectively separated from all other sub-cluster components (Figure 3.9). In contrast, sub-clusters 1A, 2A, 4A, 4B, 5A, 5B appeared cohesive as individual groups, but the RBS sites comprising their edges were interspersed among each other. This gave the impression that these sub-clusters, while representing different 'associations' of vegetation, were very similar to each other. Sub-cluster 6A was the only exception to this pattern. It appeared different to the other sub-clusters as: (i) its component RBS sites were spaced further apart (and hence less similar) from each other and from components of the other sub-clusters and (ii) the proportion of its RBS sites that were interspersed with the other sub-clusters was smaller relative to the other sub-clusters.

The ordination of sub-clusters within Figure 3.10 yielded, yet again, sub-clusters that appeared cohesive and similar in terms of the distance between these groups. However, the RBS components of these sub-clusters appeared less interspersed with other groups. The only exception to this trend was sub-cluster 9A which was divided into two distinct groups within the ordination plots. This division corresponded to a split in geographical space, with three of the RBS sites were in south-western Trinidad, while the remaining four were in the north-western region (Figure 3.6).

3.3.2.2 Summary NMDS ordinations

The stress level (0.14) for the two-dimensional summary NMDS ordination plot (Figure 3.11) means little emphasis should be placed on the details of these ordinations. Sub-clusters appeared to be arranged in a gradual ‘continuum’ with no sharp division among them except for sub-cluster 3A. In this continuum sub-clusters located in the north-eastern Trinidad were located at one extreme of the two or three-dimensional NMDS space, at the other end of the continua were sub-clusters to the south-west.

3.3.2.3 Superimposed Precipitation bubble plots

A distinct gradient was observed when the two-dimensional scatter plots of Groups 1 and 2, as well as the summary NMDS, were superimposed with annual precipitation data for Trinidad (Figures 3.12, 3.15 and 3.18). There was a high visual concordance between the order of sub-clusters arrangement within the NMDS plots and amount of annual precipitation received. Annual precipitation levels were highest at sub-clusters located in the upper and lower right-hand corners of the summary plot (corresponding to the north-east of the island) and gradually decreased towards the left of the graph (south-west of the island) (Figure 3.21).

3.3.2.4 Superimposed Altitude plots

A similar, but less distinct gradient was observed when the two-dimensional NMDS scatter plots were superimposed with altitude above sea level data (Figures 3.13, 3.16 and 3.19). Visual concordance was observed between the sub-clusters and altitude above sea level. As with annual precipitation, the sub-clusters situated to the right (Figure 3.19) occurred at relatively high altitudes; whilst those to the left of the plot were in areas of low altitude (Figure 3.22). Sub-clusters within the Northern Range were clearly defined in this NMDS, with 3A occurring at the highest altitude. This was followed by sub-clusters 2A and 4B; 5B; 4A; 8B and 6A in decreasing order of altitude. The remaining sub-clusters: 1A, 5A, 7A, 8A and 10 A were all situated at relatively low altitudes of the Northern Range.

3.3.2.5 Superimposed Soil Drainage Capacity plots

When the two-dimensional NMDS scatter plots were superimposed with Soil Drainage Capacity (SDC) (Figures 3.14, 3.17 and 3.20) no distinct pattern or gradient was observed. Additionally, no distinct relationship between altitude above sea level and SDC existed (Table 3.1, Figure 3.23), except for sub-clusters located at high altitudes (sub-clusters 2A, 3A and 4B), which were all characterised by a fast SDC and high annual precipitation.

In summary, the NMDS bubble plots (Groups 1, 2, and the summary plots) of annual precipitation and, to a lesser extent, altitude above sea level, suggest potential gradients. These gradients are indicated by high visual concordance of the gradation of symbol size among different sub-clusters within one or both of these parameters. The gradient across the annual precipitation summary diagram (sub-clusters 1A, 2A, 3A, 5B, 4A characterised by high precipitation located to the right of the diagram grading to low precipitation 10A to the bottom left), suggests that annual precipitation is the best overall explanatory variable. In addition, altitude above sea level appears to be a secondary explanatory variable for sub-clusters 2A, 3A, 4B.

3.3.2.6 Comparison of patterns derived from the presence/absence versus the square root transformation of the abundance data

A comparison of cluster and ordination results from a presence/absence transformation (Appendix A) instead of the above described square root transformation of the modified abundance index revealed the same general patterns with respect to the placement of sub-clusters and their concordance with gradients of precipitation and altitude. However, presence/absence transformation yielded less well refined results with respect to sub-cluster definition in geographical space, as well as with respect to concordance with the precipitation and altitude gradients.

3.3.3 Ecologically-important tree species

Based on the SIMPER results (Appendix B) the number of ecologically-important tree species (those that contributed to the top 35% of cumulative similarity) within a given sub-cluster ranged from three (sub-cluster 3A) to twelve species (sub-cluster 5B). Additionally, the collective contribution of these tree species within a sub-cluster to the top 35% of cumulative similarity was highest in sub-cluster 1A at 25.72%, and lowest in cluster 3A at 9.32% (Table 3.2).

Furthermore, ecologically-important tree species were not necessarily confined to just one sub-cluster; 40% of species were found in two or more (maximum of eight) sub-clusters (Table 3.3). This provides support for the hypothesis that Trinidadian vegetation is not composed of unique vegetation types, but is instead, a continuum within which the abundance and combination of ecologically-important species change in response to gradual changes in precipitation and altitude across the island.

3.4 Discussion

3.4.1 Synopsis

Three inferences about Trinidadian forests can be made from the results of these analyses. Firstly, forests are continua rather than distinct vegetation types. Secondly, within the continuum there are zones (sub-clusters) of variation in species composition and abundance which appear to be influenced by precipitation and, to a lesser extent, altitude. Finally, dominant tree species within vegetation zones may not be zone-specific; rather they occur within several zones, in each case, varying in their contributions towards within-zone similarity.

3.4.2 Interpretation of ordination results

If one looks at the cluster analysis results (3B2 and 3D2) in isolation from the NMDS ordinations, it might appear that seemingly discrete sub-clusters are indicative of discrete vegetation types/ associations, similar to those described by Beard (1946b). This is especially the case since the RBS components of these groups occur in well-defined geographic zones (Figure 3.6). However, the algorithm used to create these dendograms was designed solely to delineate ‘natural groupings’ of RBS sites, such that RBS sites within one sub-cluster are more similar in terms of community structure than RBS sites belonging to other sub-clusters. Hence, from cluster analyses alone, one should not assume that inter-relations among sub-clusters are discrete or continuous. This is especially the case in situations with a steady gradation of community structure across sites in response to strong environmental forcing (Clarke and Gorley 2006).

Superimposition of sub-clusters on a NMDS means the similarities between these sub-clusters may be visually displayed. However, the high stress levels in the NMDS ordinations means plot interpretation be restricted to the overall 'big-picture' perspective with no elaboration of plot details. High stress levels were unsurprising due to the combination of two different abundance indices into the 'modified' abundance index. Additionally, there was much observed variation of local details within the environments the RBS plots sampled. However, the interpretation restrictions coincided with the overall study objectives, which required general, rather than detailed descriptions, of the sub-clusters and their ecology for the development of a list of tree species for SDM.

The ordination results showed that sub-clusters were arranged within a continuum of very similar rather than distinct groups. This was interpreted to imply that Trinidad forests do not comprise distinct vegetation types but instead exist as a continuum within which there are gradual, subtle variations in community structure (vegetation zones) as one progresses from the north-east to south-west of the island. This continuum is thought to be a response to gradual changes in precipitation and to a lesser extent altitude across the island. Indeed, it is noteworthy that the only distinct sub-cluster (3A) within the ordination plots (Figure 3.11) was characterised by the combination of high precipitation and altitude, which were among the highest within the RBS sites.

This inference is supported by the observation that a gradual precipitation gradient stretches from the north-east to the south-west, and there are no sharp environmental discontinuities or climatic divides (Figure 3.21 and 3.22). The failure of these conditions to result in distinct vegetation types across the island is strongly supported by the concordant arrangement of sub-clusters in relation to gradually decreasing quantities of precipitation (Figures 3.12, 3.15 and 3.18) and altitude (Figures 3.13, 3.16 and 3.19) within the bubble plots. The secondary influence of altitude can be attributed to the observation that most of the island is flat with no large area of 'high' altitude terrain apart from the Northern Range. Additionally, even within the Northern Range, the highest altitudes are confined to well below 1,000 m above sea level.

The analyses did not show any correlation between soil drainage capacity and the sub-clusters, which does not concord with Beard's view that Trinidadian vegetation depends upon soil moisture holding abilities. However, soil drainage capacity data used for these analyses are a coarse representation of reality, therefore more detailed soil drainage data may indicate otherwise.

Finally, the absence of distinct vegetation types conforms to field observations which show no dramatic changes in forest vegetation. Instead, field observations conform to Marshall's (1934) description of subtle transitions of dominant tree species over distances of tens of kilometres. Exceptions to this trend include sudden vegetation alterations due to changes in edaphic characteristics that give rise to savannahs and swamps.

3.4.3 Distribution of tree species support continuum concept

The SIMPER routine was applied to the cluster results to highlight ecologically-important species within different parts of this continuum (Appendix B). While the combinations of ecologically-important species differed among sub-clusters, forty percent of these species were not confined to a specific vegetation zone but were categorised as being ecologically-important within more than one sub-clusters. For example, *Sterculia puriens* var. *glabrescens* was an ecologically-important species within eight of the thirteen sub-clusters; while *Virola surinamensis* was categorised as ecologically-important within four sub-clusters (Table 3.3). Furthermore, many of these ecologically important species were also found to occur within other sub-clusters where they were not categorised as ecologically important. For example, *Manilkara bidentata* ssp. *bidentata* was categorised as ecologically important for sub-cluster 1A, but was also found to be present in sub-clusters 2A, 4A, 5A, 5B, 6A, 7A and 8b (Appendix B). Hence, it was seen that many tree species exist in several vegetation zones within the island but vary in terms of their ‘ecological importance’ within a given zone. These observations provide further support for the existence of a vegetation continuum within the island’s forests.

3.4.4 Abundance data: presence/absence versus square root transformed

This robust response of the NMDS ordinations to manipulations of statistical transformations (square root versus presence/absence [Appendix A]) stems from the observation that the ordinations were non-metric and therefore based solely on rank similarity rather than absolute similarity values. Hence, transformations of different severities would only serve to compress the absolute similarity values without affecting the relative structure between the similarity ranks.

The difference between both sets of results may be a consequence of presence/absence transformation being the most extreme form of transformation; all the taxa within RBS samples are rendered uniform. Hence clusters and sub-clusters defined from a matrix based only on variation of species composition per RBS sample would not give as much defining detail as groups that have been defined based on variation of species composition and species abundance within a given sample.

The lack of abundance detail may contribute to the following differences between the results of the two analyses:

(i) The presence/absence cluster analyses produced clusters at higher similarity levels than those produced from following square root transformation. The clusters were therefore less distinct than those produced from square root transformed data.

(ii) Sub-clusters derived from presence/absence transformed data did not map within well-defined geographic regions when compared to sub-clusters derived via square root transformation (Appendix A). For example, clusters g and k continued to span the entire north-south length of the island – even after sub-division at an 18% similarity level (Figures A.2 to A.4).

(iii) Within the bubble plots of the summary NMDS graphs visual concordance between the presence/absence sub-cluster arrangement (Figures A.9 to A.12 and Figures A.14 to A.17) and the precipitation and altitude gradients were similar to but not as well defined as those of the square root transformed data (Figures 3.12, 3.13, 3.15, 3.16, 3.18 and 3.19).

However, equally significant from this comparison is the power of the species composition data (presence/absence transformation) which, on its own, was able to effectively define the general delineations of the vegetation zones within the island.

3.4.5 Final Remarks

A visual comparison of the most popular classification of Trinidad's vegetation, that of Beard (1946b), with the sub-clusters defined within this study revealed very little similarity between both maps. The map of the former is dominated by one type of vegetation: Evergreen Seasonal Forest – which was spread across approximately 75% of the area for which vegetation was classified within the island. This included very large, continuous areas within the south-western, south-eastern, central, north-eastern and north-central regions of Trinidad. Indeed, the area covered by this vegetation type coincided with the majority of sub-clusters defined within this study (1A, 2A, 3A, 4A, 5A, 5B, 6A, 7A, 8A, and 8B). Additionally the distribution of other vegetation types described by Beard were usually too small and scattered across multiple regions of the island to conform to any of the sub-clusters defined by this study.

Apart from this visual comparison of both maps, it was not possible to further compare the results of the present study to that of Beard due to fundamental differences in approach. Firstly, identification of different vegetation zones in the present study was based on the abundance of all the plant species within a given site, not only the enumeration of large trees; dominant tree species within each of zone were identified subsequently. This reverses Beard's logic, who used dominants to define vegetation within a given area. Secondly, RBS sites were scattered in a near to uniform distribution across the island and also included private land holdings. Beard's study, based on line transects, was confined to Crown Lands and did not effectively integrate a large proportion of forested land. Thirdly, this study seeks only to discern potential differences within the vegetation based on species composition and related abundance; there is no attempt to create physiognomic and structural groupings. Finally, increased intensity of forest exploitation since Beard's time may have altered many of the formations and associations he described (Chalmers 1981).

Native Trinidadian forests are under threat of being replaced by anthropogenic activities, such as settlement, industry and agriculture. In addition, the designation of many PAs within the island has been informed by out-dated, equilibrium-based studies, such as Beard (1946b), which do not acknowledge that species responses to disturbance are individualistic (Nelson 2004). Finally, despite studies stressing the strong dependence of vegetation types upon moisture availability; there has been no conservation study or plan thus far which attempts to incorporate the effects of a potentially warmer and drier climate into the management of remaining forest resources.

3.5 Tables

	Environmental Concordance range		
Sub-cluster	**Annual Precipitation**	**Altitude**	**Soil Drainage Capacity**
1A	2	5	2 to 4
2A	1	1 to 3	1
3A	1	1	1
4A	1 to 3	3 and 5	1 to 3
4B	1 to 2	1 to 3	1
5A	3 to 4	5	2 to 3
5B	1 to 2	4	1 to 2
6A	2 to 5	3 to 5	1
7A	1 to 4	5	4 to 5
8A	4	5	3 to 4
8B	3 to 4	4 to 5	1
9A	3 to 4	3 and 4	1 and 3
10A	3 to 4	4 to 5	2 to 3

Table 3.1: Variation of environmental parameters among sub-clusters. Where:

1 = Very high OR Very fast for Soil Drainage Capacity
2 = High OR Fast for Soil Drainage Capacity
3 = Medium OR Moderate for Soil Drainage Capacity
4 = Low OR Slow to moderate for Soil Drainage Capacity
5 = Very low to absent OR Slow for Soil Drainage Capacity

The NMDS bubble plots of Annual Precipitation, Altitude and Soil Drainage Capacity (Groups 1 and 2 as well as the summary plots) indicate potential gradients with symbols proportional in size to 1 or more of these parameters showing high visual concordance with the different sub-clusters. The gradient across the Annual Precipitation summary diagram (sub-clusters 1A, 2A, 3A, 5B, 4A being high precipitation to the right of the diagram grading to low precipitation 10A to the left bottom), suggests that Annual Precipitation is the best overall explanatory variable with altitude in addition for sub-clusters 2A, 3A, 4B.

Sub-cluster	**Average similarity within sub-cluster (%)**	**Tree species (contributing to the top 35% of cumulative similarity within sub-clusters)**	**Contribution of individual tree species to within sub-cluster similarity (%)**	**Total contribution of tree species to within sub-cluster similarity (%)**
1A	**23.19**			25.72
		Sterculia pruriens var. *glabrescens*	7.54	
		Manilkara bidentata ssp. *bidentata*	7.22	
		Virola surinamensis	5.74	
		Pentaclethra macroloba	5.22	
2A	**30.58**			21.11
		Ryania speciosa	5.21	
		Eugenia confusa	4.06	
		Tabebuia stenocalyx	3.25	
		Cassipourea guianensis	3.21	
		Sterculia pruriens var. *glabrescens*	2.84	
		Manilkara bidentata ssp. *bidentata*	2.54	
3A	**36.47**			9.32
		Coccoloba ascendens	3.31	
		Sterculia pruriens var. *glabrescens*	3.17	
		Licania heteromorpha var. *heteromorpha*	2.84	
4A	**32.34**			17.01
		Carapa guianensis	3.4	
		Sterculia pruriens var. *glabrescens*	2.97	
		Brownea coccinea ssp. *capitella*	2.54	
		Eschweilera subglandulosa	2.35	
		Virola surinamensis	1.99	
		Terminalia amazonia	1.98	
		Andira inermis	1.78	
4B	**30.57**			10.36

		Sterculia pruriens var. *glabrescens*	3.35	
		Tabernaemontana attenuata	2.5	
		Ryania speciosa	2.4	
		Byrsonima spicata	2.11	
5A	**34.1**			13.49
		Terminalia amazonia	2.64	
		Sterculia pruriens var. *glabrescens*	2.5	
		Eschweilera subglandulosa	2.43	
		Protium guianense	2.06	
		Virola surinamensis	1.95	
		Byrsonima spicata	1.91	
5B	**34.68**			24.56
		Sterculia pruriens var. *glabrescens*	2.63	
		Ryania speciosa	2.63	
		Carapa guianensis	2.44	
		Terminalia amazonia	2.15	
		Tovomita eggersii	2.09	
		Attalea maripa	1.96	
		Licania heteromorpha var. *heteromorpha*	1.95	
		Virola surinamensis	1.89	
		Laetia procera	1.77	
		Abarema jupunba	1.74	
		Simaba multiflora	1.72	
		Calliandra guildingii	1.59	
6A	**23.02**			15.99
		Protium guianense	3.56	
		Attalea maripa	3.51	
		Terminalia amazonia	3.16	
		Coccoloba latifolia	3.15	
		Rollinia exsucca	2.61	
7A	**33.35**			14.23
		Brownea coccinea ssp. capitella	3.32	
		Spondias mombin	2.36	
		Swartzia pinnata	1.88	
		Trichilia pallida	1.84	
		Guarea glabra	1.67	
		Eschweilera subglandulosa	1.64	

		Pentaclethra macroloba	1.52	
8A	**33.92**			14.96
		Cecropia peltata	2.1	
		Spondias mombin	2.04	
		Zanthoxylum martinicense	2	
		Trichilia pallida	1.91	
		Andira inermis	1.86	
		Sapium glandulosum	1.86	
		Casearia spinescens	1.64	
		Guapira salicifolia	1.55	
8B	**29.96**			14.62
		Brownea coccinea ssp. *capitella*	2.94	
		Protium guianense	2.7	
		Swartzia pinnata	2.12	
		Attalea maripa	1.8	
		Swartzia simplex	1.69	
		Chrysophyllum argenteum ssp. *argenteum*	1.69	
		Sterculia pruriens var. *glabrescens*	1.68	
9A	**22.78**			16.3
		Brosimum alicastrum	3.37	
		Spondias mombin	3.19	
		Melicoccus bijugatus	2.66	
		Trichilia pallida	2.57	
		Coursetia ferruginea	2.37	
		Cordia panamensis	2.14	
10A	**23.53**			18.91
		Spondias mombin	3.25	
		Cecropia peltata	3.23	
		Cordia curassavica	2.94	
		Andira inermis	2.51	
		Psidium guajava	2.47	
		Cordia collococca	2.3	
		Casearia guianensis	2.21	

Table 3.2: SIMPER analyses results of tree species contributing to similarity within sub-clusters. The species listed accounted for top 35% of the cumulative similarity within each sub-cluster.

Ecologically Important species	**Number of clusters where important**	**Present in top 25 commercially important species list?**	**Star rating**
Abarema jupunba (Willd.) Britton & Killip	1		G
Andira inermis (W. Wright) Kunth ex DC.	3	√	G
Attalea maripa (Aubl.) Mart.	3		G
Brosimum alicastrum Sw.	1	√	G
Brownea coccinea Jacq. ssp. *capitella* (Jacq.) D. Velázquez & Agostini	3		BL
Byrsonima spicata (Cav.) DC.	2		G
Calliandra guildingii Benth.	1		G
Carapa guianensis Aubl.	2	√	G
Casearia guianensis (Aubl.) Urban	1		G
Casearia spinescens (Sw.) Griseb	1		G
Cassipourea guianensis Aubl.	1		G
Cecropia peltata L.	2		G
Chrysophyllum argenteum Jacq. ssp. *argenteum*	1		G
Coccoloba ascendens Duss ex Lindau	1		G
Coccoloba latifolia Poir.	1		GD
Cordia collococca L.	1		G
Cordia curassavica (Jacq.) Roem. & Schult.	1		G
Cordia panamensis Riley	1		G
Coursetia ferruginea (Kunth) Lavin	1		BL
Eschweilera subglandulosa (Steud. ex O. Berg) Miers	3	√	BL
Eugenia confuse DC.	1		GD
Guapira salicifolia (Heimerl) Lundell	1		BL
Guarea glabra Vahl.	1		G
Laetia procera (Poepp. & Endl.) Eichler	1		G

Licania heteromorpha Benth. var. *heteromorpha*	2		G
Manilkara bidentata (A.DC.) A. Chev. ssp. *bidentata*	2	√	G
Melicoccus bijugatus Jacq.	1		G
Pentaclethra macroloba (Willd.) Kuntze	2		G
Protium guianense (Aubl.) Marchand	3		G
Psidium guajava L.	1		G
Rollinia exsucca (DC. ex Dunal) A.DC	1		G
Ryania speciosa Vahl	3		G
Sapium glandulosum (L.) Morong	1		G
Simaba multiflora Juss.	1		G
Spondias mombin L.	4	√	G
Sterculia pruriens (Aubl.) K. Schum. var. *glabrescens* E. Taylor	8		G
Swartzia pinnata (Vahl) Willd.	2		BL
Swartzia simplex (Sw.) Spreng.	1		G
Tabebuia stenocalyx Sprague & Stapf	1	√	G
Tabernaemontana attenuata (Miers) Urban	1		GD
Terminalia amazonia (J. F. Gmel.) Exell	4	√	G
Tovomita eggersii Vesque	1		GD
Trichilia pallida Sw.	3		G
Virola surinamensis (Rol. ex Rottb.) Warb.	4	√	G
Zanthoxylum martinicense (Lam.) DC.	1	√	G
⇓	⇓	⇓	⇓
Remainder of top 25 commercially important species	**Number of clusters important within**	**Present in Top 25 commercially important species list?**	**Star rating**
Aniba panurensis (Meisn.) Mezzat.	0	√	G

Bravaisia integerrima (Spreng.) StandI.	0	√	G
Buchenavia tetraphylla (Aubl.) R. A. Howard	0	√	G
Calophyllum lucidum Benth.	0	√	GD
Cedrela odorata L.	0	√	G
Cordia alliodora (Ruiz & Pav.) Oken	0	√	G
Hernandia sonora L.	0	√	G
Hymanea courbaril L.	0	√	G
Mora excelsa Benth.	0	√	BL
Ocotea glomerata (Nees) Mezzat.	0	√	G
Protium sagotianum Marchand	0	√	G
Schefflera morototoni (Aubl.) Maguire, Steyermark & D. G. Frodin	0	√	G
Symphonia globerifera L.f.	0	√	G

Table 3.3: Star ratings of ecologically important and commercially important species within Trinidad. Where: G = Green; BL = Blue; GD = Gold and BK = Black.

Star Ranking	**Details**	**Derived IUCN short-list**
None	Data quality too poor	Data Deficient (DD)
Green	Global distribution extending across South America – unlikely to be threatened by serious extinction	Least Concern (LC)
Blue, Gold	Dependant on Range size and proximity to forms of irreversible development	Vulnerable (V)
Blue, Gold		Near Threatened (NT)
Black, Gold, Blue		Endangered (EN)
Black	Endemics and near-endemics	Critically Endangered (CR)

Table 3.4: Correlation of Star rankings with IUCN conservation status.

Global range	Meaning of Global range category	Subconditions, if any, to qualify for Star to right	Star Code
1	Endemic or near endemic to T&T. Near endemics are, for example, on Venezuela's Patos island, Paria peninsular, in the Dutch Antilles or Grenada, not more widespread in S. America or Lesser Antilles.		Black (BK)
2	EITHER found also more widely in, for example, Venezuela or Guyana, and southern Lesser Antilles; not just a small extension beyond T&T. OR apparent T&T endemics but with very plausible records or (including likely synonymy) from well outside T&T.		Gold (GD)
3	EITHER fairly widespread across Venezuela, the Guianas, southern Caribbean. OR widespread in Caribbean (to Greater Antilles) and also in northern S. America...	..but sparsely distributed, for example, scattered on a few higher Caribbean mountain tops	GD
		..in most or all countries in range with several distant localities, or known to be very abundant in part of range	Blue (BU)
4	As 3, but extending, for example, to Brazil, Bolivia, Peru OR to Mexico and N. America (if both, see 5)	If, for example, only known in a distinct patch of northern Brazil, S. Guyana; or very scattered throughout	BU
		As far as known, found throughout most of range at least on a 1 degree resolution.	Green (GN)
5	Widespread in the Americas, but either not generally in the Caribbean, or scattered throughout range	Normally distributed in range, for example, in most degree squares throughout forest or savanna belts	BU
		Unusually scattered or sparse (allowing for the fact that some groups are little-collected, so more evidence is needed to upgrade them to BU), even allowing for restriction to forest, savanna or similar broad formations, for example, montane endemics on scattered peaks would belong here.	BU
6	Widespread neotropical (as 5 but more densely distributed plus Caribbean)		GN
7	Globalised floristic elements	Widespread in Americas (probable origin), but also known today in the Old World	GN
8		Widespread global weeds; or seeds of global strand and seashore; origin obscure or Old World	GN
9		Exotics and garden or crop plants, commonly planted, not indigenous, at least to T&T	GN

Table 3.5: Plant species global range categories and their translation to Star ratings in Trinidad and Tobago. Table taken from Baksh-Comeau et al. 2011.

Category	**Species**	**Ecologically Important**	**Commercially Important**	**Star rating**
Combination of (i) Ecologically important (ii) Commercially important and (iii) Global/Regional rarity	*Andira inermis*	√	√	G
	Brosimum alicastrum	√	√	G
	Brownea coccinea ssp. *capitella*	√		BL
	Calophyllum lucidum		√	GD
	Carapa guianensis	√	√	G
	Coccoloba latifolia	√		GD
	Coursetia ferruginea	√		BL
	Eschweilera subglandulosa	√	√	BL
	Eugenia confusa	√		GD
	Manilkara bidentata ssp. *bidentata*	√	√	G
	Mora excelsa		√	BL
	Spondias mombin	√	√	G
	Swartzia pinnata	√		BL
	Tabebuia stenocalyx	√	√	G
	Tabernaemontana attenuata	√		GD
	Terminalia amazonia	√	√	G
	Tovomita eggersii	√		GD
	Virola surinamensis	√	√	G
	Zanthoxylum martinicense	√	√	G
+	+	+	+	+
Endemic	*Ilex arimensis*			BK
Ubiquitous ecological importance	*Sterculia pruriens* var. *glabrescens*	√		G

Table 3.6: Final list of species chosen for species distribution modelling in Chapters 4 to 6.

3.6 Figures

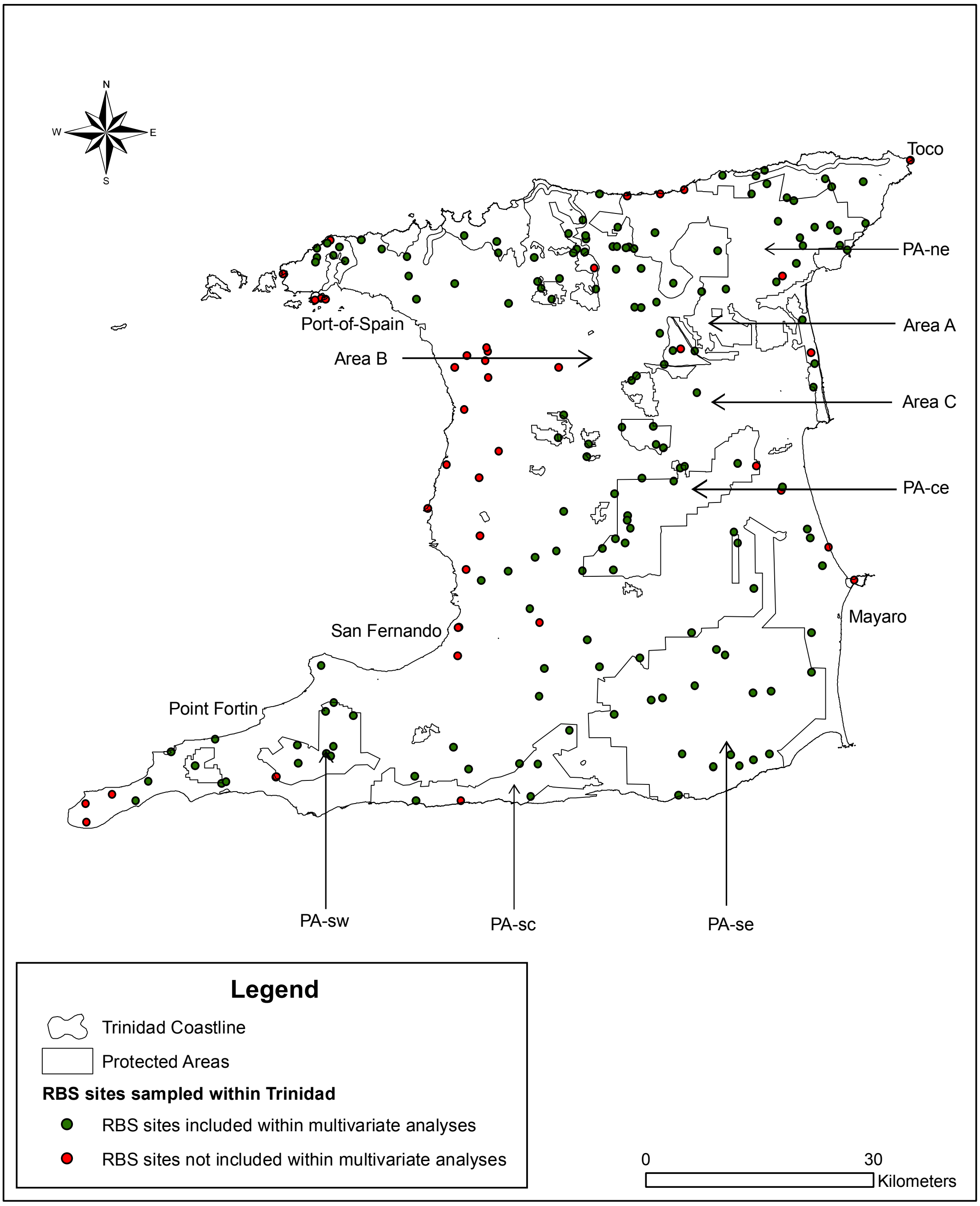


Figure 3.1: Rapid Botanical Survey sites sampled within Trinidad.

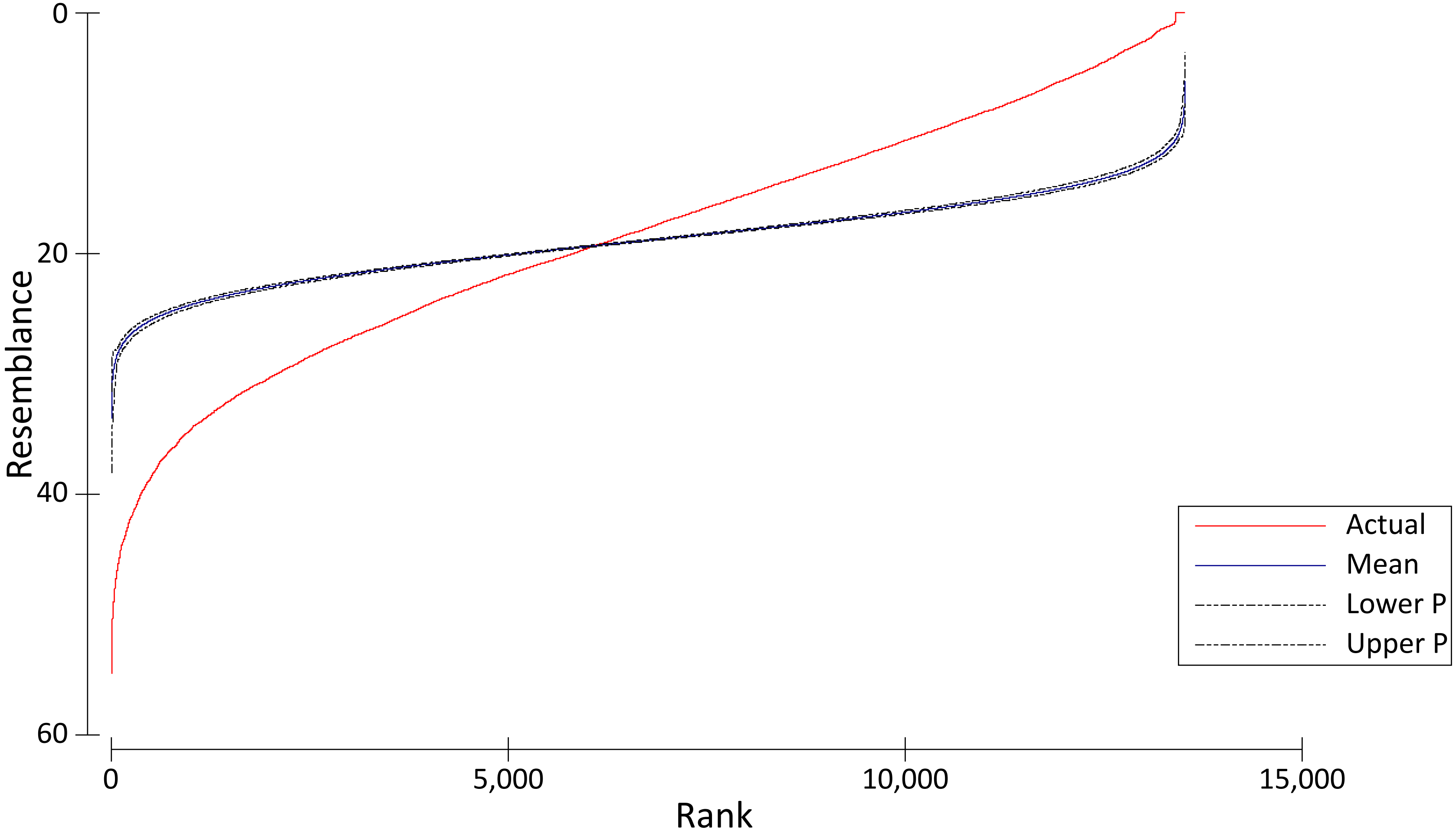


Figure 3.2: SIMPROF test of modified abundance data for all sites.

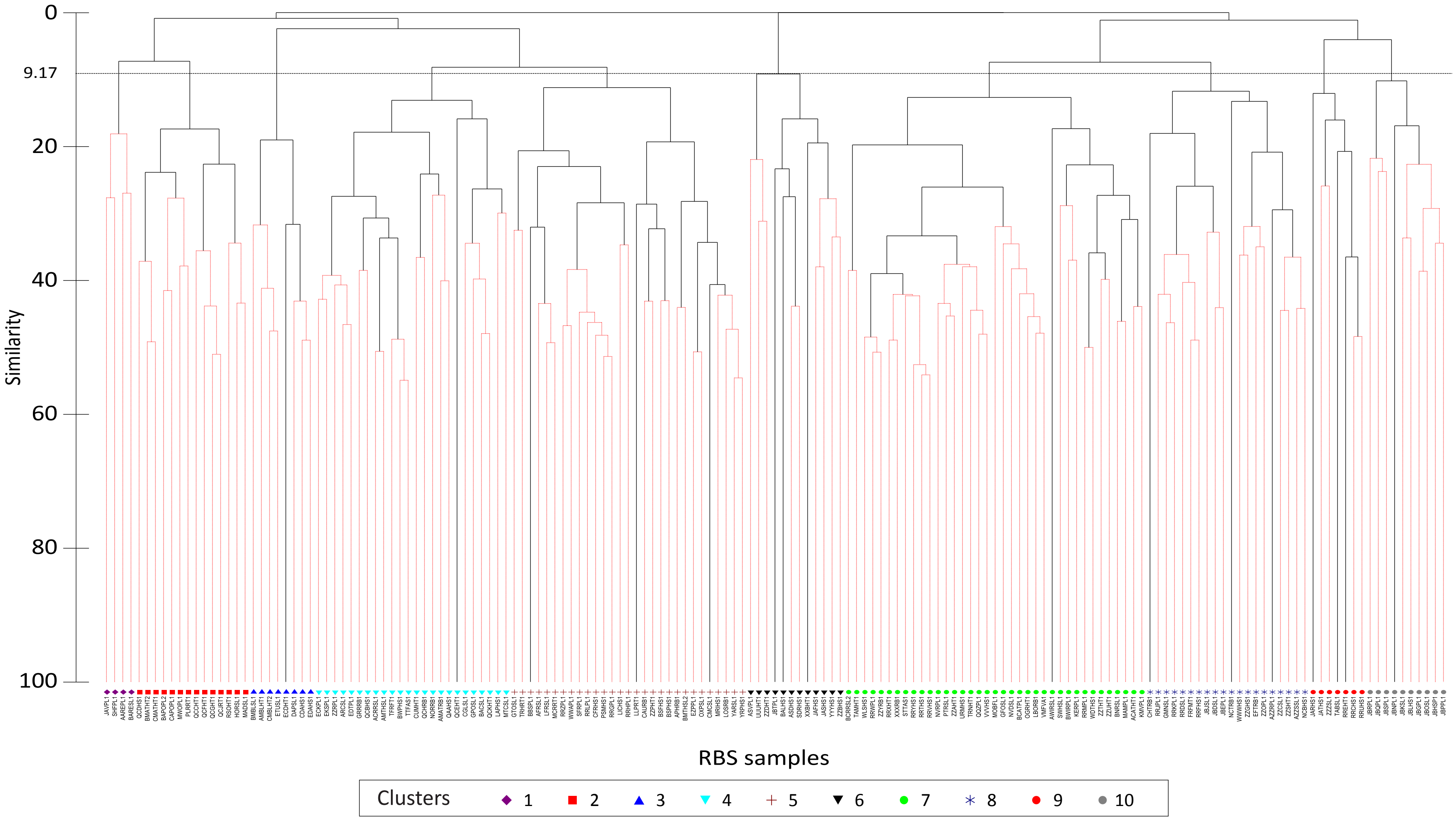


Figure 3.3: Cluster dendrogram at a 9.17% similarity level.

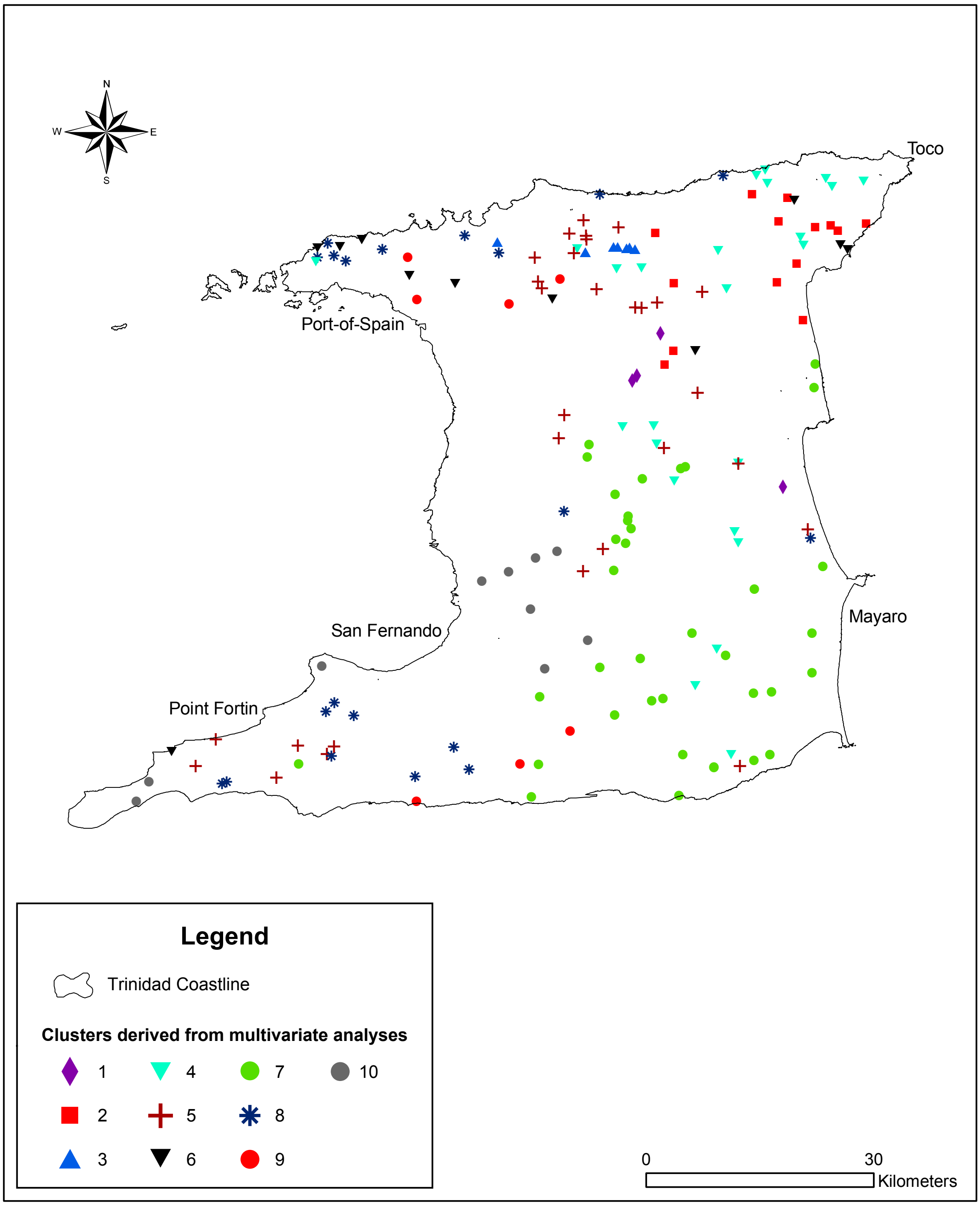


Figure 3.4: Clusters derived from multivariate analyses.

Figure 3.5: Cluster dendrogram showing sub-cluster arrangement.

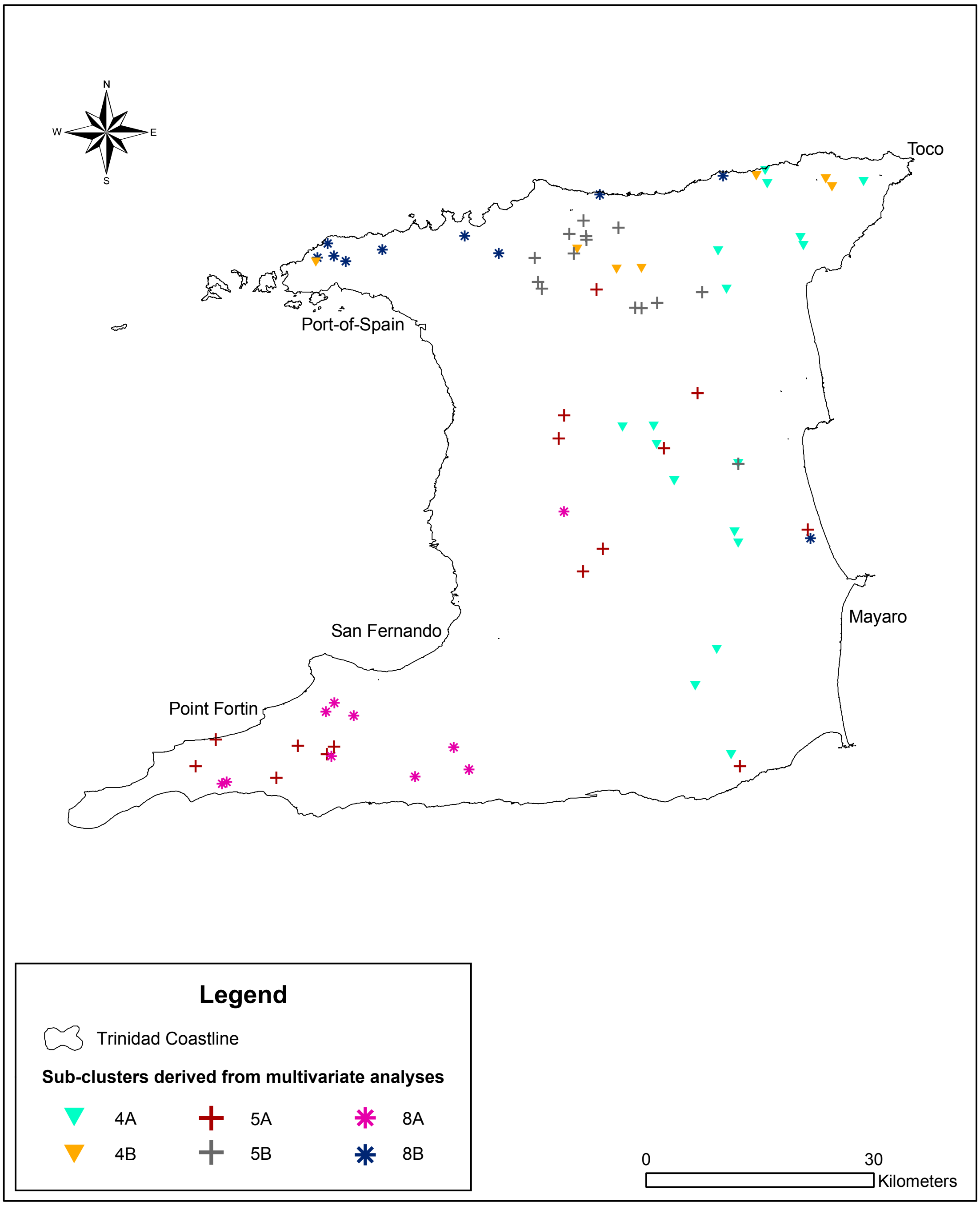


Figure 3.6: Sub-clusters derived at a 13.26% similarity level.

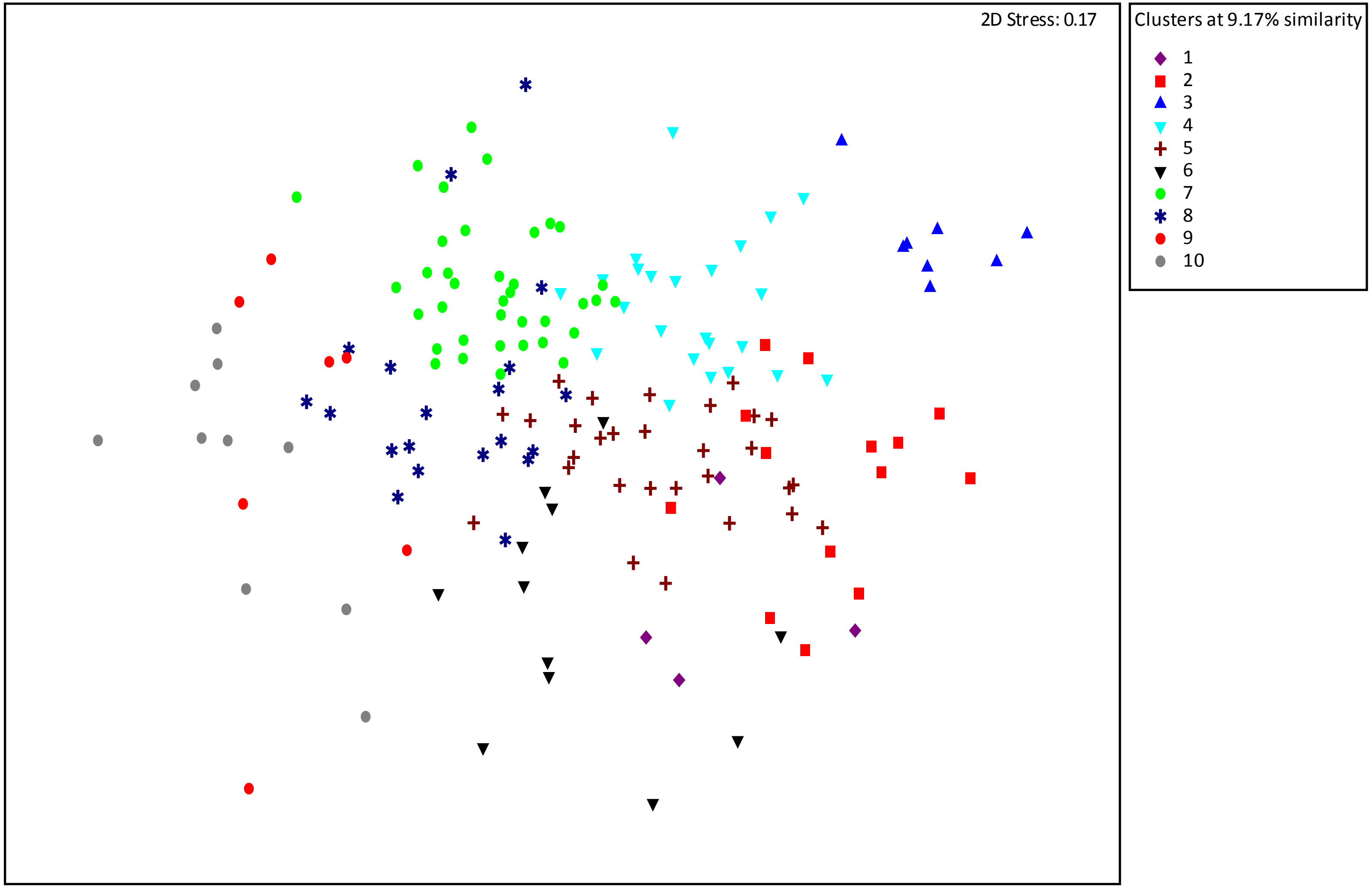


Figure 3.7: 2D NMDS: A two-dimensional representation of among site resemblances within each cluster.

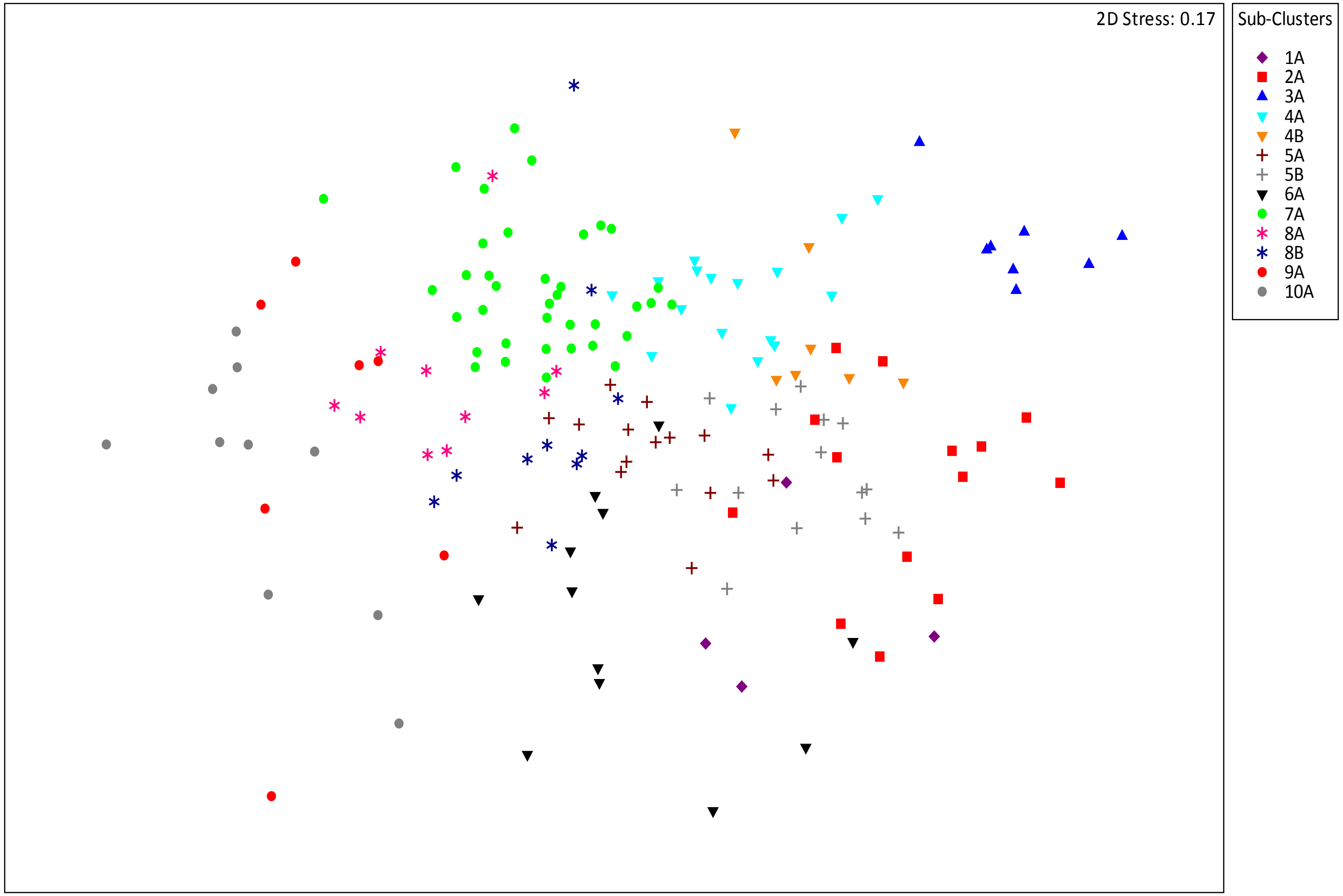


Figure 3.8: 2D NMDS: A two-dimensional representation of among site resemblances within each sub-cluster.

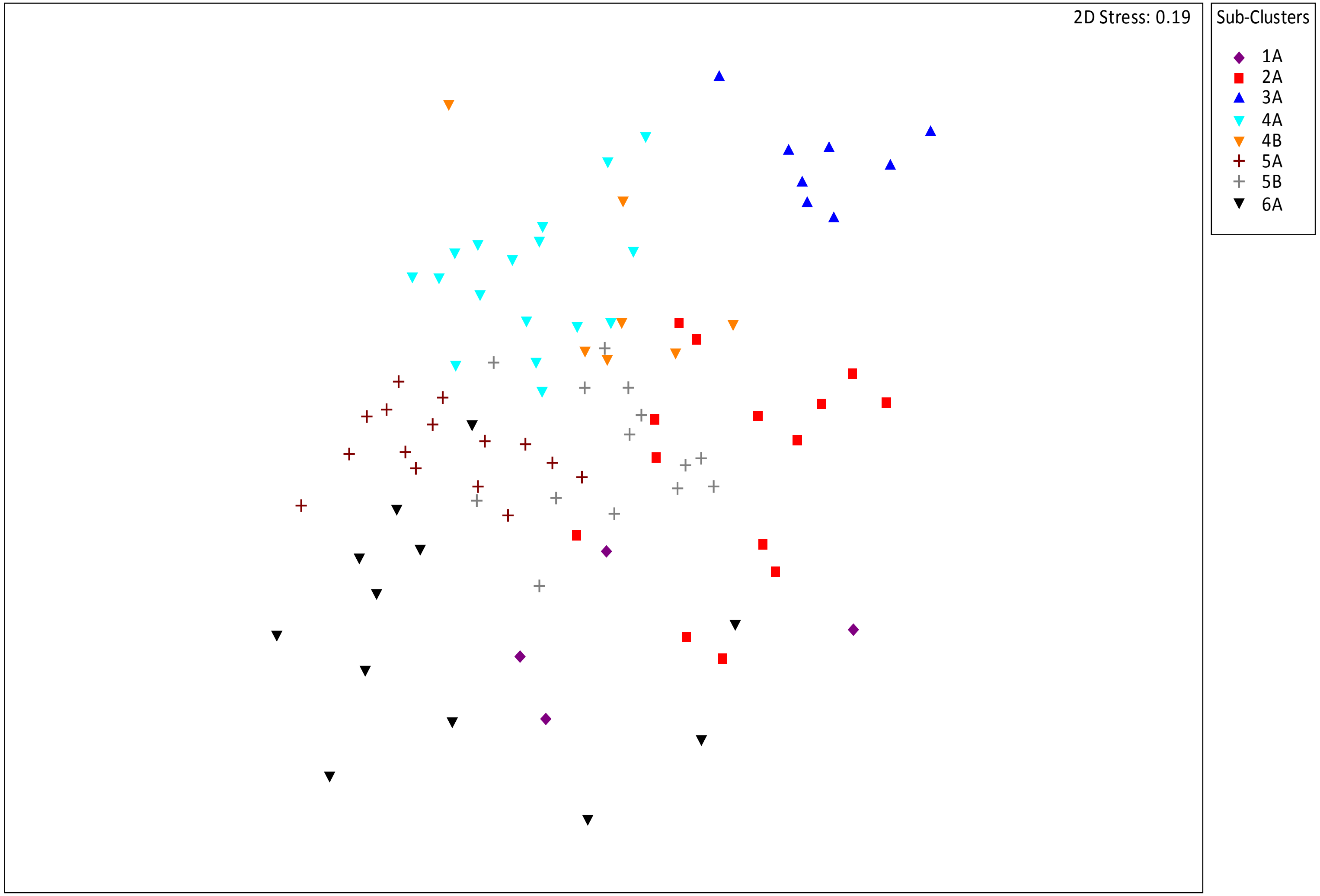


Figure 3.9: 2D NMDS: A two-dimensional representation of among site resemblances within each sub-cluster: Group 1.

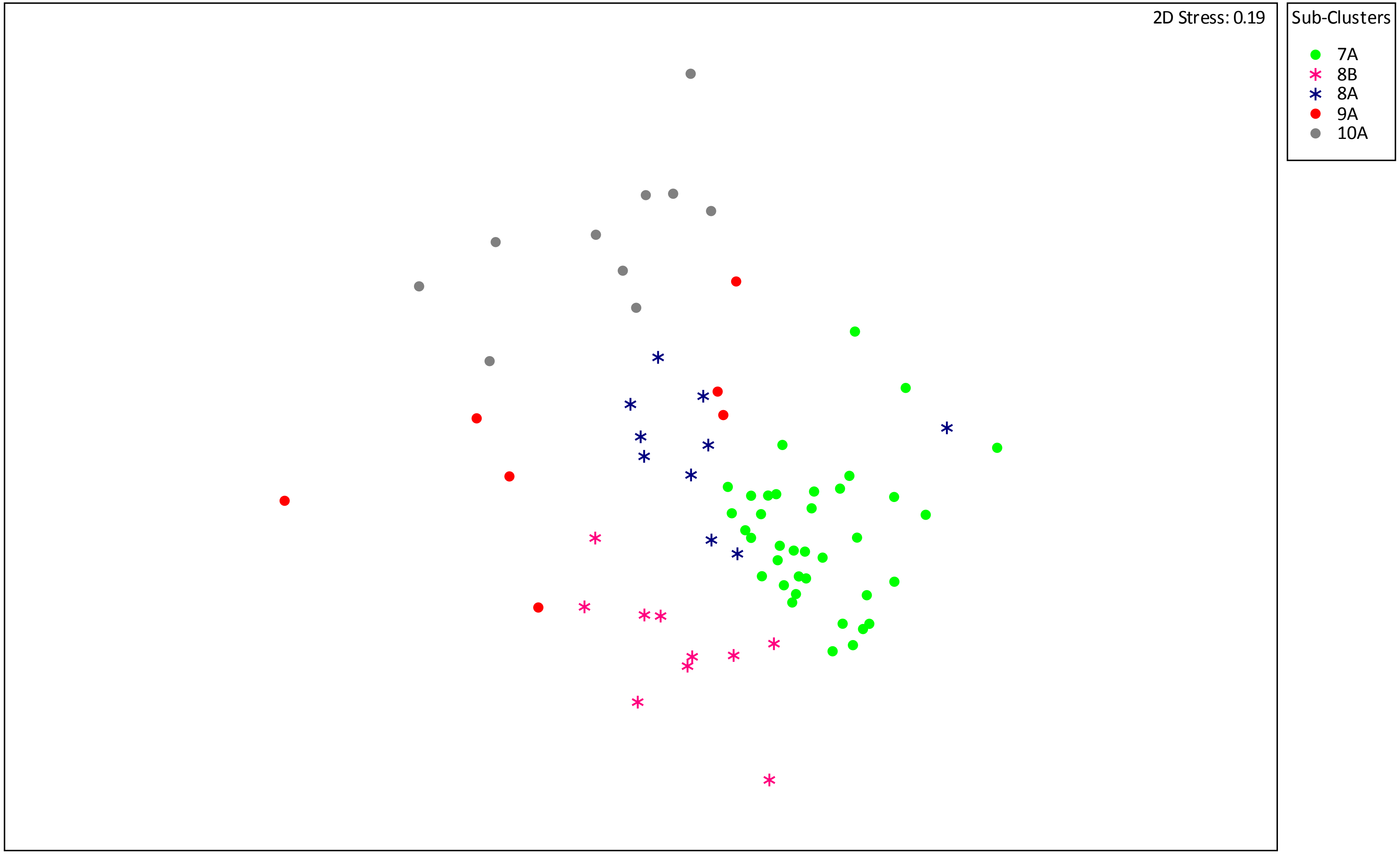


Figure 3.10: 2D NMDS: A two-dimensional representation of among site resemblances within each sub-cluster: Group 2.

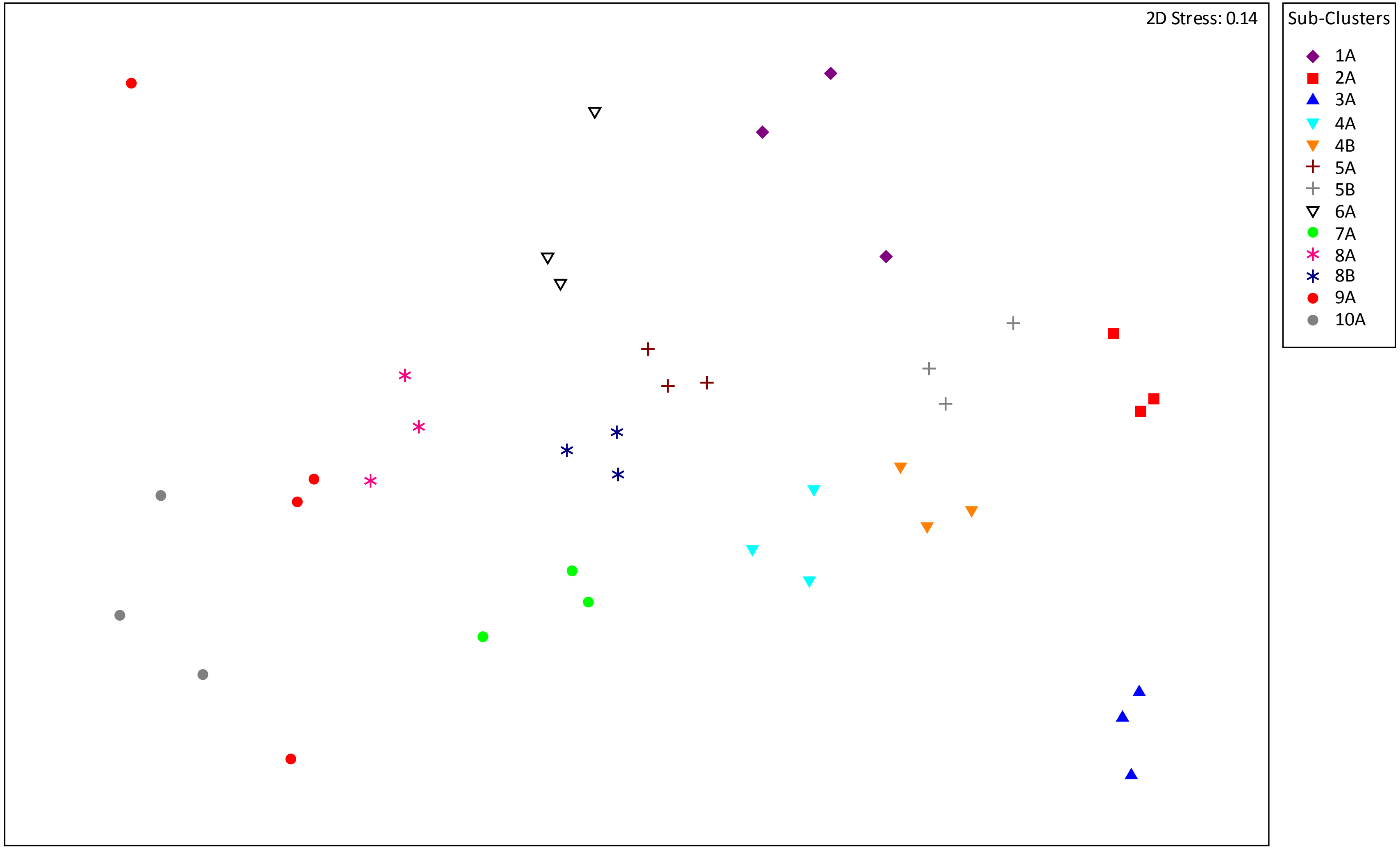


Figure 3.11: Summary 2D NMDS: A two-dimensional illustration of resemblance among the sites selected to represent each sub-cluster (Groups 1 and 2)

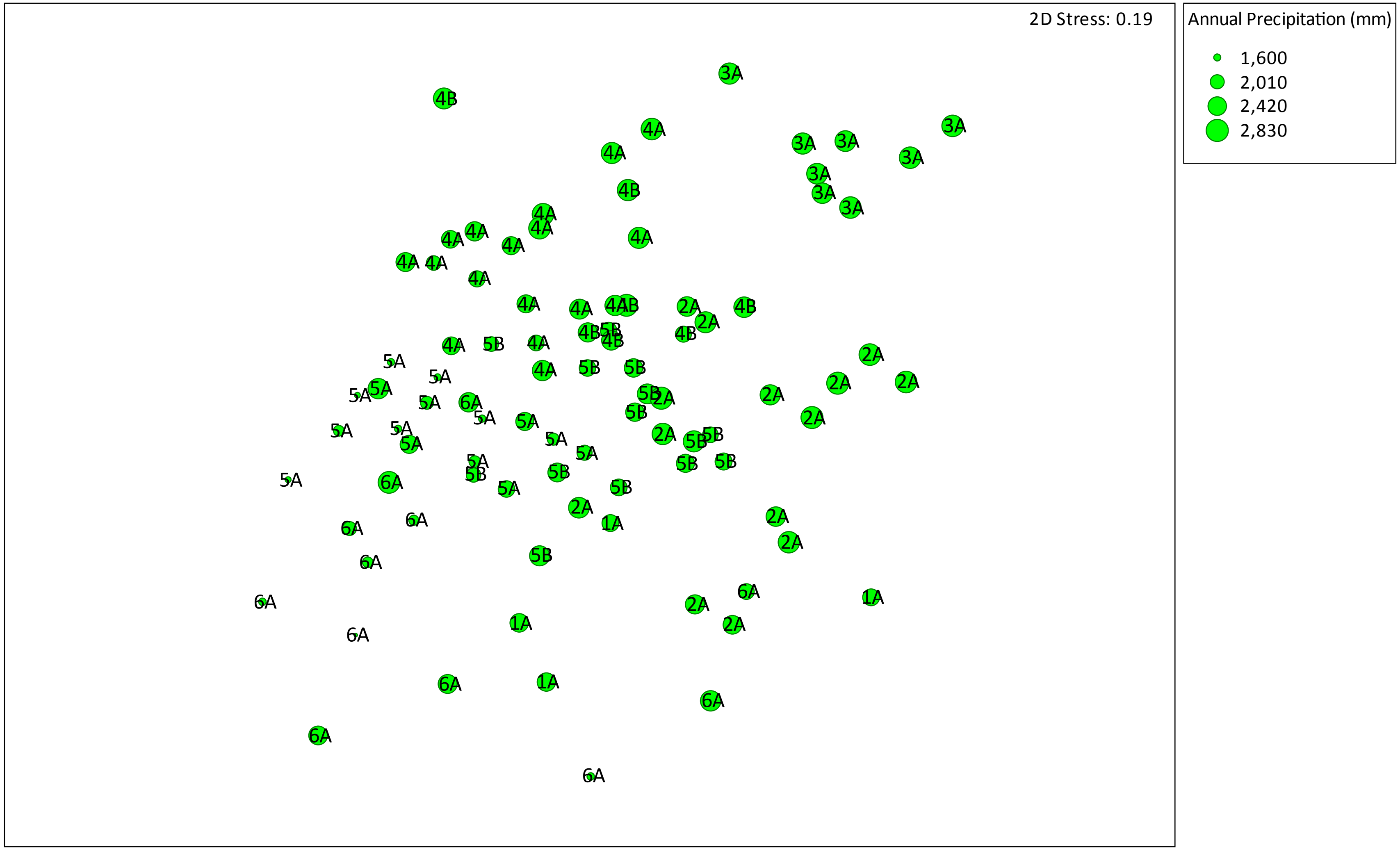


Figure 3.12: 2D NMDS of sub-clusters for Group 1 overlaid with a bubble plot of Annual Precipitation at each site.

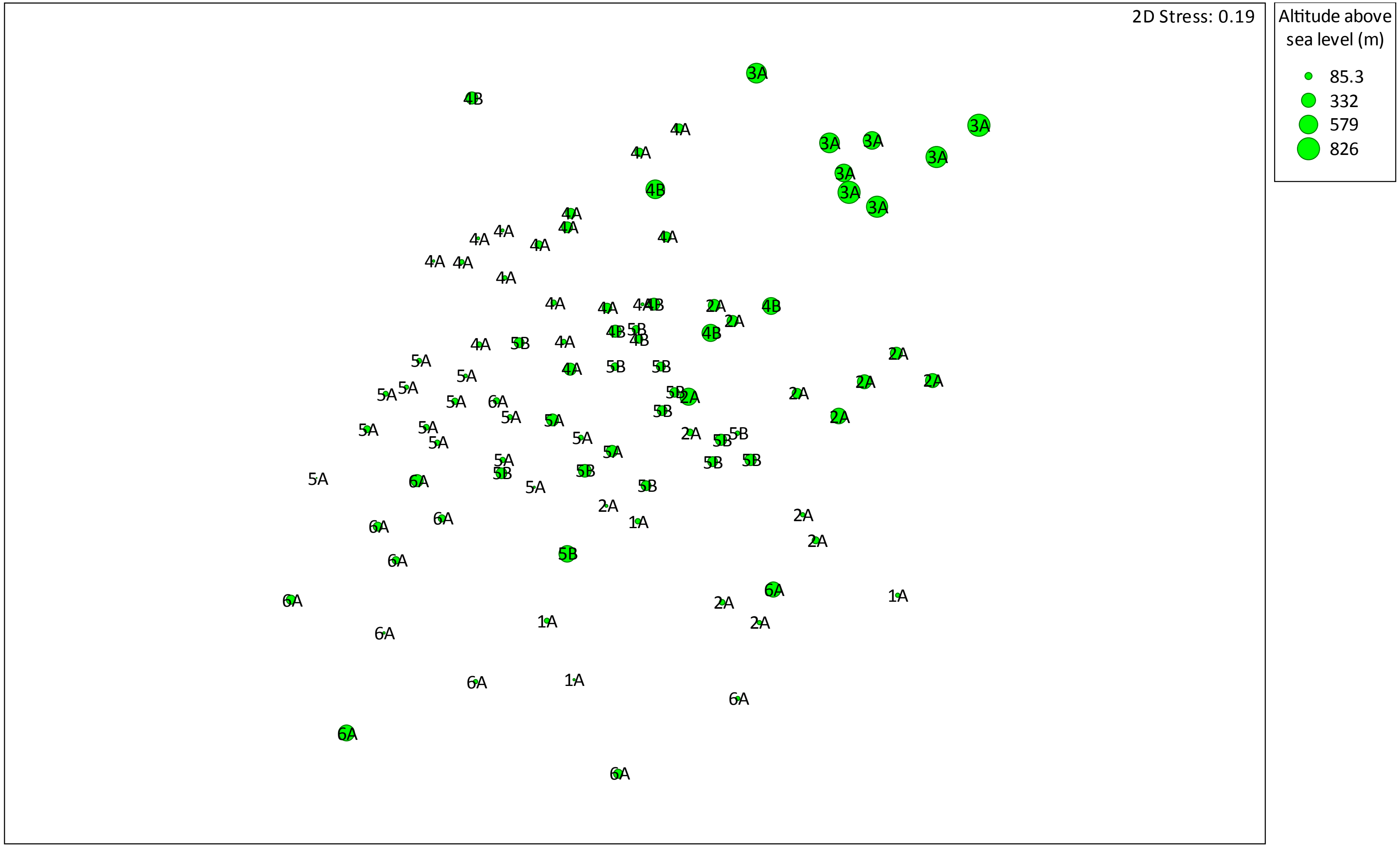


Figure 3.13: 2D NMDS of sub-clusters for Group 1 overlaid with a bubble plot of Altitude above sea level at each site.

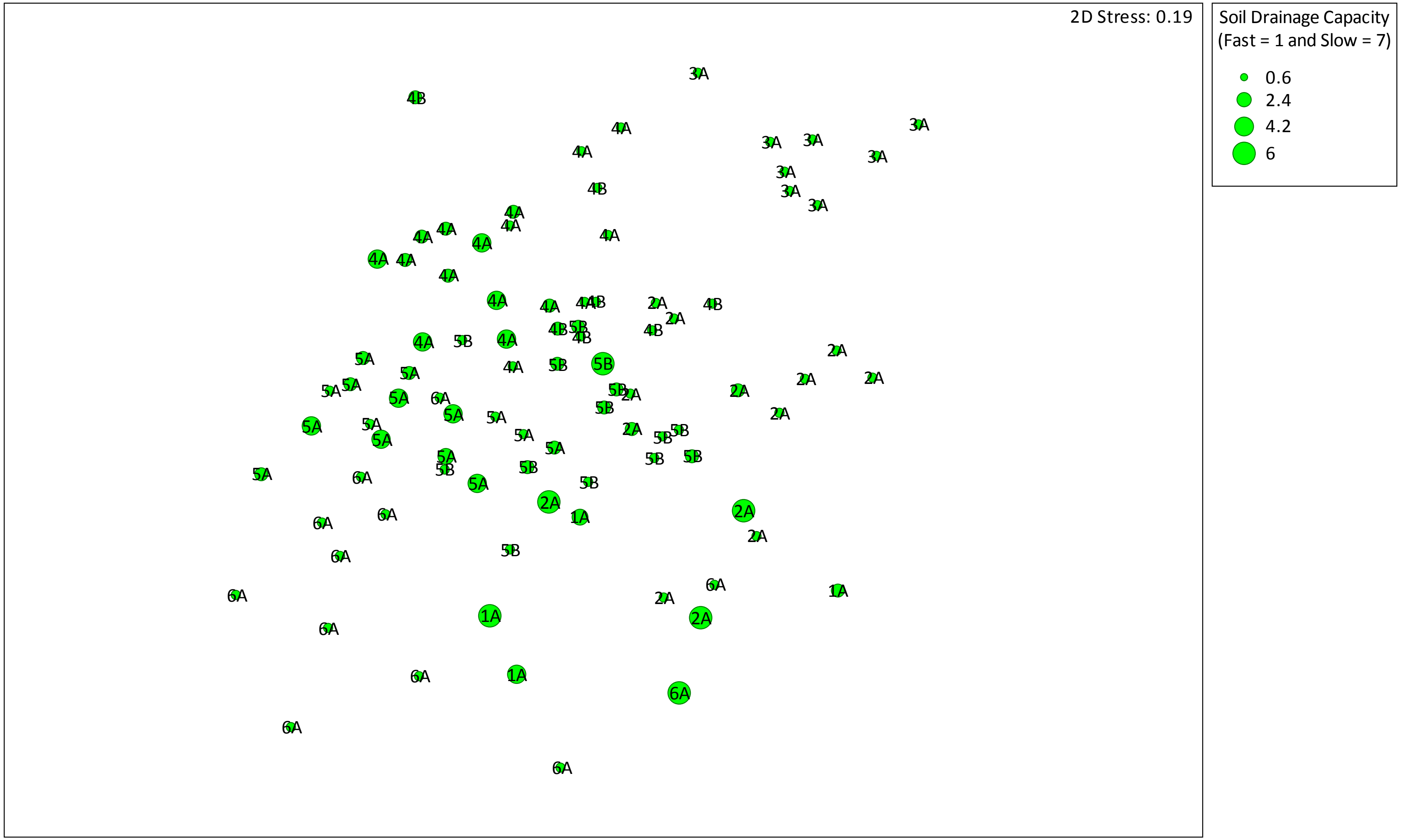


Figure 3.14: 2D NMDS of sub-clusters for Group 1 overlaid with a bubble plot of Soil Drainage Capacity at each site.

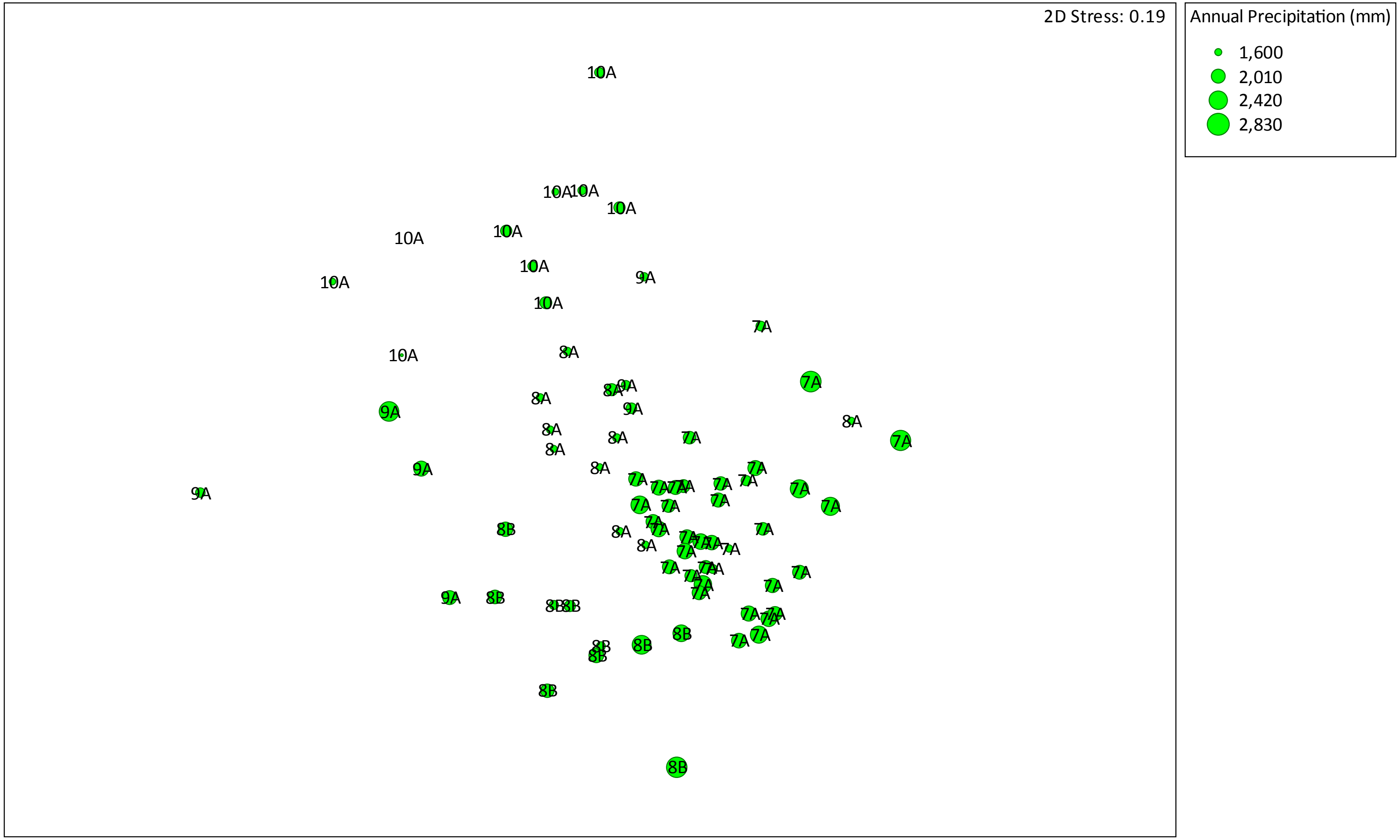


Figure 3.15: 2D NMDS of sub-clusters for Group 2 overlaid with a bubble plot of Annual Precipitation at each site.

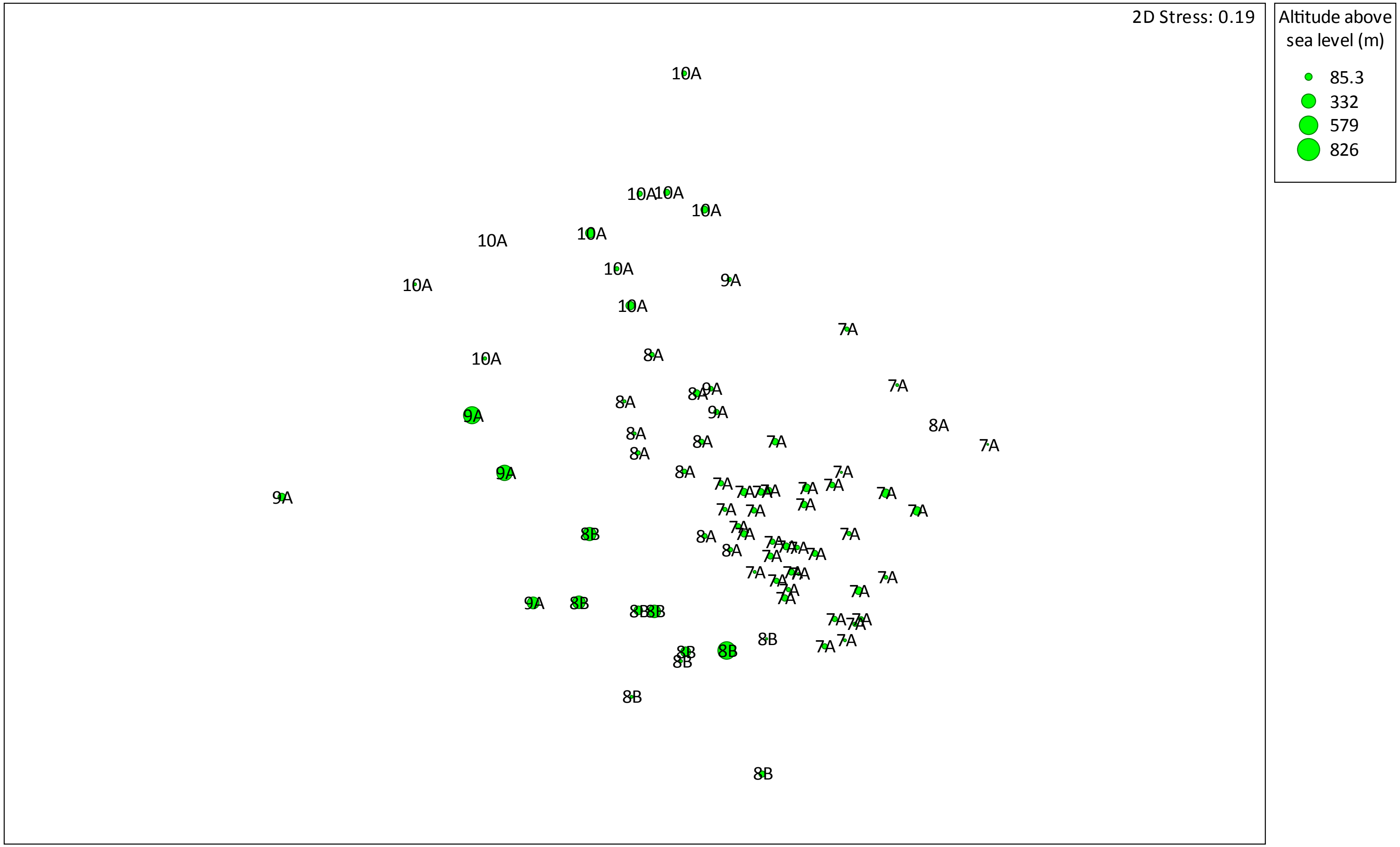


Figure 3.16: 2D NMDS of sub-clusters for Group 2 overlaid with a bubble plot of Altitude above sea level at each site.

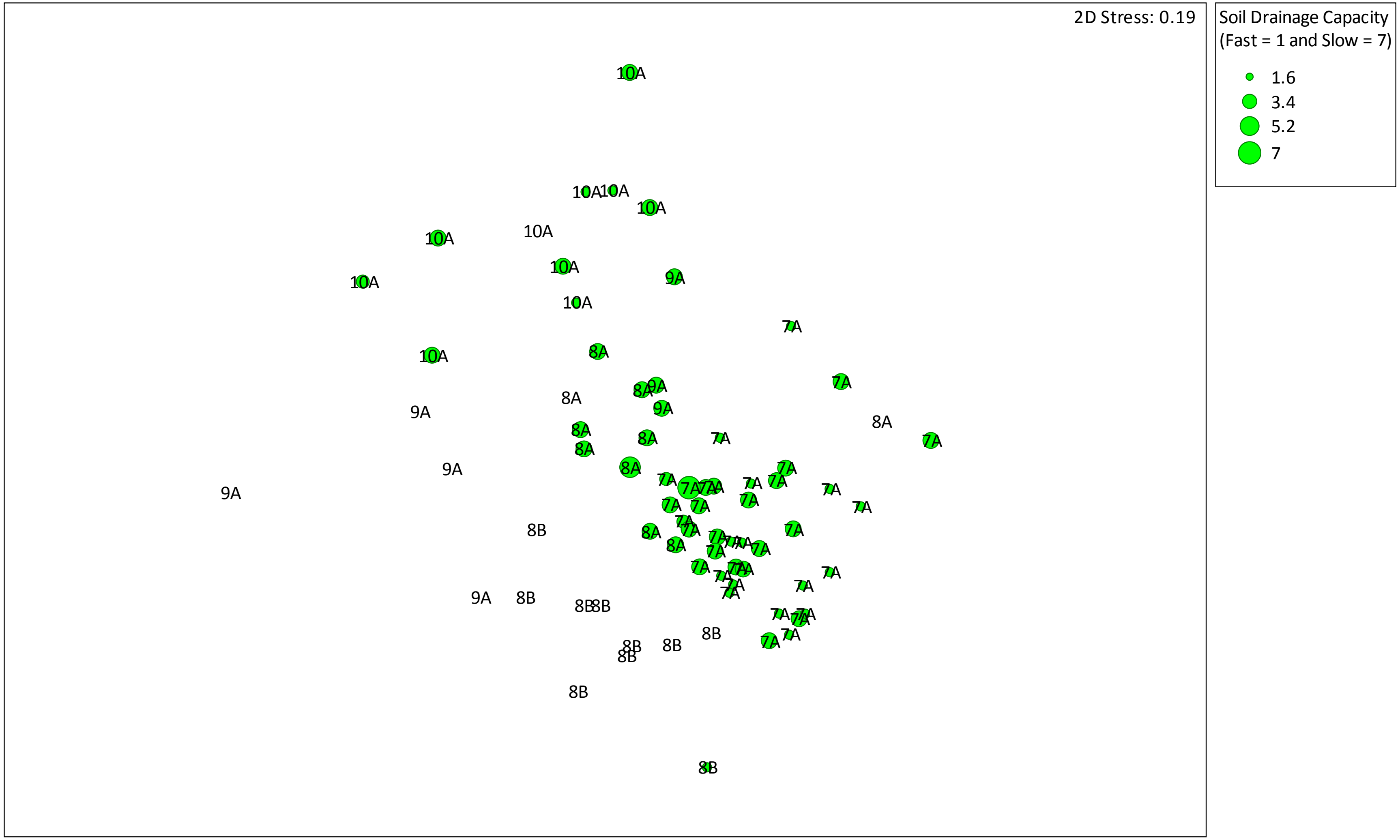


Figure 3.17: 2D NMDS of sub-clusters for Group 2 overlaid with a bubble plot of Soil Drainage Capacity at each site.

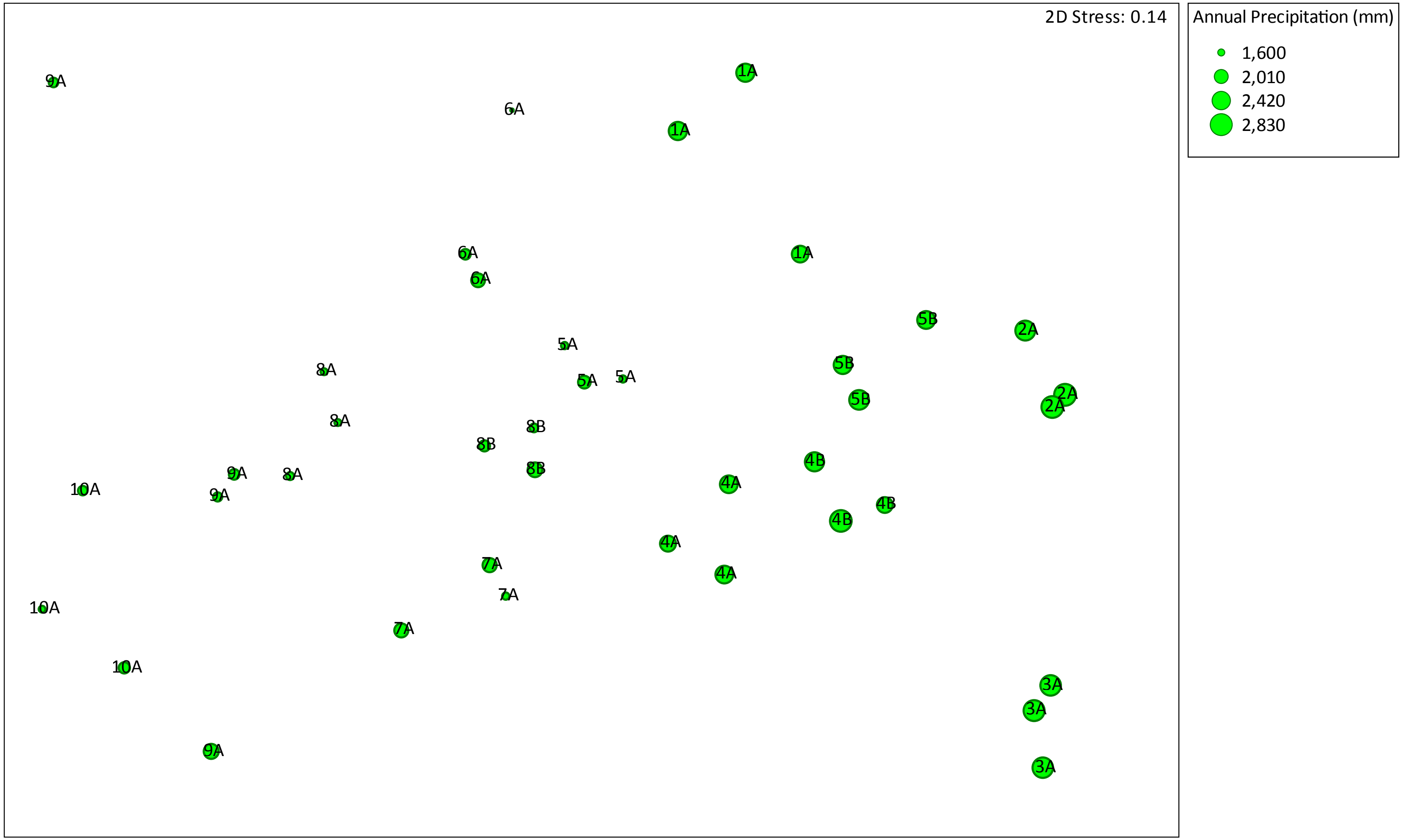


Figure 3.18: Summary 2D NMDS illustrating the representative sites of sub-clusters within Groups 1 and 2 overlaid with a bubble plot of corresponding Annual Precipitation values.

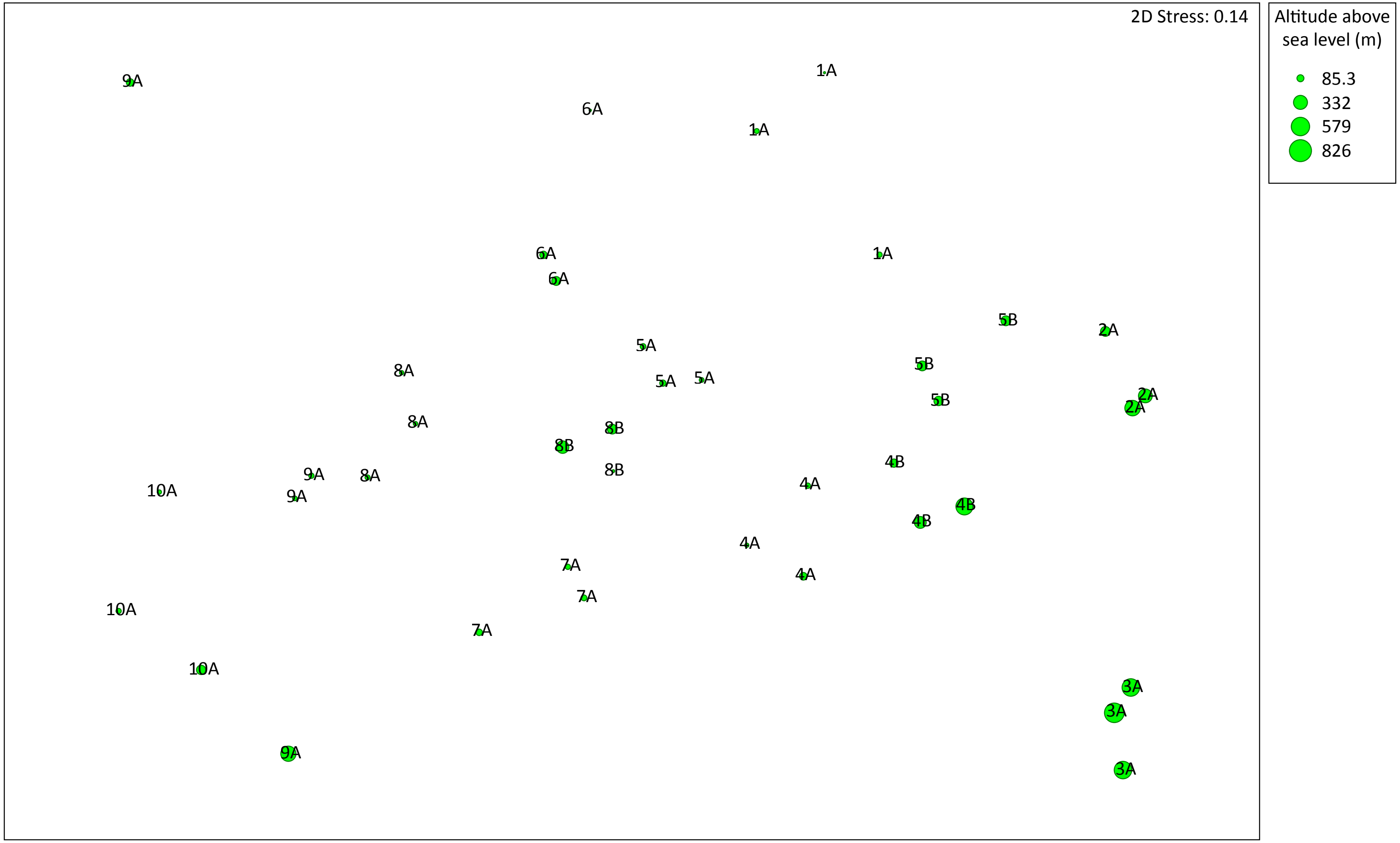


Figure 3.19: Summary 2D NMDS illustrating the representative sites of sub-clusters within Groups 1 and 2 overlaid with a bubble plot of corresponding Altitude above sea level.

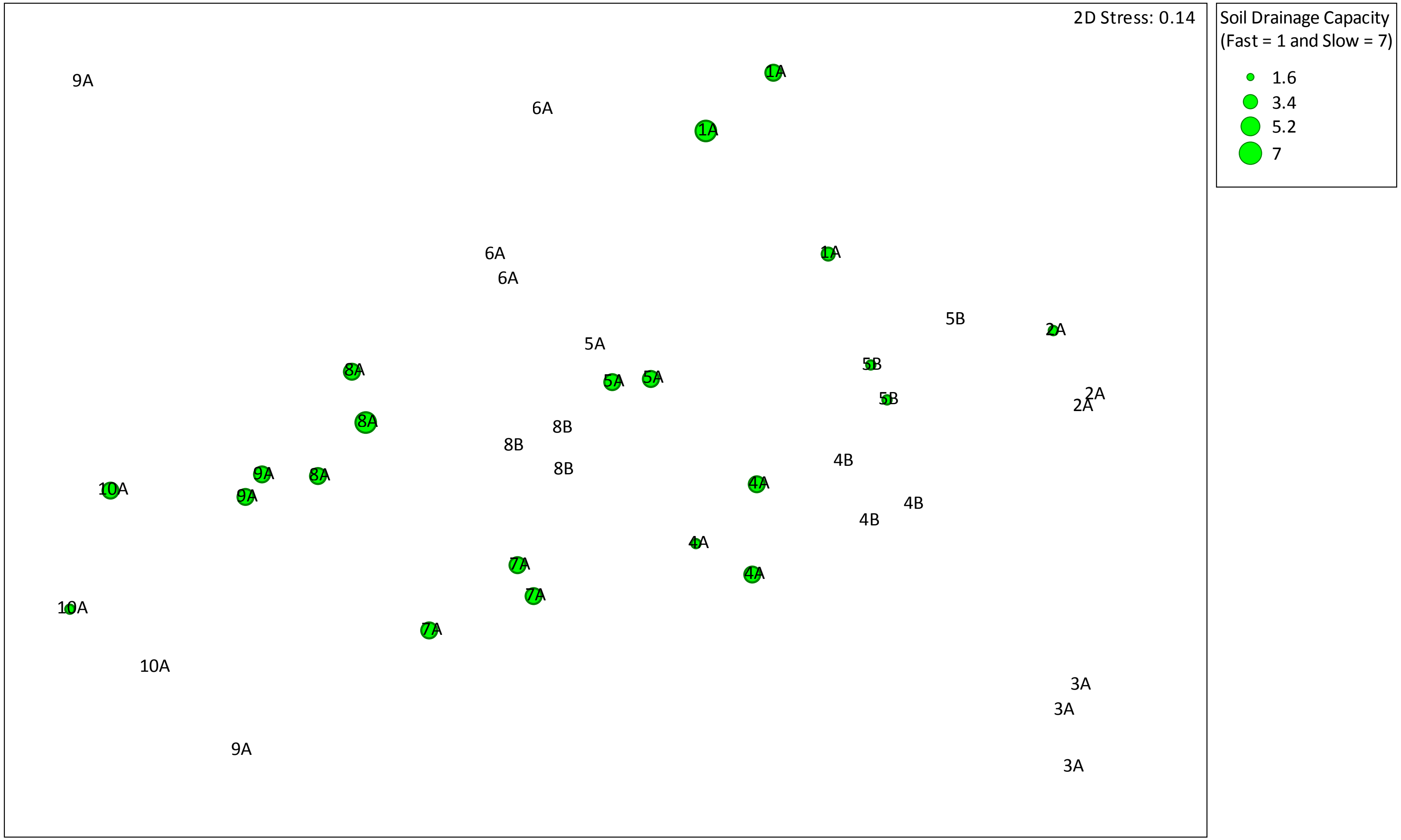


Figure 3.20: Summary 2D NMDS illustrating the representative sites of sub-clusters within Groups 1 and 2 overlaid with a bubble plot of corresponding Soil Drainage.

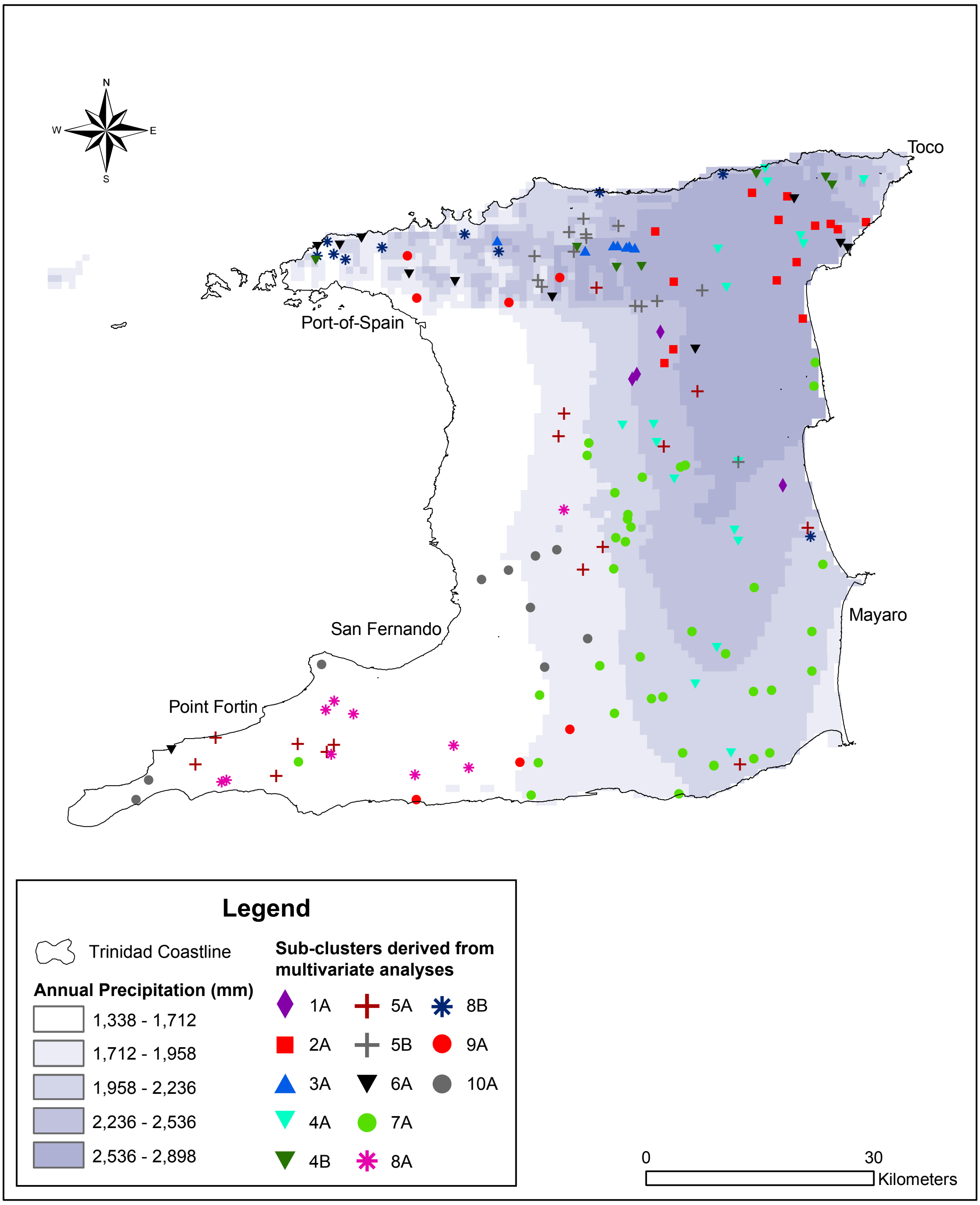


Figure 3.21: Sub-clusters superimposed with Annual Precipitation pattern.

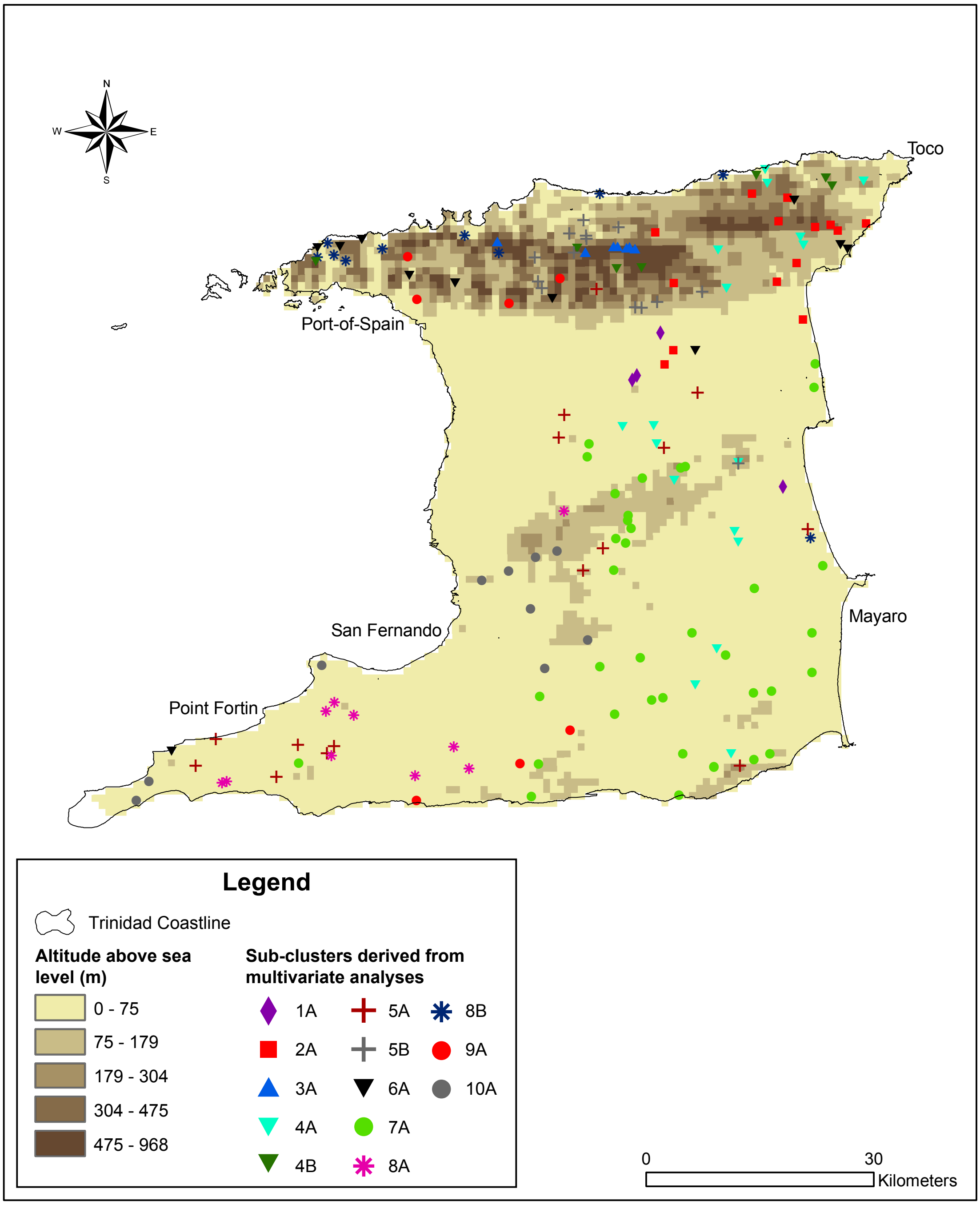


Figure 3.22: Sub-clusters superimposed with Altitude above sea level.

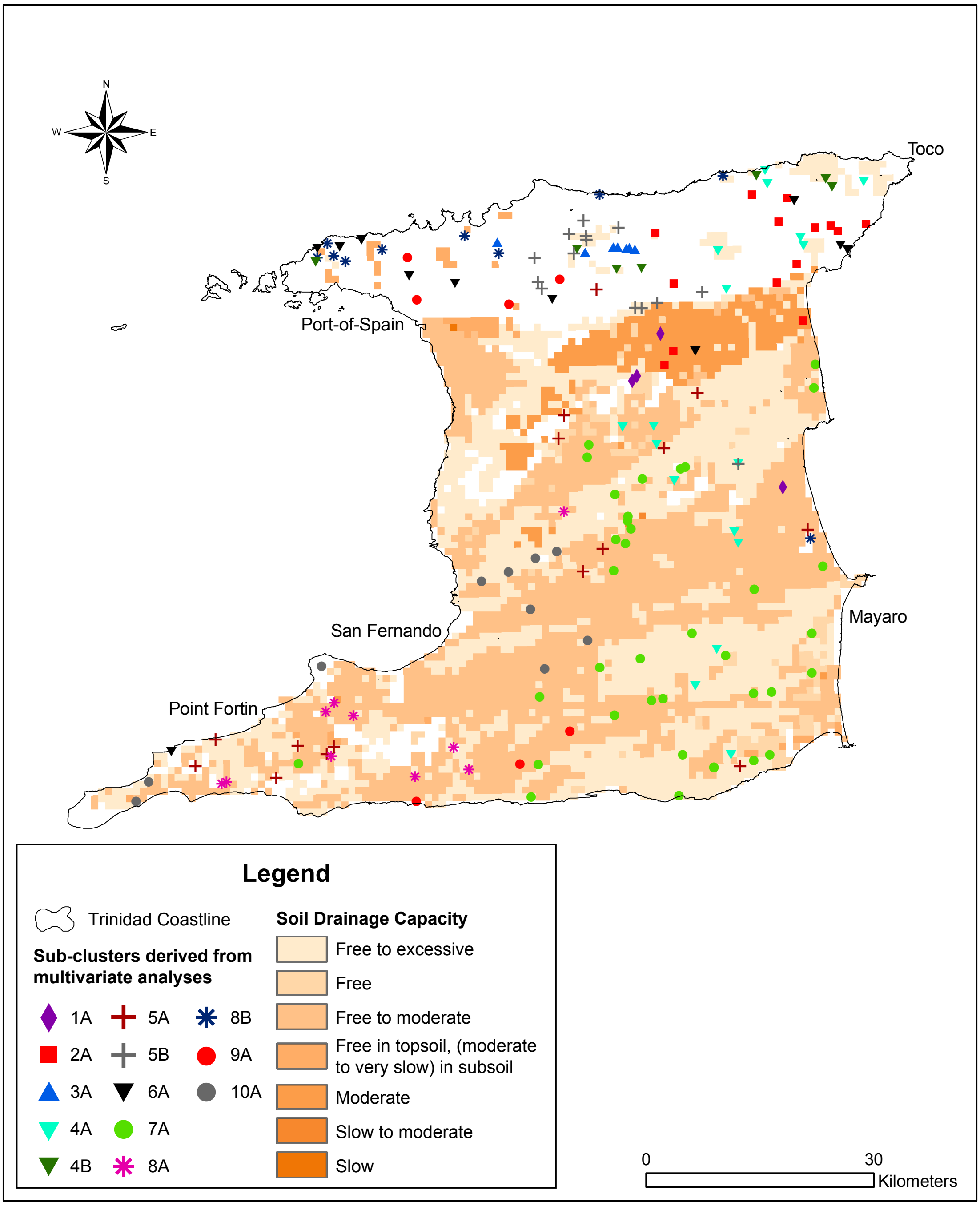


Figure 3.23: Sub-clusters superimposed with Soil Drainage Capacity.

Chapter 4

Modelling present-day distributions of selected tree species within Trinidad

4.1 Introduction

This chapter represents the first of two parts of an investigation into the use of SDM as a potential tool for informing conservation planning in the face of climate change. It provides an introduction to SDM and focuses on the use of the MaxEnt algorithm to generate models of the potential present distributions of selected species under present climatic conditions. Based on the small scale of the Caribbean island of Trinidad, the Methods Section outlines data requirements and treatments and also provides suggestions for the manipulation and assessment of model output. It further discusses specific problems associated with SDM at scale of the Caribbean SIDS and suggests possible solutions.

4.1.1 Species Distribution Models – What and Why?

There has been a remarkable surge in SDM over recent decades – both in the scientific literature and by governmental and non-governmental institutions that are involved in conservation and resource assessment at large spatial scales (Ferrier et al. 2002; Franklin et al. 2009; Iverson and Prasad 1998). This has been due to a combination of (i) the increasing demand for geographical descriptions of biodiversity and (ii) the steady stream of novel and improved techniques and data in response to this demand (Elith et al. 2011).

SMs are numeric instruments designed to combine and relate species distribution data (occurrence or abundance at known locations) to the environmental and/or spatial characteristics of these locations. SMs sometimes involve extrapolation beyond the current known range through space and/or time and are used to gain ecological insight by predicting species' distributions across landscapes (Franklin 2009).

According to Franklin (2009), the roots of SDM can be traced back to a combination of biogeography (Box 1981), ecological gradient analysis (Whittaker 1960; Whittaker et al. 1973), and remote sensing and GIS (Franklin 1995). Additionally, according to Elith and Leathwick (2009), a powerful conceptual argument in favour of modelling individual species instead of communities was provided by studies [e.g., vegetation (Whittaker 1956) and birds (MacArthur 1958)] which drew attention to the 'individualistic responses of species' to their environments.

4.1.2 Main applications of SDM

SMs are applied in four main forms: (i) interpolation of the (relative) suitability of the habitat that is known to be occupied by a species; (ii) estimation of the relative suitability for habitat within geographic areas that are known to be uninhabited by a species; (iii) estimation of changes in habitat suitability over time in response to a specific scenario of environmental change; and (iv) estimations of species niche (Franklin 2009). There are many published examples which indicate that interpolation-based SMs can perform well when describing the natural distribution of a given species within its current range. Interpolations with strong predictive ability and ecological insight can be derived when functionally relevant predictor variables and well-designed survey data are applied to the appropriate algorithm (Guisan and Thuiller 2005). Such SMs are often considered reliable enough to support effective decision-making.

However, transferability of SMs – which involve extrapolation to areas where a species could occur (ii and iii) as well as niche estimates (iv) have been intensely debated in the literature, as they are characterised by a host of conceptual and practical problems (Hampe 2004; Menke et al. 2009; Soberón and Peterson 2005). In particular, there is a high uncertainty associated with extrapolations conducted to predict species distributions within novel conditions – which involve the use of new combinations or values of predictor variables outside the original ranges of the training data. This is due to the absence of species occurrence data within the training data that can be used to directly test/support these predictions. This high uncertainty is also associated with possibilities which are difficult to predict under training/present conditions. These include: (i) species' distribution under novel conditions being influenced by factors such as phenotypic plasticity and genetic variability; (ii) novel (combinations of) environmental conditions altering the context within which mechanistic/process-based interactions (such as biotic interactions) may influence species distribution; and (iii) dispersal pathways being altered by these novel conditions (De Marco et al. 2008; Dormann 2007). Such uncertainty makes the output of these models difficult to assess. However, in many cases these SMs (ii to iv) are still used – as they are the only tools available.

4.1.3 Species niche versus geographic space

Also known as 'ecological niche models' or similar derivatives, the relation of SDM to the species niche concept has been, and still is often debated in the literature (Guisan and Thuiller 2005; Hirzel and Le Lay 2008; Jiménez-Valverde et al. 2008; Soberón 2007). However, this debate has been afflicted by a series of technical and conceptual difficulties and has yet to be resolved. The terminology varies in the literature and SMs are usually described with respect to the (i) fundamental and (ii) the realized niche concepts. The geographic area which, according to the SM output, meets the environmental conditions required by a species describes some part of its fundamental niche. This is not necessarily the same as areas that are actually occupied by this species, which represent some part of its realized niche (Jiménez-Valverde et al. 2008; Peterson et al. 2008; Phillips et al. 2006).

However, outputs of the majority of SDM studies are described with respect to the realized niche (Austin 2002; Guisan and Thuiller 2005; Thuiller et al. 2004). This is because these SMs are usually constructed based on conditions associated with actual species occurrences within environmental space. The mapped extrapolation of this output within geographic space is referred to as the potential distribution or habitat suitability of that species (Araújo and Guisan 2006; Soberón 2007).

Despite the niche theory strongly underpinning SDM, the view adopted by this thesis follows that of Franklin (2009) who argues that correlative SMs are not actual representations of species niches but are simply empirical correlations between species occurrences and the environmental variables at these locations. Moreover, when extrapolated from environmental to geographic space, these SM outputs represent the potential geographic distribution or suitable habitat for a given species. Furthermore, while it is accepted that that these models should always be evaluated for 'ecological realism', the availability of data rarely allows the fundamental or realised niche of a species to be completely described or confirmed. Finally, SMs are increasingly being used to predict the geographical distribution of a given species rather than for studying the details of its distribution in any of its niches (Pearson and Dawson 2003; Thuiller et al. 2011). Hence, SMs in this thesis are considered to depict potential species distributions which are based on the availability of required environmental conditions for species occurrence within geographical space – rather than any aspect of its niche.

4.1.4 Different types of SDM algorithms

Over the last two decades, the on-going developments within the field of SDM have yielded a multitude of methods/algorithms. These algorithms can be distinguished based on the type of species data they use. Systematic collection of species data from biological surveys of sites – from which the presence-absence or abundance of a species are recorded, have been applied to regression-based algorithms such as Generalized Linear Models (GLMs), Generalised Additive Models (GAMs) and Boosted Regression Trees (BRTs) (Elith et al. 2011; Franklin 2009). However within most areas of the world there is a paucity of such systematic biological survey data. Instead, there is a greater prevalence of species occurrence data in the form of presence-only records within herbarium and museum collection databases. Representing over a century of collecting efforts across many areas of the globe, these data represent a valuable source of species occurrence data. Some algorithms, such as logistic regression, decision trees and GAMs which have been traditionally used for presence-absence or abundance data have also been applied to presence-only data (Franklin 2009). However, the increasing availability of presence-only data over recent years has inspired the development of several SDM algorithms designed specifically for presence-only data. These include Ecological Niche Factor Analysis (ENFA), Genetic Algorithms for Rule Production (GARP) and MaxEnt.

Apart from the type of data available, the choice of which model to use for a study has also been based upon factors such as the characteristics of the species being modelled (their distributions and life histories) and the scale of analysis (Franklin 2009). However, several authors have pointed out that ultimately it is the experience of the practitioners in conjunction with the type of data available that determines the algorithm used in any particular application (Austin et al. 2006; Burgman et al. 2005). The remaining analyses of this thesis are based upon the MaxEnt algorithm (Phillips and Dudík 2008; Phillips et al. 2006).

4.1.5 Presence-absence versus presence-only

As the term implies, presence-only data consist of the occurrence locations of species without any information about known absences. The most well used example is the now wide availability of occurrence data derived from the millions of herbaria and museum records that have been compiled in electronic form within natural history collection databases. These have been and continue to be used for a variety of modelling applications including conservation, macro-ecology, evolutionary biology and climate change modelling (Graham et al. 2004).

Justification for the steadily increasing use of such presence-only data comes from the fact that there is a lack of systematic survey data in many regions of the world in conjunction with the widespread demand for mapped predictions (Pearce and Boyce 2006). Additionally, apart from being time and resource consuming, there is no guarantee that systematic biological surveys will yield rare (but present) species or sufficient numbers of observations that are needed for the SDM of many species. For example, a recent survey in Madagascar resulted in the compilation of data for 2,315 species across six taxonomic groups on the island, however, more than 60% of these had fewer than eight observations, hence SMs could not be generated (Kremen et al. 2008).

There is also great variation in opinions about the value of presence-only data in the literature. Some researchers have surmised that more robust SM output would be obtained with the availability of absence data as this would facilitate analyses of (spatial) bias and of prevalence (Phillips et al. 2009). However, others highlight the advantages of not including absence data, they argue that absence data can be confounding and misleading because it may not possible to distinguish whether an absence indicates that a habitat is not suitable or whether it is suitable but not occupied due to a variety of reasons including disturbance, biotic interactions, dispersal constraints and ‘non-equilibrial’ phases such as invasions of exotic species.

About a decade ago, the original modelling methods which were used to fit presence-only data [e.g., BIOCLIM (Busby 1991)] employed only occurrence data and ignored incorporating environmental conditions that were available to a given species within (other parts of) the study region. In contrast, more recent algorithms such as MaxEnt which are designed specifically for presence-absence data, generally require a sample of observations that characterise the range of environments that are available within the entire study area (Phillips et al. 2006). This enables these models to incorporate the relative suitability of available environmental conditions in the form of ‘pseudo-absence’ (or background) points. Within MaxEnt, these pseudo-absence points are not used as species absences but instead provide a sample of conditions which are available to the species within the region. Comparison of known occurrence records with these pseudo-absence points increases the discriminative ability of the algorithm by enabling a clearer understanding of the conditions which shape the occurrence of the species within a region. These pseudo-absence points are extracted from anywhere within the study area (grid cells) using different sampling techniques, for example random or stratified random sampling. Furthermore, studies have suggested that the inclusion of background observations from beyond the species range or from areas that are environmentally dissimilar from the location points of the species being modelled yields more accurate results (Chefaoui and Lobo 2008; Le Maitre et al. 2008). This is especially the case when the objective of the modelling is to project changes in species range under novel conditions such as climate change. However, these analyses did not incorporate this technique because, as discussed in Chapter 6, the range of several of these species also included other islands within the Caribbean. However, the lack of unbiased, occurrence data (or in some cases any occurrence data whatsoever) within these islands, prevented reliable definition of these species ranges beyond the island of Trinidad. Hence, the range of these analyses was limited solely to Trinidad.

4.1.6 MaxEnt

MaxEnt is a software application designed specifically for the SDM of presence-only data and to overcome the problems of small, unplanned, un-designed samples of species occurrence (Phillips and Dudík 2008; Phillips et al. 2006). It is a nonlinear, nonparametric, presence-only model which is also insensitive to multicolinearity. The output of MaxEnt is a value between 0 and 1 and not binary (0 or 1), this allows the programme to introduce individual thresholds – which seems to be more precise (Phillips et al. 2006). It also provides the percentage contribution of each predictive variable within the models that are built.

MaxEnt is based on a principle of maximum entropy from statistical mechanics which, when applied to SDM, states that the best approximation of an unknown (species) distribution is the one with maximum entropy (the most spread out and uniform) subject to known constraints. These constraints are defined by the expected value of the distribution, which is estimated from a set of species presence observations, and excludes all conditions and assumptions which are not supported by the occurrence data (Phillips and Dudík 2008). Three aspects distinguish it from other SDM algorithms. Firstly, as mentioned above, locations within a study area that are not known occurrences are not interpreted as absences, but instead as pseudo-absences (possible presence or absences) which are used to represent the background environment. Secondly, it includes a regularisation term which prevents over-fitting by constraining the modelled distributions to be fitted within a certain interval around the empirical mean instead of matching it exactly (Phillips et al. 2006).

Finally, unlike most other SDM algorithms which tend to be discriminative, MaxEnt is generative in nature. For a given prediction, where X = inputs and Y = the response or probability of occurrence:

Discriminative approaches model the probability of a response given the inputs [Pr(Y/X)].

The generative approach of MaxEnt instead, models the probability of inputs given the response [Pr(X/Y)]. Bayes' rule is then used to get from Pr(X/Y) to Pr (Y/X) (Phillips and Dudík 2008).

Since its introduction in 2006, MaxEnt has become increasingly popular compared to other presence-only algorithms because of several reasons. Firstly, its requirements are simple, consisting only of the occurrence data of the species being modelled and environmental information for the study area (Phillips et al. 2006). Secondly, it has been shown to produce very robust results with small amounts of training data (small sample sizes) (Phillips and Dudík 2008). It has also been used extensively to produce robust results in a variety of applications that have been based in many different regions of the world. Some of these include modelling the effects of climate change on species distributions (Fitzpatrick et al. 2008; Hijmans and Graham 2006); studies of endemism hotspots (Murray-Smith et al. 2009) and investigation of the degree to which climate constrains distributions of species (Echarri et al. 2009; Wollan et al. 2008). Finally, several comparative studies have demonstrated that MaxEnt either outperforms other algorithms (both presence-onlu and presence-absence) or is among the top-performing methods with respect to several measures of prediction accuracy (Elith and Graham 2009; Hernandez et al. 2006; Pearson et al. 2007; Phillips et al. 2006).

4.1.7 The problem of spatial autocorrelation

A central concept to SDM is the distinction between environmental and geographic space. While the latter is defined either by two-dimensional map coordinates or three-dimensional digital elevation models, the former has the potential to be multi-dimensional because it is defined by the set of predictor variables (Franklin 2009). When a SDM algorithm is fitted with environmental predictors alone, its output depicts the variation of a species' distribution solely in environmental space instead of geographic space. It is important to note such models do not incorporate geographic proximity into the generation of their predictions – despite the fact that the generated model is mapped in geographic space as one of the final steps of creating the model output. The fact that these mapped outputs may show clustering in geographic space is simply an artefact of spatial autocorrelation among the environmental parameters input into the model (Franklin 2009).

Sample selection bias is a serious source of error, especially for SMs that have been built from presence-only data. Biased occurrence data include those that have been obtained from purposive sampling, historical surveys, natural history collections (herbaria and museums) and other opportunistic sources of species observations. These occurrence data usually exhibit strong spatial bias in survey effort and are typically strongly skewed towards more accessible areas (Reddy and Dávalos 2003; Schulman et al. 2007). In the recent years, there have been several papers which have warned against the use of such non-randomly distributed location data, as this can dramatically lower their predictive ability by resulting in unrealistic bias among the environmental parameters during the generation of an SM (Elith et al. 2011; Phillips et al. 2009).

Such bias is a problem in SDM because it violates one of the most basic statistical assumptions of most SDM methods: that the presence data are sampled independently (without any bias) within the study area (Phillips et al. 2006). This in turn affects the modelling process (which assumes no bias) during which the training data are selected uniformly at random from the biased set of sites that have been input into the model. This often results in the model being fitted closer to environmental characteristics of, for example, a biased herbarium collection than to a model of the true distribution of the species. Further, because the test and training data derived from a biased occurrence dataset will not be independent of each other, this can result in inflated model performance assessments in addition to misleading interpretation of the importance and influence of environmental parameters upon the species' distribution.

This spatial bias is known to be a greater problem for presence-only models than for presence-absence models (Zadrozny 2004) as it affects solely presence data and not background data. Hence all SDM algorithms which incorporate the modelling of presence occurrences in relation to a background (e.g., MaxEnt and GARP) will be influenced by this bias in sample selection (Phillips et al. 2009).

4.1.8 Possible solutions to spatial autocorrelation

Perhaps the most obvious way of addressing this problem of spatial bias would be the manipulation of the occurrence data in order to remove this bias by surveying in under-represented areas and down-weighting or discarding records in over-sampled areas. However, in large study areas it may not be possible to conduct new surveys due to impractical logistics and/or a lack of resources. Further, bias in sample selection may be an inherent part of the current, realised distribution of a species where the landscape has been modified by activities such as deforestation; such scenarios cannot be ‘fixed’ by collecting new data. Additionally, the scarcity of records makes the discarding of usually hard-won records unpalatable, while the down-weighting of records in oversampled areas may be obstructed by incomplete information regarding the distribution of the survey effort.

The only example found to improve upon this problem encountered in the literature was the work of Phillips et al. (2009). They proposed a technique for methods such as MaxEnt, BRTs, GAMs and GLMs, which helps to reduce the error introduced by sample bias. This involves using background data that reflects the same spatial bias as the occurrence data for building SMs in order to achieve the same environmental bias in both datasets. This is based on the premise that a model built on occurrence and background data which share a common a spatial bias will not be focused upon the sample selection bias but instead on any existing differentiation between the distribution of the occurrences and the background. Such a model would highlight the habitats of the species within the biased sample (and background) space instead of focusing on areas that are more heavily sampled within the entire study area.

Because detailed information about the spatial bias for the survey of the species being modelled may be unavailable and hence difficult to re-create, they propose constructing this biased-background based on sites that have been sampled from a broad set of similar species referred to as a 'target group' (Anderson et al. 2003; Ponder et al. 2001). For example, presence records from a natural history collection could be used to create a target group based on broad biological groups such as vascular plants, birds or lizards. However, they specify that these target groups should contain species that have been collected or observed using the same methods or equipment. Sites for all records from all of the species that comprise this group would then represent the full set information for the survey effort of the given species – which could be used as the background data. They argue that it is likely that the species within a target group that have been observed by similar methods will also share similar bias. Further, they conclude that an appropriate choice of background data that utilises a target-background approach can be effective in removing some of this bias by spreading model predictions into unsampled areas of the study area with similar conditions to the areas where the species is known to be present. However, this technique was not incorporated into these analyses due to the availability of a spatially unbiased global set of sample points (discussed further in Section 4.4.6.

4.1.9 Evaluation of models

All SMs have projection errors because these models are simplifications of reality. Sufficient attention should be given to the nature and degree of such errors and their costs; furthermore, caution should always be practiced when applying the mapped output of these models (Barry and Elith 2006; Liu et al. 2005). However, within the literature, evaluation of SMs has been focused on predictive performance rather than other criteria such as calibration (comparison of the average probability of species presence projected by an SM to the proportion of positives correctly projected), credibility (to the user community) and ecological realism (Franklin 2009).

Because of this attention to predictive ability, especially associated with the probability of a binary outcome (presence/absence), there has been extensive focus on threshold-independent measures of prediction accuracy – especially the Area Under the Curve (AUC) (Section 4.2.8.3). However, it is important to note that the AUC and other threshold-independent methods used to evaluate model accuracy need to be interpreted in a somewhat different manner for presence-only models. This is because their application would be to presence and pseudo-absence data rather than presence and absence data (see Section 4.2.8.3).

Evaluation of predictive performance can be severely limited due to a paucity of independent and adequate data available for evaluation (Lobo et al. 2004). Moreover, some of the most popular applications of SDM, such as projections of species distributions under future scenarios of climate/environmental change are, at best, challenging to evaluate (Elith and Graham 2009).

Finally, SDM has, over recent decades, been proven be a useful tool in the estimation of primary order relationships between species distribution and environmental factors. However, it is important to remember that these models are simply tools that can be used as estimates within a given application and should not be misinterpreted to be exact or near exact representations of the distribution of a given species.

4.1.10 SDM within the Caribbean SIDS

Caribbean SIDS contain many endemic and endangered species which are under intense pressure due to the increasing human populations within these small, fixed geographic spaces. SDM has been used as a tool for aiding conservation planning and management in many regions across the continents and sub-continents of the world (Franklin 2009). However, there is an acute paucity of SDM studies or applications within small geographic spaces, such as the Caribbean SIDS, and in particular, within terrestrial regions of these islands (see Section 5.1.13).

Trinidad is, in several ways, an ideal case study for exploring the potential of SDM within Caribbean SIDS.

Its topography ranges from flat alluvial plains which are situated between almost equidistant areas of high elevation along (i) the northern coast (Northern Range), (ii) central region (Central Range) and (iii) southern coast (Southern Range) of the island (see Section 4.2.3 for problems posed to SDM by areas of high elevations). These are interspersed with a variety of different habitats, some of which are characterised by sharp boundaries due to edaphic features. Apart from almost fifty percent of the island still being under forest cover, it has resources that can effectively facilitate an SDM study. These include a well inventoried and documented flora, a comprehensive, data-based collection of its flora (within the National Herbarium of Trinidad and Tobago) and access to up-to-date and reliable GIS and remote sensing data.

This chapter will explore the feasibility of using SDM within the Caribbean island of Trinidad. This is accomplished by (i) generating SMs of the potential present distributions of selected tree species (from Chapter 3); and (ii) discerning which environmental predictor variables are most relevant in defining the distribution of these species.

4.2 Methods

To model the potential present distributions of the list of tree species (Chapter 3) several steps were essential.

4.2.1 Data requirements for Species Distribution Modelling

The following input data were used to model the potential distribution of a given species during present climate conditions: (i) species distribution data (recorded presence locations) within the island – in terms of geographic co-ordinates (latitude/longitude) (Section 4.2.2); (ii) present climate data for Trinidad – expressed in the form of Bioclim variables (Section 4.2.3), (iii) soil drainage data (Section 4.2.4); (iv) Slope data (Section 4.2.5) and (v) Elevation data (Section 4.2.6).

4.2.2 Species distribution data

4.2.2.1 Sources of species location data

For each of the twenty-one species defined in Table 3.6 (Chapter 3), geographic co-ordinates of recorded presence locations were determined. The majority of these co-ordinates were extracted from the RBS inventory described in Chapter 3. However, a total of twelve co-ordinates were also extracted from the following databases: (i) voucher specimens of the National Herbarium of Trinidad and Tobago; and (ii) the National Forestry Division PSPs. These twelve co-ordinates were included in order to both augment species occurrence points for the rarer species as well as to honour the use of data provided by partner institutions that were involved in the RBS survey.

4.2.2.2 Spatial resolution of species location data

Once geographic co-ordinates for all species were compiled, a ‘global location dataset’ was created by merging the locations (geographic co-ordinates) of all 21 species and removing the replicates. The points of this global location dataset were mapped in geographic space using ArcGIS 9.3. By overlaying the WorldClim 1 km^2 grid (see 4.2.3.1) onto this global location dataset, location points were edited so that no two points were with a 1 km radius to each other (Figure 4.1). This spatial resolution threshold was administered in order to conform to the spatial resolution of the present climate data described in Section 4.2.3.3 below. The list of geographic co-ordinates for each species was re-defined to exclude any points which were not part of the global location dataset. This was done to ensure that the environmental conditions associated with the species occurrence data corresponded to the environmental conditions depicted by the climate data.

4.2.2.3 Testing of global dataset for spatial bias

The global location dataset was tested for spatial autocorrelation using the Average Nearest Neighbour Index test within ArcGIS 9.3 (Figure 4.2). This measures the degree of spatial dispersion in a distribution based on the distance between adjacent points (Ebdon 1985; Mitchell 2005). Based on the null hypothesis that the points within the distribution are randomly distributed, it is expressed as the ratio of the observed distance divided by the expected distance; where the expected distance is the mean distance between neighbouring points in a hypothetical distribution. Index values of less than 1 indicate a tendency towards clustering, while values greater than one suggests that the trend is towards dispersion or competition. The statistical significance of the result is measured by the z-score and the p-value – which indicate whether or not the null hypothesis should be rejected (Mitchell 2005).

4.2.3 Present climate data for Trinidad

4.2.3.1 WorldClim data

A fundamental premise of biogeography is that climate is a major factor that influences the natural distribution of species. Evidence for this comes both from palaeoecological studies (Clark 1998; Woodward 1987), as well as documentation of recent trends of changes in species range (Botkin et al. 2007; Pearson and Dawson 2003; Thuiller et al. 2006). Hence it is important to first look at the relationship between present climate conditions and the distribution of the species selected for this study before attempting to project the impacts of a future changed climate (Chapter 5).

The WorldClim website (Hijmans et al. 2005b) provides access to global climate data layers (climate grids) for past, present and future climate scenarios. Its present climate data is based on observed data (between 1950 and 2000) that were collected from a multitude of weather stations across the globe. These observed data were interpolated (thin-plate smoothing spline) to create climate grids of mean monthly climate data (monthly: total precipitation (P), maximum (Tmax), minimum (Tmin) and mean (Tmean) temperatures). These climate grids in addition to nineteen derived bioclimatic variables, are available on the WorldClim website at different resolutions which range from 30 arcseconds to 10 arcminutes (Hijmans et al. 2005b).

Monthly averages of the 30 arcseconds (1 km^2) resolution for P (mm), Tmax (°C x 10), Tmin (°C x 10) and Tmean (°C x 10) were downloaded from Tile 23 within the WorldClim present climate dataset in a generic grid format. These generic grids were imported into a DIVA GIS (Hijmans et al. 2005a) environment – within which the spatial extent of Trinidad was cropped then converted into American Standard Code for Information Interchange (ASCII) files (e.g., Figures 4.3 to 4.6).

Hijmans et al. (2005b) note that there are areas of uncertainty associated with the WorldClim data at a 30 arcsecond resolution. These are due the quality of the observed on data in conjunction with the interpolation method used. They explained that the quality of the interpolated climate surfaces would depend on (i) "the local climate variability", (ii) "quality and density of the observations" and (iii) "the degree to which the spline could be fitted". The distribution of the weather stations that were used to generate the climate surfaces were not random, with a dearth of these stations within (i) areas with low population densities and (ii) high elevations.

Indeed, little weather station data were available for many islands of the Caribbean which are characterised by high elevations and associated complex topography. Additionally, the WorldClim data omits locally important variables (which are especially within areas of complex topography) such as aspect. This leads to the inability of the 1 km^2 data to adequately capture all the variation at this resolution.

4.2.3.2 Bioclim(atic) variables

Bioclimatic (Bioclim) variables are biologically meaningful variables which have been derived from monthly precipitation (P) and temperature (Tmax, Tmin and Tmean) values over a given number of consecutive years (Hijmans et al. 2005b). They represent patterns which are useful in ecological niche modelling – such as annual means (e.g., annual precipitation, mean annual temperature); seasonality (e.g., annual range in precipitation and temperature) as well as limiting environmental factors (e.g., precipitation of the wet and dry quarters (three consecutive month period) and temperature of the coldest and warmest month).

4.2.3.3 Generation of Bioclim variables for present climate conditions

Because of the uncertainty associated with the WorldClim data for the Caribbean islands (particularly the low density of weather station data) (Section 4.2.3.1), the degree of variation across Trinidad captured by the Bioclim variables was unknown. In order to determine which of these variables were adequately captured for the island, the surfaces for all thirty-five Bioclim variables were calculated from the ASCII files of the cropped WorldClim's monthly P, Tmax, Tmin and Tmean data for Trinidad (Section 4.2.3.1). Table 4.1 below lists these Bioclim variables and the formulae used for their calculation (where applicable). The resolution of these Bioclim surfaces was the same as that of the P, Tmax, Tmin and Tmean data (1 km^2) that were initially downloaded from the WorldClim website.

A comparison of Bioclim data generated using the methods published by WorldClim and the original Bioclim surfaces that are published on the WorldClim website revealed further inconsistencies for some variables. The published WorldClim method states the values generated for all climate surfaces were rounded but this was not consistently done; values for BIO3, BIO8, BIO9, BIO10, BIO11 were chopped rather than rounded. To avoid this inconsistency, these analyses were based on newly generated Bioclim surfaces with consistently rounded values.

Inspection of these generated Bioclim grids revealed questionable patterns for several of the temperature-derived variables (BIO2, BIO3, BIO5, BIO6 and BIO7). Some of these suspect Bioclim grids showed concentric circles radiating from a single point situated along the North-Western peninsula of the island

(BIO2, BIO3 and BIO7), and were linked to two issues of concern. Firstly, the WorldClim database used temperature data for Tmax and Tmin from just one point within Trinidad. Secondly, due to many more records being available for Tmean than for Tmax and Tmin, all WorldClim Tmax and Tmin surfaces were not calculated directly from Tmax and Tmin data – but instead from the Tmean surface plus or minus half the temperature range (Hijmans et al. 2005b). Therefore, these Bioclim variables (BIO5, BIO6 and BIO7) were also omitted as possible predictor variables to be used for the SDM analyses (Table 4.1). Maps of the selected Bioclim variables are illustrated in Appendix C.

4.2.4 Soil Drainage data

Substrate characteristics are frequently used to model the distribution of plant species because of their nutrient and drainage characteristics (Franklin 2009). Soil drainage was included as a predictor variable for these analyses as it has been identified by local experts as an important factor that influences the distribution of vegetation across Trinidad (Baksh-Comeau, pers. comm. 2010).

A coarse soil drainage index – was developed to express the drainage capacity of all soils across Trinidad. The index was created from the ‘Summary of Soil Data’ tables taken from the Land Capability Survey (GOTT 1972c). Within these tables, each soil type within Trinidad is labelled with a unique numeric id that is representative of its soil drainage capacity.

These numeric ids were categorised into a ‘soil drainage index’ which ranged from 1 (free drainage in sandy soils) to 7 (slow drainage in heavy clays) (Table 4.2). This index was then mapped in ArcGIS 9.3 by adding a ‘soil drainage’ category to the attribute tables of the ‘Soils of Trinidad’ polygon shape file. This shape file, which was derived from the 1:25,000 Soil Map Series (GOTT 1972a), was provided by the DGLM at the St. Augustine Campus of the UWI. Within the attribute tables, the ‘soil drainage’ column was populated with soil drainage index values corresponding to the unique numeric soil id for each soil type polygon.

The resulting map of the soil drainage index was then converted from a polygon to an ASCII format, which was then input into MaxEnt for modelling.

4.2.5 Generation of Slope data

4.2.5.1 Contours to Triangulated Irregular Network (TIN)

Within the terrain of a study region, slope influences overland and subsurface flows of water, and hence, affects potential soil moisture and a range of other soil characteristics (e.g., moisture regime) which can impact upon the distribution of plant species. Additionally, it has been suggested that the inclusion of predictor variables from more than one hierarchical scale may help to yield more accurate SMs (Meyer and Thuiller 2006). Hence the incorporation of ‘meso-scale’ predictor variables such as slope (and soil drainage above) in conjunction with the ‘macro-scale’ climate parameters was selected for these analyses.

Slope data for the extent of Trinidad was generated within ArcGIS 9.3 from a 10 m contour shape file obtained from the DGLM at the St. Augustine Campus of the UWI. The contour shape file was derived from the 1:25,000 Topographic Map Series (GOTT 1972b) to a ±5 m accuracy.

The 3-D Analyst extension within ArcGIS 9.3 was used to build a TIN for the island based on this contour data. TINs are vector-based digital geographic data commonly used to represent the surface morphology of landscapes. TINs are constructed by the triangulation of vertices within a given surface – which are connected via a series of edges to create a network of triangles. The edges of this triangular network form contiguous, non-overlapping facets which are used to define and capture linear features within the landscape, such as ridges (Lillesand et al. 2008).

4.2.5.2 TIN to Slope

The slope function of the Surface Analysis Tool within the 3-D analyst was then used to create a slope grid from the TIN. This tool computes the maximum rate of change between each cell and its 8 neighbours. The value of each pixel within the output slope grid was expressed as degrees (Lillesand et al. 2008).

The Slope grid was then converted to an ASCII grid format (for input into MaxEnt) within ArcGIS 9.3.

4.2.6 Generation of Elevation Data

Land surface elevation has been known to affect several parameters which directly influence the distribution of plant species. These include temperature and radiation regimes, as well as precipitation via orographic lifting and geology (which affects the availability of mineral nutrients) (Franklin 1995). Elevation data was therefore included as another meso-scale predictor variable for these analyses.

The TIN created in Section 4.2.5.1 above was also used to create a Digital Elevation Model (DEM). A DEM is a regularly spaced raster grid, within which pixel values correspond to elevation points recorded from the terrain of the area.

Within ArcGIS 9.3 the TIN was converted to a raster format (DEM) by using the ‘TIN to raster’ function within the 3D Analyst Tools. This DEM was then converted to an ASCII grid format for input into MaxEnt.

4.2.7 Removal of highly correlated variables

Because MaxEnt does not detect multicollinearity, correlation tests on the predictor variables to be used for the modelling were performed to identify and remove highly correlated variables. This was necessary to ensure that the distribution models would not be over-parameterised with redundant climatic information.

A rectangular matrix was created within an SPSS Statistics environment (SPSS Inc. 2008) containing the values of each pixel (1 km^2) within the surfaces generated (Sections 4.2.3.3 to 4.2.6) for: (i) each of the thirty-five Bioclim variables, (ii) the soil drainage index, (iii) the slope and (iv) the elevation across Trinidad. As the values of these data varied in orders of magnitude, these data were square-root-transformed.

A two-tailed Pearson's correlation coefficient (significance level = 0.01) matrix was then generated from the transformed data. Treating all correlations which were $\geq \pm 0.85$ as highly correlated, the parameters were arranged in groups of highly correlated predictor variables (Rissler et al. 2006; Rissler and Apodaca 2007).

The correlation values between each parameter within a given group – and all parameters external to the group were then summed and the average 'external correlation' calculated. The parameter with the lowest average external correlation within a given group was taken as the representative predictor variable (from that group) to be used in the modelling.

This list of least externally correlated predictor variables to be used in the modelling consisted of BIO4 = Temperature Seasonality (standard deviation x 100), BIO13 = Precipitation of Wettest Month, BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO18 = Precipitation of Warmest Quarter, BIO19 =

Precipitation of Coldest Quarter, BIO9m4 = Mean Temperature of Driest Third (4 months) as well as elevation, slope, drainage (Table 4.1).

BIO12 = Annual Precipitation, BIO14 = Precipitation of Driest Month, BIO16 = Precipitation of Wettest Quarter and BIO17 = Precipitation of Driest Quarter were also added to the above list because of their ecological meaningfulness (Table 4.1).

4.2.8 Calibration of MaxEnt

4.2.8.1 MaxEnt

SDM analyses were conducted using the MaxEnt software (version 3.3.3e; `http://www.cs.princeton.edu/~schapire/maxent/`; Phillips et al. (2004, 2006)). Details of this model are included in Section 4.1.6.

4.2.8.2 Input into MaxEnt

The input requirements into MaxEnt consisted of (i) species location data in terms of geographic co-ordinates (latitude/longitude) and (ii) a directory of selected predictor variables.

The geographic co-ordinates for all 21 species were input into MaxEnt as a multi-species dataset csv file which consisted of species names, followed by the geographic coordinates (longitude, latitude).

The environmental directory consisted of layers within which the selected continuous environmental variables (Table 4.1) were expressed within ASCII raster grids (ESRI's .asc format). Categorical data (soil drainage) was also included within the environmental directory (indicated in the run window). It was necessary that all ASCII file headings were identical, in order to have the same geographic boundaries and cell size. It was also imperative that the same coordinate system (in this case WGS 84) be used for both the location data and the environmental layers.

4.2.8.3 Maximising AUC accuracy

This study used the AUC of the Receiver Operating Characteristic (ROC) of the test data (test-AUC) to evaluate the predictive accuracy of the species distribution models that were generated by MaxEnt (Peterson et al. 2008). The ROC curve expresses the relationship between the proportion of true positives (sensitivity) and the proportion of false negatives (1-specificity) across the range of possible probability thresholds (Pearce and Ferrier 2000), where sensitivity refers to the proportion of presences selected within a model, and specificity is a measure of correctly projected absences.

In essence, test-AUC values generated by presence-absence models are interpreted as the probability that a model will correctly distinguish between a presence and an absence record if each record is selected randomly from the set of presences and absences (Fielding and Bell 1997; Pearce and Ferrier 2000). However, as outlined by Phillips et al. (2006), for presence-only models, AUC values instead express the probability of the model classifying a presence more accurately than a random prediction (rather than the ability to distinguish presence from absence).

There are subjective guidelines within the literature as to what test-AUC values constitute 'good model performance'. For presence-absence models, test-AUC values range from 0.5 – where the model's predictive ability is no better than random to 1.0 for perfect predictive ability. Test-AUC values of >0.9 denote very good predictive ability while a test-AUC value between 0.7–0.9 is good and test-AUC values <0.7 are considered to be uninformative (Baldwin 2009). But according to Phillips et al. (2009), the AUC values for presence-only models are not as easy to interpret; while 0.5 still indicates that the model's ability to discriminate is no better than random, the maximum attainable test-AUC score is usually less than 1.0 (Phillips et al. 2006).

Additionally, it is useful to keep in mind that many authors (e.g., Franklin 2009; Peterson et al. 2008) have suggested that a true test of the model is whether it is useful for a given application. While subjective, it is worth considering that, for example, if the aim of the application is to predict the actual distribution of a species, a presence-absence algorithm is preferable; with a good model predicting both presences and absences with equal frequency. However, such models also consider the prediction of an unoccupied area to be environmentally suitable as a model error; hence these models may be assessed as poor despite them providing biologically sound output. In contrast, presence-only algorithms may be the preferred option if the aim of the study is to estimate the potential distribution of a species. Because of the lack of absence data, such models are categorised as useful (versus correct) if they are able to successfully predict the presence of species within most/all test localities. However, if such a model does successfully predict all test locations – but within the entire study area, it will be accurate but not useful – as its output will not be more insightful than a random prediction. As this study sought to generate the potential distributions of selected species, the use of the presence-only technique MaxEnt was considered relevant. The usefulness of these SMs were assessed by a combination of the AUC scores and expert opinion (Section 4.2.13).

4.2.8.4 MaxEnt settings used for developing the species distribution models

Once the location and environmental data were input into MaxEnt, a choice among six options (ranging from linear to hinge features) was required to determine how the predictor variables (*or features*) should be treated during model generation. Based on exploratory model runs of all six options on a subset of the species selected for these analyses, hinge features (which applies both linear and step functions to the predictor variables) consistently produced the strongest models – for the majority of species.

For each species, the final SM used for these analyses was hence based on the mean output of cross-validation model runs (see Section 4.2.9) which were generated using hinge features and an accompanying regularisation parameter of 0.5. According to the work of Phillips and Dudík (2008), the use of hinge features has been shown to increase significantly the average test-AUC values (of 226 species found within a variety of global environments), compared to models run without. Hinge features are thought to increase a model's performance by allowing for simpler and more succinct estimations of the 'real' species response to the environment, and can be used with both random and biased backgrounds. This feature is however based on the limitations that: (i) the number of presence records is at least 15; and (ii) the regularisation parameter is set to 0.5. As mentioned above, the regularisation parameter affects how closely-fitted the output should be to the presence records with values less than 1.0 resulting in a closer fit, while those greater than 1.0 result in a model output that is relatively more dispersed. Additional features selected included the 'Make pictures of the predictions' and the 'Do jackknife to measure variable importance' options. The former results in the inclusion of jpeg map images of the projected species distribution niche the within the output file and the latter results in the inclusion of jackknife test plots which indicate variable importance (Section 4.2.12).

4.2.8.5 MaxEnt Output

Details of the final SM (mean output from cross-validation runs) generated for each species were output within an html file. From this file, the (i) 'Omission and Predicted Area' curve and the (ii) ROC curve were both checked in order to verify that (i) test and training datasets remained independent of each other and (ii) the model's test-AUC performed better than random.

Additionally, MaxEnt's output included a probability distribution grid map within which each pixel illustrates the probability of finding the species of interest within that given area (Phillips and Dudík 2008). These maps were expressed in a logistic format, which according to Phillips and Dudík (2008), improves model calibration by expressing large differences in output values as corresponding large differences in suitability.

4.2.9 Choice of species for further analyses (Test AUC threshold)

Test-AUC (referred to as AUC) performance for the model of a given species was tested by conducting a series of cross-validation runs for each species. These runs varied in the number of cross-validation replicates – which ranged from 10 to 100 (Table 4.3). This was done to ensure that the accuracy of the AUC values used for each species' potential distribution was robust and maximised. From these results, graphs of 'Number of replicates' versus 'Average Test AUC' (Figure 4.7) and 'Number of replicates' versus 'Standard deviation of the individual AUC scores' (Figure 4.8) were used to discern the species which produced robust models (AUC > 0.7). From these graphs, 11 species (out of the initial 21) were used for further analyses (Table 4.3).

4.2.10 Correlation of distribution maps to model strength

Maps of the presence locations recorded for each of the original 21 species were plotted using ArcGIS 9.3 (Table 4.8). These were visually inspected to determine any correlation between distribution extent and model strength (AUC value).

4.2.11 MaxEnt – present output

4.2.11.1 MaxEnt output

MaxEnt's logistic output for the potential present distribution of each of the selected 11 species was expressed as a continuous grid map (e.g., Figure 4.9) – within which the value (ranging from 0 to 1) of each pixel represented the probability of presence within the given pixel (Section 4.2.8.5).

4.2.11.2 Threshold of Occurrence

Binary categorisation of the logistic output into 'present' or 'absent' was necessary for further analysis of the distribution patterns of the 11 species. To do this, a 'threshold of occurrence' needed to be decided upon. Several methods for determining such a threshold are available in the literature (Liu et al. 2005; Pearson et al. 2006; Pearson et al. 2004; Phillips et al. 2006) with the choice depending both on the type of data that is available and the objective of the research. For presence-only data, one approach involves the use of an arbitrary fixed probability level (e.g., 50%) derived from the model output (Robertson et al. 2001). However, this method is subjective and the chosen probability level may not be ecologically relevant to each species being modelled. Hence, other methods have been used in the literature that are based upon data that are used to calibrate the model (e.g., occurrence records) such as the 'lowest predicted value' of an observed occurrence record (Pearson et al. 2006) or 'fixed sensitivity' approach (Pearson et al. 2004).

As the objective of this study was to define the potential distribution niche of the selected tree species within Trinidad, the fixed sensitivity approach was employed. A threshold was selected that maximised the number of observed presences categorised as 'present', but imposed standardisation to accommodate: large differences in the number of observed localities among the eleven species being modelled. This is in complete contrast, for example, to a scenario where the objective of the study is to reintroduce an endangered species. Such an objective would instead require a much higher threshold in order to reduce the risk of choosing unsuitable areas and also to facilitate choosing sites with the highest suitability for the species survival (Pearce and Ferrier 2000).

The threshold of occurrence was set at a 5% omission level (analogous to setting a fixed sensitivity of 0.95). This was achieved by ordering the logistic probabilities of presence (from the MaxEnt output grid) of all observed localities for a given species in ascending order of magnitude and selecting the probability value representative of the first 5% of the locality points as the threshold. This threshold of occurrence value varied from species to species (Table 4.4) depending on the distribution of the logistic probability of presence across the number of observed localities.

4.2.11.3 Presence/absence maps

From the raw MaxEnt logistic output grid for each species (e.g., Figure 4.9), all pixels with probabilities less than the selected threshold of occurrence were given the value ‘0’ (absent) while all pixels with values more than or equal to the threshold of occurrence were labelled as ‘1’ (present). The resulting ASCII binary grid was then imported into ArcGIS 9.3 as a raster image of the potential distribution of the given species under present climate conditions (Figure 4.10).

The presence/absence raster image of the potential distribution of each of these eleven species was then clipped with the GIS forest cover polygons for 1969 and 2007 (Chapter 2) in order to discern the net loss of each species’ potential distribution due to limitations in forest cover during both these years (Table 4.5). The resulting proportions of each species’ potential distribution range being encompassed by forest cover during 1969 and 2007 were then used to calculate the percent change in the area of each species’ potential distribution from 1969 to 2007 (as a result of alterations in forest cover during this period).

4.2.12 Variables which contributed the most to models

4.2.12.1 Jackknife tests

For each species, the results of the Jackknife test, which was carried out while the model was being built by MaxEnt, were used to determine the variables which contributed the most to explaining the species’ potential distribution. Put simply, the jackknife test tracks the contribution of each predictor variable at each step in the building of the model and displays these results in three formats: (i) gain of the model with all predictor variables; (ii) gain of the model with just one predictor variable in isolation; and (iii) gain of the model exclusive of the predictor variable. These results of all three jackknife plots were compared and incorporated to determine the four variables which contributed most to the model's gain (Table 4.6). Collated results show the frequencies at which individual predictor variables contribute to the models generated within the set of 11 (Figure 4.11).

4.2.12.2 Climate space graphs

The validity of the top two contributing predictor variables (Table 4.6) responsible for defining the potential present climate niche of a given species was tested by the construction of a climate space graph (e.g., Figures 4.12 and 4.13).

Within Microsoft Excel, the relationship between the values of the two top predictor variables at each pixel within their ASCII grids was plotted. Additionally, the locations of all known presences of the species were also incorporated into the graph. The inclusion of all/most of the latter within the former was used as a method of understanding how widely distributed the species is (expected to be) in these environmental spaces (of the top two predictor variables) during both the present and future (SRES A2 scenario) climates.

4.2.13 Assessment of the presence/absence maps by 'expert knowledge'

An estimation of the field accuracy of the present distribution models, which were generated for these eleven species, was done by the assessment of the presence/absence maps described above (Section 4.2.11.3), by 'experts' in the field who were well acquainted with the distribution of each of these species.

Within ArcGIS 9.3 each of the presence/absence raster images above (Section

4.2.11.3) were clipped with the Dissolved Forest Cover polygon for 2007 (Section 2.5.2) using the Data Management Tools. The resulting images showed the potential distribution of a given species within the present forested areas of Trinidad, effectively excluding all other areas of forest within Trinidad which had been cleared for development.

Each of these modified presence/absence images were then overlain with the 'Major Roads' and 'Major Towns and Cities' shape files (acquired from the DGLM, UWI, St. Augustine) (Figures 4.14 to 4.24). However the known occurrence points of the species were excluded in order to prevent biased assessments.

These resulting maps of the potential distributions of the species within existing forested areas (together with major towns, cities and roads for reference) were then sent to four Foresters within the Forestry Division of Trinidad and Tobago each of whom have been involved in the island-wide management of these species for over 20 years. They were asked to use their knowledge of the species' distribution over the last 20 years to rate the accuracy of the maps (Table 4.7). The ranking scheme was simple and consisted of four categories:

- Poor = ≤50% accuracy
- Fair = >50% and <70% accuracy
- Accurate = ≥70% and <90% accuracy
- Very accurate = ≥90% accuracy

Additionally, the foresters were asked to indicate their level of confidence/skill regarding the distribution of each species. Again, this ranking scheme was simple, consisting of five categories: poor, fair, good, very good and excellent. The forester skill level for each species was also included in Table 4.7. Foresters were also asked to indicate, by drawing on a printed copy of the map, areas where they believed: (i) should be included as part of the species' distribution (under-estimated model) and (ii) areas which they believe should be excluded from the species' distribution (over-estimated model).

4.3 Results

4.3.1 Spatial Autocorrelation

The results of the Average Nearest Neighbour Index test (Figure 4.2) indicated that the global set of species locations used for these SDM analyses were near to random (very small degree of clustering which is more than likely due to random chance) with respect to their spatial arrangement. This increases confidence that the species distribution models created during the analyses would not be affected by inflated AUC scores.

4.3.2 Variation of AUC scores

Fluctuation of AUC values decreased as the number of cross-validation replicates increased (Table 4.3, Figures 4.7 and 4.8). Further, for each given species, AUC values and their standard deviations eventually stabilised beyond a certain number of cross-validation replicates. These points of stabilisation coincided in all cases with the number of occurrence points for that given species. A good example of this is the occurrence dataset of species *Mora excelsa* which consisted of 18 location sites. As seen in Figures 4.7 and 4.8, the AUC and its standard deviation became constant from twenty replicates onwards. This is due to the fact that for cross-validation replicates, the occurrence data of a species is divided into equal sized groups called replicate folds. As the replicates within a run progress, models are created by omitting each fold in turn (the omitted folds are used to test the model's performance). Hence, once the number of replicate folds is exhausted, the AUC value becomes constant. The biggest advantage of cross-validation is that it makes use of all of the data for validation, and hence is ideal for making better use of small datasets which are typical of occurrence datasets of many tropical plants (Feeley and Silman 2011).

4.3.3 Change in potential species distribution range resulting from alterations in forest cover between 1969 and 2007

Net losses in species' potential distributions for this group of eleven species as a result of restrictions in forest cover availability ranged between 29.8% and 18.4% during 1969, and 29% and 16.2% during 2007 (Table 4.5).

However, it was found that the alteration in forest cover across Trinidad from 1969 to 2007 yielded no large changes in the area of these species' potential distributions (that were supported by available habitat). During this period, species' potential distributions varied from an increase of 5.3% (*Tabernaemontana attenuata*) to a decrease of 5% (*Brosimum alicastrum*). Additionally, the majority of these species were shown to experience slight increases in their potential distribution ranges, with just three species (*Brosimum alicastrum*, *Carapa guianensis* and *Sterculia puriens* var. *glaberscens*) experiencing slight decreases, and only one species' *Virola surinamensis* distribution range remaining unchanged.

4.3.4 Correlation of AUC scores with the distribution range of a species

Test-AUC scores were lower for species with ubiquitous sets of occurrence points (Table 4.8), while species with restricted ranges consistently scored high test-AUC values. That is, MaxEnt creates an 'environmental envelope' for a given species based on the combination of predictor variable conditions occurring at all of its location points. It then identifies and highlights the probability of the species existing within other parts of the study area based on the combination of environmental conditions defined within the species' climate envelope. A ubiquitous species which exists within the majority of a given study area will have a climate envelope which leaves very little room for such interpolation. Hence such species will accrue lower AUC scores than range restricted species, the climate envelopes (well defined and narrow) of which have a lot more room within the study area for such interpolation.

4.3.5 Most frequent top contributing predictor variables

For each species model, confirmation of the importance and relevance of the top two contributing predictor variables (outlined in Table 4.6) was provided by the construction of climate space graphs (e.g., Figures 4.12 and 4.13). As seen in the examples, this confirmation lies in the fact that the entire set of location points for *Tabernaemontana attenuata* and *Brosimum alicastrum* were each encompassed within the 'climate space' of their top two contributing predictor variables. Similar patterns were observed for the remaining nine species.

It is noteworthy that these climate space graphs do not imply that the remaining predictor variables were redundant. Instead, these graphs were meant to simply illustrate how each species fit in the leading environmental variables – i.e., that within the environmental hyperspace, each species' occurrence was well encompassed within the envelope of the two variables – which were shown by the model breakdown to be major contributors to the final output (Table 4.6). This does not automatically imply that the species distribution is not also a consequence of the distribution of other environmental variables to an equal or lesser extent. Hence if the model breakdown of variable importance is robust (determined by the AUC value) – then it is likely that the envelope coverage of these occurrences would vary depending on how much the selected variables (used to create the envelope) contributed to the model output.

Finally, it was shown (Table 4.6 and Figure 4.11) that BIO17 (precipitation of driest quarter) was the predictor variable with the greatest frequency of occurrence (as one of the top four contributing predictors) among the eleven species models that were generated. This was followed by BIO13 (precipitation of wettest month) and a tie for the third most frequent place between BIO14 (precipitation of driest month) and Elevation.

4.3.6 Assessment of model accuracy by foresters

Assessment of the present distribution models by the foresters showed that the majority of the models appeared to represent an accuracy level greater than 50% (Table 4.7). Eight of the eleven species models were ranked as either a combination of Fair and Accurate or better, with just three models being ranked as only Fair. The best performing species (in decreasing order) were *Mora excelsa*, *Sterculia puriens* var. *glabrescens* and *Virola surinamensis* while the species which performed the poorest was *Ilex arimensis*. It was also clear from Table 4.7 that the SMs which were ranked as Excellent or Accurate were generally associated with species for which the foresters reported higher confidence levels compared to those SMs which were ranked as Fair or Poor. According to the foresters, species for which their confidence levels were rated Fair or Poor were all those which were not commonly observed within the island's forests.

Additionally, none of the foresters suggested that areas within any of the model outputs should be excluded, however, they did suggest that the distributions projected for for *Ilex arimensis*, *Tabernaemontana attenuata* and *Brosimum alicastrum* were under-estimated. Apart from being a subset of those for which the foresters reported low confidence levels, all three of these species distributions were assessed to have been under-estimated within the same region of the island – the area between the central and eastern portions of the Northern Range (e.g., Figure 4.22). According to the foresters, despite these being uncommon species, this area of underestimation was obvious to them because of historical observations which clearly place these species within this area.

4.4 Discussion

The above analyses suggest that SDM can be used to model the present potential distributions of tree species within the Caribbean SIDS. However, several factors need to be taken into consideration when designing these analyses:

4.4.1 Importance of forest cover change upon species' potential present distributions

It has been well established in the literature (e.g., Parmesan and Yohe 2003) that habitat availability, and not solely climate change, may be a major determinant of whether a species will be able to survive into the future. Indeed, the potential distributions of majority of species within this group would automatically be decreased by 20% or more because of limited habitat availability during both 1969 and 2007 (Table 4.5).

However, from 1969 to 2007, the effect of changes in habitat availability (forest cover) was minimal on the change in area of the potential distributions of species within this group. The (i) near congruence of the net losses among species' potential distributions during 1969 and 2007 and (ii) the small overall changes in the area of species' potential distributions as a result of alterations in forest cover from 1969 to 2007 (Table 4.5) can be attributed to two factors. Firstly, there was a less than 10,000 ha decrease in forest cover across Trinidad from 1969 to 2007 (Figure 2.3). Additionally, examination for Figures 2.4 and 2.5 revealed that the distribution patterns of forest cover across the island during both these years were strikingly similar in geographical space. Such unsubstantial changes of forest cover in both area and geographical space therefore led to minimal changes in the potential distributions of these species during this period of time. However, this also implies that if the rate of deforestation continues to increase (Section 2.5.3), continued and accelerated encroachment of forested areas by anthropogenic activity will lead to the potential distributions of these species decreasing with time.

4.4.2 Useful for conservation planning of range-restricted species

The above described pattern of range restricted species giving rise to models which have generally higher AUC scores than ubiquitous species conforms to the findings of other studies which have shown that model accuracy increases with species range restriction (Franklin et al. 2009; Segurado and Araújo 2004). This suggests that range-restricted species may be specialists that have more predictable patterns of occurrence relative to environmental gradients within the island. The application of SDM within the Caribbean SIDS is likely to be more useful for the rare and endemic species with restricted ranges rather than those that are widespread across these island. Any range-restricted island endemic or endangered species should give rise to species distribution models with satisfactory to high levels of predictive performance (AUC test scores >0.7). However, this is not expected to be the case for ubiquitous species, which are likely to produce models that have lower levels of predictive performance associated with them. Although less than ideal, this situation shows potential for SDM to be very useful in conservation management and planning endeavours which focus on the conservation of endemic and rare species populations that are highly vulnerable because of their restricted habitats within these islands. Additionally, the potential for the generation of more robust models for ubiquitous species may be enhanced by both the incorporation of data from, and increasing the size of, the study area to include other islands of the Caribbean and/or mainland South America.

Within the short and medium term (before a larger climate signal needs to be considered) SMs based on present climatic conditions may aid the above mentioned conservation management efforts within these islands in several ways. For example, SMs of invasive species, pests and disease carriers can be used to highlight areas within islands' PANs that are most susceptible and which require more careful management. Additionally, SMs of timber species can be used to inform and prioritise harvesting based on suitability of conditions, with the least suitable areas being harvested before those where environmental conditions presently promote maintained growth and the establishment of seed banks. Although, the latter may be considered a double-edged sword – as it also has the potential to reduce the genetic diversity of the species, hence reducing its capacity to adapt to climate change. In general however, such applications are particularly valuable given the small scale of the PAN within these islands.

4.4.3 Concurrence with results of ecological analyses

Because of the dominance of precipitation-based predictor variables used to develop these SMs, it cannot be assumed that it is more than co-incidental that the most frequent of the top contributing predictor variables outlined were related to precipitation. However, the top contributing variables being related to precipitation and elevation (Table 4.6 and Figure 4.11) also conforms to the results of the ecological analyses (Chapter 3) – which identified precipitation and elevation as major factors influencing the distribution and ecology of Trinidad's vegetation. This concordance of both sets of results from independent analyses may provide increased confidence that precipitation-based and elevation predictor variables are important factors influencing the distribution of the modelled species.

4.4.4 Expert evaluation of models

The prospect of using location points in conjunction with environmental data to estimate the species distribution has led to opportunities in conservation and planning impossible without SDM. However, this prospect comes with the caveat that inferences are only as good as the models themselves. This can be particularly problematic given the frequent inability to assess how well these models reflect ecological reality (Elith and Leathwick 2009). Expert assessment has been traditionally used in many ecological studies to derive or assess solutions when detailed empirical data are lacking or when uncertainty is large (Daehler et al. 2004; Grist et al. 2005; Petersen et al. 2003). Hence, expert opinion as a possible means of model evaluation was seen as a way of gauging the reality associated with this study; especially given that the availability of such knowledge is rare and has been infrequently mentioned in the SDM literature to date.

Despite this survey of expert opinion consisting of a very small sample size (four foresters), the results in Table 4.7 were still considered to be useful as this group of foresters was comprised of individuals who are experienced in identifying trees across the entire island. Additionally, each forester's experience does not represent just a snapshot of one point in time, but instead encompasses a period of more than twenty years of species observation per forester. This temporal perspective was seen as being particularly valuable in the assessment of these models.

The assessment of the eleven species distribution models by these foresters was interpreted to be positive as: (i) with the exception of one rating for one species, none of the models were ranked as poor (less than 50%); (ii) the majority of these species were assessed as being over 70% field accurate and (iii) none of the models were judged to be over-estimations of the foresters' perception of the species' distributions.

However, with respect to the under-estimation of the distribution of three species (Section 4.3.6), the (same) area which was assessed as being under-estimated within all three SMs also happens to be the only area within the Northern Range that was sparsely represented within the global set of species location points used for these analyses (Figure 4.1). Indeed, only one RBS site was located within this area (between the central and eastern portions of the Northern Range). Given the complex topography of this region, it is likely that high variation in the distribution of parameters such as elevation (a top contributing predictor variable for all three species) may have resulted in little or no correlation from lower, less complex terrain to this region. This highlights the high uncertainty associated with developing SMs within regions of complex terrain without relatively high resolution, evenly distributed occurrence data.

Both under-estimation and over-estimation are equally important in analyses such as this – which seek to assess the potential of PANs within the Caribbean SIDS to support species survival into the future. Indeed both the assessed absence of over-estimation, as well as indications of under-estimation in three out of the eleven models, was instrumental in indicating persistent strengths and potential weaknesses of these models. That the models were effective in excluding localities that the species were not known to exist (absence of false-positive errors) is particularly valuable as it does not facilitate the planning of conservation efforts in areas which are not suitable for species survival. This is particularly important within small islands which are typically characterised by extremely limited space available for the establishment of PAs. However, a few of these models were not as good in representing the entire realised distributions of a few species; such false-negative errors could lead to application errors such as the design of PAs that are too small or which do not adequately encompass areas that are necessary for the species survival. However, generally speaking, these results indicate that cautious interpretation of SDM can be a very instrumental tool in the prediction of the potential distributions of range restricted species with the Caribbean SIDS. Further, the supplementation of SDM results with independent forms of verification such as expert assessment and/or independent occurrence databases (e.g., herbarium) also provides a means of refining the area within which the distribution of the species has been defined.

4.4.5 Need for more detailed climate data within the Caribbean

It should be acknowledged that seven out of nine of the ‘least externally correlated predictor variables’ used for these analyses (Section 4.2.7) were precipitation-based variables. This is may be a result of the exclusion of all Bioclim variables derived from Tmax and Tmin data due to suspect patterns – which is elaborated upon in Section 4.2.3.3. Indeed, the perceived usefulness of these SMs by the foresters is remarkable, especially in light of the fact that the climate data (from the WorldClim website) used for these analyses were not perceived to be very good representations of climate across the island. As explained above, the WorldClim climate grids are interpolations based on climate data collected from weather stations across the globe. However, the number of data points on the island of Trinidad was limited to just a few points across the island. The paucity of data collection points across not just Trinidad, but most of the Caribbean region implies high observational uncertainty – which could limit the accuracy of the climate layers required for SDM analyses within most of the Caribbean SIDS (Tabor and Williams 2010).

This has resulted in a paucity of sound temperature-based predictor variables that can currently be used for SDM analyses within most of this region. This certainly introduced a bias regarding the results of this SDM exercise by increasing the likelihood of a precipitation-based variable featuring as a top predictor within a given SM. According to some authors such as Graham et al. (2009) and Franklin (2009), there is to date, no simple guideline with respect to how many predictor variables should be used in a modelling exercise. However, these variables, apart from being direct, should have a hypothesised direct mechanistic influence upon a species' distribution – as a result of their influence on bioenergetics and hence population parameters (Guisan and Thuiller 2005). Local experts believe that precipitation meets both these requirements, however, there is no literature or expert opinion of how temperature influences the distribution of these species (Baksh-Comeau, pers. comm. 2010). Indeed, the inclusion of precipitation-based ecologically meaningful predictor variables was done based upon the strong suggestion of local experts. Given the lack of knowledge on the effect of temperature upon the distribution of these species, it is unsurprising that no temperature-based predictor variables were suggested as ecologically meaningful. Indeed it may not be co-incidental that there is both a paucity of sound temperature-based climate data as well as literature or expert opinion on the mechanistic impact of temperature upon the flora within these islands. Perhaps the latter is symptomatic of the former.

Climate scientists across the region echo the sentiment that there is a need for more accurate climate data that detail regional variation of climate and complex topography across the Caribbean (Charlery and Nurse 2010). They cite the lack of historical climate observations as one of the main contributors to this paucity. The solution to this problem may lie both in (i) the mining of such data within the region and (ii) developing a means of generating sound temperature-based climate surfaces from the scarce, poorly distributed and usually intermittent temperature data that have been collected within these islands.

Several sources of historical precipitation and temperature data, dating back to the early 1800s were stumbled across while researching the early ecological studies done in Trinidad (Chapter 3). As many of these islands were centres of the nineteenth century cocoa, coffee and sugar-cane industries, it seems plausible that similar data may also have been recorded at several stations across many of these islands. Perhaps the mining and incorporation of these and similar data could be used to contribute to the development of more detailed climate data in the future. Additionally, a search for more recent data held by local oil refineries, the Water and Sewage Authority and botanical gardens may help to further this cause. Furthermore, the dearth of climate data highlights the need for the establishment of strategically located weather stations across the island(s), if climate change is to be incorporated into future policy and planning within the region.

Finally, apart from the mining and pooling together of historical climate data, progress may be enhanced by the conglomeration of research efforts and expertise within the Caribbean region as a whole. Until such progress has been made, SDM efforts such as this study need to acknowledge and incorporate into interpretation – the biased usage of precipitation-based predictor variables. Additionally, the incorporation of non-climate predictor variables such as elevation may serve as indirect indicators of temperature functions.

4.4.6 Biased-background approach is not suited for SDM within the Caribbean SIDS

The stratified random sampling design that was used for development of the RBS sites (Chapter 3) contributed a great deal to the low degree of spatial bias of the global location dataset used for the SDM analyses in this chapter. This is because the distribution of the RBS occurrences (which constituted the majority of the global location dataset used in this chapter) was itself random. Hence the incorporation of just twelve occurrence points from the Herbarium and PSP datasets did not greatly alter the random nature of these points. This was ideal for the SDM analyses that occurred within this chapter since the proposed solution of modelling occurrence data against a biased background when these data are spatially auto-correlated is difficult at best within study areas as small as the Caribbean SIDS.

The biased background approach is, at its present stage of development and testing, not very suitable for small islands. There are several reasons for this, foremost of which is the fact that using a target-group background would involve selecting only of subsets of the geographic, and hence environmental space within these small islands for construction of the SMs. This could lead to predictions that are misleading, especially given the fact that many Caribbean SIDS contain a large variety of environments which are sometimes marked by sharp boundaries due to complex geographic, edaphic and topographic terrain that are accompanied by steep climate gradients (Helmer et al. 2002).

Additionally, a key assumption of the target-group approach is that data for all the species comprising the group have been collected using the same methods and equipment, as this concept aims to represent an approximation of the sampling effort for each taxa within the group. This is impractical within many of the Caribbean SIDS as despite there being a great deal of on-going collection and description of the flora in many islands by several different institutions, there is little guarantee of concordance of survey techniques for taxa that would naturally comprise a target group. A good example of this is the data used for modelling analyses of this chapter – all three sources (RBS, herbarium and PSP data) were collected using very different methods.

Furthermore, as models are built on random backgrounds, the effect and success of a target-group background has been shown to vary depending on the prevalence of the selected species within the study area, with the greatest performance being associated with species that have strong biases in occurrence data. However, because target-groups effectively decrease the size of the area being modelled (compared to the original random background of the island), this increases the similarity between the spatial distributions of the training and test sites, automatically decreasing the prediction strength of the model (compared to a model generated from a random background). There is still no clear indication in the literature as to how to interpret these lower AUC scores with respect to confidence in gauging the model's predictive ability.

Finally, Phillips et al. (2009) noted that the target-group approach was developed with the intention of generating models within fixed geographic areas and under fixed climatic conditions. They point out that these results do not necessarily transfer when the models are projected to future climate conditions (Thomas et al. 2004). Since then a study by Elith et al. (2011) has used the biased background approach in two case studies which involved projection onto future climates, however, they were unable to derive any conclusive evidence that such projections can be done with the same or more confidence than models generated from a random background. The biased-background approach therefore decreases the value of using SDM within the Caribbean SIDS by potentially limiting it to the modelling of the potential distribution of a species during the present climate. It has not been shown to produce confident projection of these results onto future climate scenarios, which is vital for the conservation planning and management of the endemic species of the Caribbean SIDS into a warmer, drier future.

4.4.7 Prospect of SDM at a regional scale within the Caribbean

One of the main drivers responsible for the surge in popularity of presence-only species distribution models is that it enables the use of large amounts of herbarium and museum data in the creation of models which portray the potential distributions of the many species within these collections. The vast potential of herbaria and museum occurrence data should certainly not be ignored as scientists scramble to develop strategies to conserve what is left of the world's biodiversity. The flora of many islands within the Caribbean have been, and still are being surveyed and documented by several institutions across the world such as the Natural History Museum, London, the New York Botanical Gardens and the Missouri Botanical gardens to name a few. There is no doubt that these data are valuable resources which will be of great use to Caribbean SIDS wishing to develop pro-active conservation planning for their endemic and endangered species.

However, as explained above, the use of herbarium data alone to develop models of species distributions can be misleading and has potential to result in erroneous conservation planning strategies when applied. This study suggests a possible solution for this dilemma: a strategic combination of stratified random RBS surveys designed to fill the gaps within existing herbarium data in order to create spatially unbiased species occurrence datasets that are well suited for SDM. While this alternate approach is certainly not a 'quick-fix' solution, the small size of these islands makes such stratified random RBS sampling logistically possible and hence presents a unique opportunity for SDM within this region that is not possible within similar large-scale studies based in continental regions. This approach also brings with it the potential for several added advantages in the long term.

Apart from these RBS surveys serving to add to or develop much needed baseline data within many of these islands, they would also provide the opportunity to detect and eliminate critical sources of error such as incorrect geographic co-ordinates which are common within online databases. Further, there is great potential in the establishment of a network of co-operation among islands of the Caribbean wishing to conduct RBS surveys – by forging agreements with the established herbaria in the region.

Finally, many of these species do not exist on one island alone. If such studies are conducted across several islands within the region, this presents the opportunity to develop and document a 'large-scale' perspective of the distribution of a given species across the entire Caribbean basin instead of within an individual island. Such an endeavour would be invaluable in promoting regional co-operation with respect to conservation planning and management across the entire basin rather than just within individual islands.

4.5 Tables

Bioclim variable	**Description**	**Selection Status for SDM analyses (X = not selected) (√ = selected)**
BIO1	Annual Mean Temperature	X Multicollinearity
BIO2	Mean Diurnal Range (Mean of monthly [max temp - min temp])	X Suspect pattern
BIO3	Isothermality (BIO2/BIO7) (* 100)	X Suspect pattern
BIO4	Temperature Seasonality (standard deviation *100)	√ Least correlated predictor
BIO5	Maximum Temperature of Warmest Month	X Unreliable Tmax data
BIO6	Minimum Temperature of Coldest Month	X Unreliable Tmin data
BIO7	Temperature Annual Range (BIO5-BIO6)	X Unreliable Tmax and Tmin data
BIO8	Mean Temperature of Wettest Quarter	X Multicollinearity
BIO8m2	Mean Temperature of Wettest consecutive 2 month period	X Multicollinearity
BIO8m4	Mean Temperature of Wettest consecutive 4 month period	X Multicollinearity
BIO9	Mean Temperature of Driest Quarter	X Multicollinearity
BIO9m2	Mean Temperature of Driest consecutive 2 month period	X Multicollinearity
BIO9m4	Mean Temperature of Driest consecutive 4 month period	√ Least correlated predictor
BIO10	Mean Temperature of Warmest Quarter	X Multicollinearity
BIO10m2	Mean Temperature of Warmest consecutive 2 month period	X Multicollinearity
BIO10m4	Mean Temperature of Warmest consecutive 4 month period	X Multicollinearity
BIO11	Mean Temperature of Coldest Quarter	X Multicollinearity
BIO11m2	Mean Temperature of Coldest consecutive 2 month period	X Multicollinearity

BIO11m4	Mean Temperature of Coldest consecutive 4 month period	X Multicollinearity
BIO12	Annual Precipitation	√ Ecologically meaningful
BIO13	Precipitation of Wettest Month	√ Least correlated predictor
BIO14	Precipitation of Driest Month	√ Ecologically meaningful
BIO15	Precipitation Seasonality (Standard deviation/mean * 100)	√ Least correlated predictor
BIO16	Precipitation of Wettest Quarter	√ Ecologically meaningful
BIO16m2	Precipitation of Wettest consecutive 2 month period	X Multicollinearity
BIO16m4	Precipitation of Wettest consecutive 4 month period	X Multicollinearity
BIO17	Precipitation of Driest Quarter	√ Ecologically meaningful
BIO17m2	Precipitation of Driest consecutive 2 month period	X Multicollinearity
BIO17m4	Precipitation of Driest consecutive 4 month period	X Multicollinearity
BIO18	Precipitation of Warmest Quarter	√ Least correlated predictor
BIO18m2	Precipitation of Warmest consecutive 2 month period	X Multicollinearity
BIO18m4	Precipitation of Warmest consecutive 4 month period	X Multicollinearity
BIO19	Precipitation of Coldest Quarter	√ Least correlated predictor
BIO19m2	Precipitation of Coldest consecutive 2 month period	X Multicollinearity
BIO19m4	Precipitation of Coldest consecutive 4 month period	X Multicollinearity
Elevation	Elevation surface over the island of Trinidad	√ Least correlated predictor
Slope	Slope surface over the island of Trinidad	√ Least correlated predictor

Soil Drainage	Soil drainage index for soils within the island of Trinidad	√ Least correlated predictor

Table 4.1: List of predictor variables considered for the Species Distribution Modelling. Where green highlighting denotes least correlated predictor variables and yellow highlighting denotes ecologically meaningful predictor variables.

Major soil categories	**Soil Drainage description**	**Soil Drainage Index**
Sands	Free to excessive	1
	Free	2
	Free to moderate	3
↓	Free in topsoil, moderate in subsoil	4
	Free in topsoil, slow in subsoil	4
	Free in topsoil, very slow in subsoil	4
	Moderate	5
Heavy clays	Slow to moderate	6
	Slow	7

Table 4.2: Soil Drainage Index.

	Number of cross-validation replicates							
Species	**10**	**15**	**20**	**25**	**30**	**40**	**50**	**100**
Andira inermis	0.6488	0.6499	0.6433	0.6396	0.6461	0.6522	0.638	0.6454
Brosimum alicastrum	0.711	0.704	0.7084	0.7013	0.7143	0.7092	0.7133	0.7133
Brownea coccinea ssp. *capitella*	0.646	0.6471	0.638	0.6374	0.6485	0.6291	0.6408	0.6408
Calophyllum lucidum	0.8381	0.827	0.8382	0.8403	0.8388	0.836	0.836	0.836
Carapa guianensis	0.7451	0.7444	0.744	0.7484	0.747	0.7518	0.7505	0.7534
Coccoloba latifolia	0.5069	0.4946	0.4917	0.5046	0.4996	0.4925	0.4975	0.498
Coursetia ferruginea	0.6572	0.6766	0.6591	0.6686	0.6686	0.6686	0.6686	0.6686
Eschweilera subglandulosa	0.6381	0.6388	0.6374	0.6426	0.6352	0.6422	0.6397	0.639
Eugenia confusa	0.8755	0.8731	0.8674	0.8799	0.8739	0.8739	0.8739	0.8739
Ilex arimensis	0.7345	0.741	0.7573	0.7516	0.7436	0.7424	0.7424	0.7424
Manilkara bidentata ssp. *bidentata*	0.6431	0.6394	0.6486	0.6527	0.6536	0.6463	0.6528	0.6528
Mora excelsa	0.7831	0.7665	0.7431	0.7431	0.7431	0.7431	0.7431	0.7431
Spondias mombin	0.6182	0.6077	0.6102	0.6122	0.6072	0.6049	0.5991	0.5989
Sterculia pruriens var.*glabrescens*	0.7055	0.711	0.7115	0.7126	0.7073	0.7078	0.7093	0.7118
Swartzia pinnata	0.6883	0.6578	0.6842	0.6726	0.6722	0.6804	0.6747	0.6747
Tabebuia stenocalyx	0.8203	0.8267	0.832	0.8299	0.8354	0.8439	0.8245	0.8245
Tabernaemontana attenuata	0.857	0.855	0.8538	0.8496	0.857	0.8471	0.8471	0.8471
Terminalia amazonia	0.6891	0.6932	0.6942	0.6915	0.6921	0.6841	0.6887	0.6996
Tovomita eggersii	0.8053	0.8042	0.8	0.8097	0.8149	0.8002	0.8002	0.8002
Virola surinamensis	0.7274	0.7223	0.7303	0.7234	0.726	0.7261	0.7259	0.7299
Zanthoxylum martinicense	0.7093	0.712	0.6918	0.6931	0.6899	0.6968	0.6968	0.6968

Table 4.3: Variation of species models strength (Test AUC) with number of cross-validation replicates. Where species highlighted in green are those with robust models that were chosen for further analyses.

Species	**5% omission probability value**	**# POINTS**
Brosimum alicastrum	0.2688	55
Calophyllum lucidum	0.3137	39
Carapa guianensis	0.1876	101
Eugenia confusa	0.1805	33
Ilex arimensis	0.2616	35
Mora excelsa	0.1733	18
Sterculia puriens var. *glabrescens*	0.214	141
Tabebuia stenocalyx	0.1519	44
Tabernaemontana attenuata	0.3121	35
Tovomita eggersii	0.0806	41
Virola surinamensis	0.2067	98

Table 4.4: 5% omission threshold values used to create species presence/absence maps.

Species	**Net loss of potential present species range due to the limitations of forest cover during 1969 (%)**	**Net loss of potential present species range due to the limitations forest cover during 2007 (%)**	**Change in area of potential present species range resulting from alterations in forest cover between 1969 and 2007 (%)**
Brosimum alicastrum	24	**29**	-5
Calophyllum lucidum	22.5	20	2.5
Carapa guianensis	20.3	21	-0.7
Eugenia confusa	**18.4**	**16.2**	2.2
Ilex arimensis	**29.8**	27.2	2.6
Mora excelsa	21.5	18.7	2.8
Sterculia puriens var. *glabrescens*	22	22.4	-0.4
Tabebuia stenocalyx	21.5	19.5	2
Tabernaemontana attenuata	22.5	17.2	5.3
Tovomita eggersii	28	25.1	2.9
Virola surinamensis	22.5	22.5	0

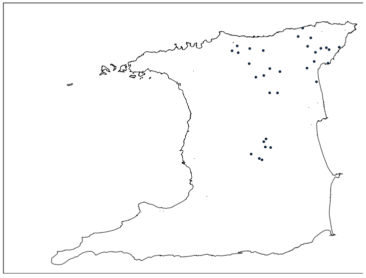
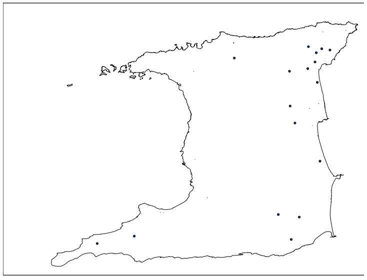
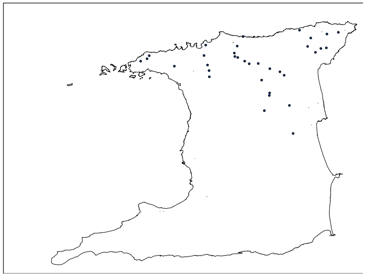
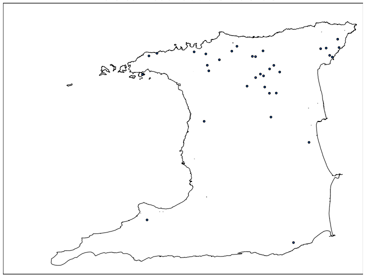
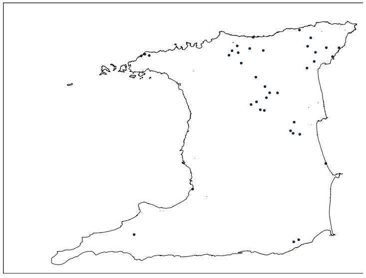
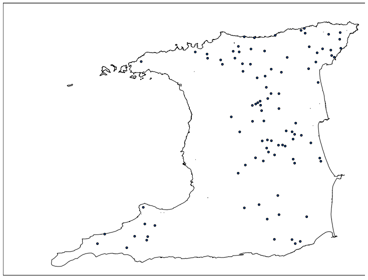
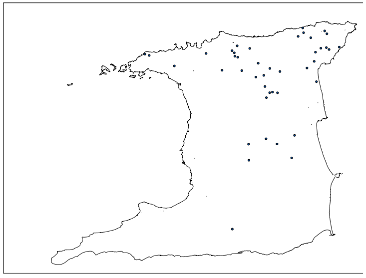
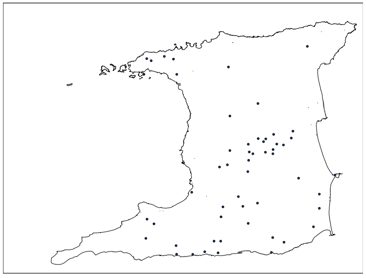
Table 4.5: Change in area of potential present species distribution range resulting from alterations in forest cover between 1669 and 2007.

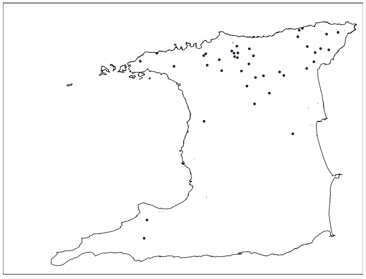
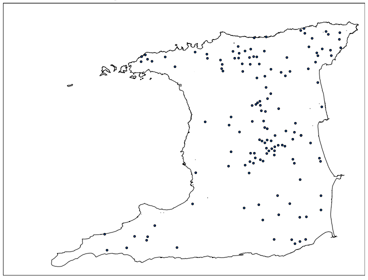
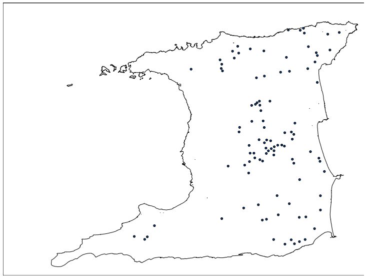
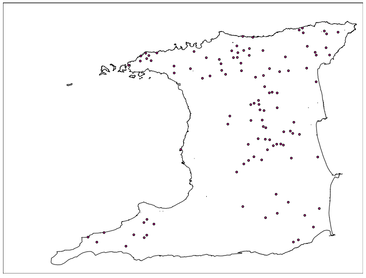
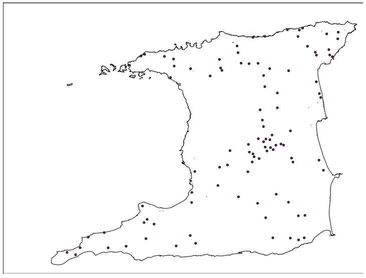
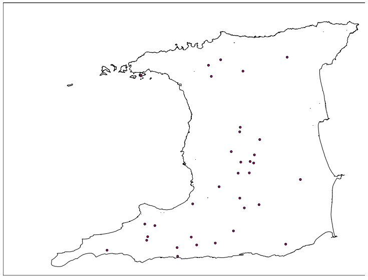
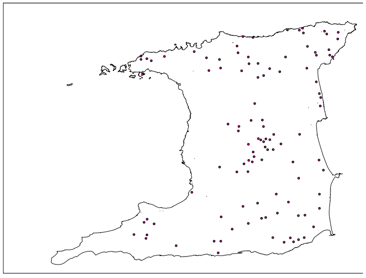
	Contributing importance of parameters to present climate models			
Species	**1st**	**2nd**	**3rd**	**4th**
Brosimum alicastrum	Elevation	BIO17	BIO14	BIO15
Calophyllum lucidum	BIO17	BIO13	BIO14	Elevation
Carapa guianensis	BIO17	BIO12	BIO14	BIO13
Eugenia confusa	BIO17	BIO12	BIO13	BIO14
Ilex arimensis	Slope	Drainage	Elevation	BIO9m4
Mora excelsa	BIO17	BIO15	BIO14	BIO12
Sterculia puriens var. *glabrescens*	BIO13	BIO17	Elevation	BIO12
Tabebuia stenocalyx	BIO13	BIO16	Drainage	BIO17
Tabernaemontana attenuata	Drainage	Elevation	BIO13	BIO17
Tovomita eggersii	Slope	Elevation	BIO13	BIO16
Virola surinamensis	BIO13	BIO17	BIO12	BIO14

Table 4.6: Contributing importance of Bioclim and topographical parameters to present climate models of species.

	Accuracy ranking of Species Distribution Model Map				
Species	**Poor**	**Fair**	**Accurate**	**Excellent**	**Comments**
Brosimum alicastrum		$\surd^{3}$ $\surd^{3}$ $\surd^{5}$ $\surd^{4}$			Under-prediction
Calophyllum lucidum		$\surd^{4}$ $\surd^{2}$	$\surd^{3}$ $\surd^{2}$		
Carapa guianensis			$\surd^{2}$ $\surd^{2}$ $\surd^{2}$ $\surd^{1}$		
Eugenia confusa		$\surd^{5}$ $\surd^{5}$	$\surd^{5}$ $\surd^{4}$		
Ilex arimensis	$\surd^{5}$	$\surd^{4}$ $\surd^{4}$ $\surd^{4}$			Under-prediction
Mora excelsa			$\surd^{2}$ $\surd^{1}$ $\surd^{2}$	$\surd^{1}$	
Sterculia puriens var.*glabrescens*			$\surd^{2}$ $\surd^{1}$ $\surd^{2}$	$\surd^{2}$	
Tabebuia stenocalyx		$\surd^{3}$	$\surd^{2}$ $\surd^{2}$ $\surd^{1}$		
Tabernaemontana attenuata		$\surd^{4}$ $\surd^{5}$ $\surd^{4}$ $\surd^{4}$			Under-prediction
Tovomita eggersii		$\surd^{4}$ $\surd^{3}$	$\surd^{4}$ $\surd^{3}$		
Virola surinamensis			$\surd^{3}$ $\surd^{3}$ $\surd^{2}$	$\surd^{2}$	

Table 4.7: Accuracy assessment of species distribution models (present climatic conditions) by Foresters of the National Forestry Division of Trinidad and Tobago. Where 1 to 5 represent the skill/confidence of the forester with respect to a given species: 1 = Excellent; 2 = Very Good; 3 = Good; 4 = Fair and 5 = Poor.

Distribution of species with Test AUC scores ≥0.7			
Species	**Test AUC values**	**Species**	**Test AUC values**
Eugenia confusa 	0.8739	*Mora excelsa* 	0.7431
Tabernaemontana attenuata 	0.8471	*Ilex arimensis* 	0.7424
Calophyllum lucidum 	0.836	*Virola surinamensis* 	0.7299
Tabebuia stenocalyx 	0.8245	*Brosimum alicastrum* 	0.7133

Tovomita eggersii 	0.8002	*Sterculia pruriens* var. *glabrescens* 	0.7118
Carapa guianensis 	0.7534		
Distribution of species with Test AUC scores <0.7			
Terminalia Amazonia 	0.6996	*Andira inermis* 	0.6454
Zanthoxylum martinicense 	0.6968	*Brownea coccinea* ssp. *capitella* 	0.6408

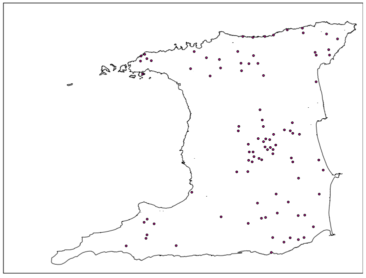
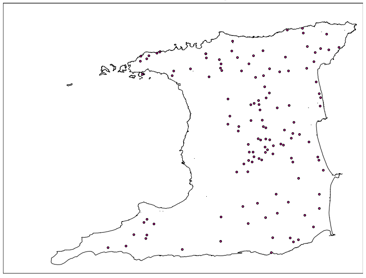
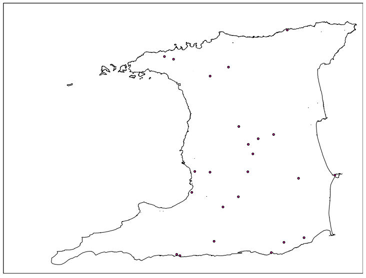
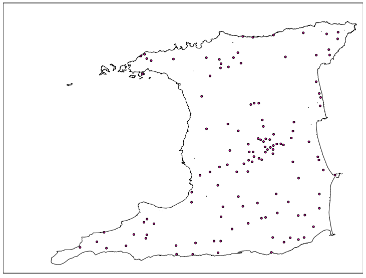
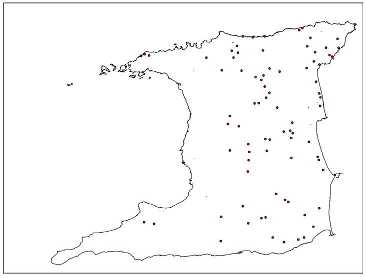
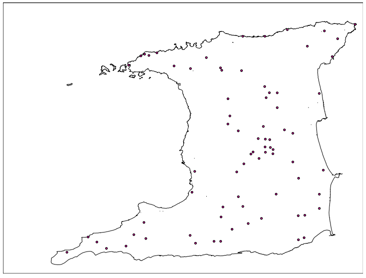
Swartzia pinnata 	0.6747	*Eschweilera subglandulosa* 	0.639
Coursetia ferruginea 	0.6686	*Spondias mombin* 	0.5989
Manilkara bidentata ssp. *bidentata* 	0.6528	*Coccoloba latifolia* 	0.498

Table 4.8: Variation of model strength with species distribution within Trinidad.

4.6 Figures

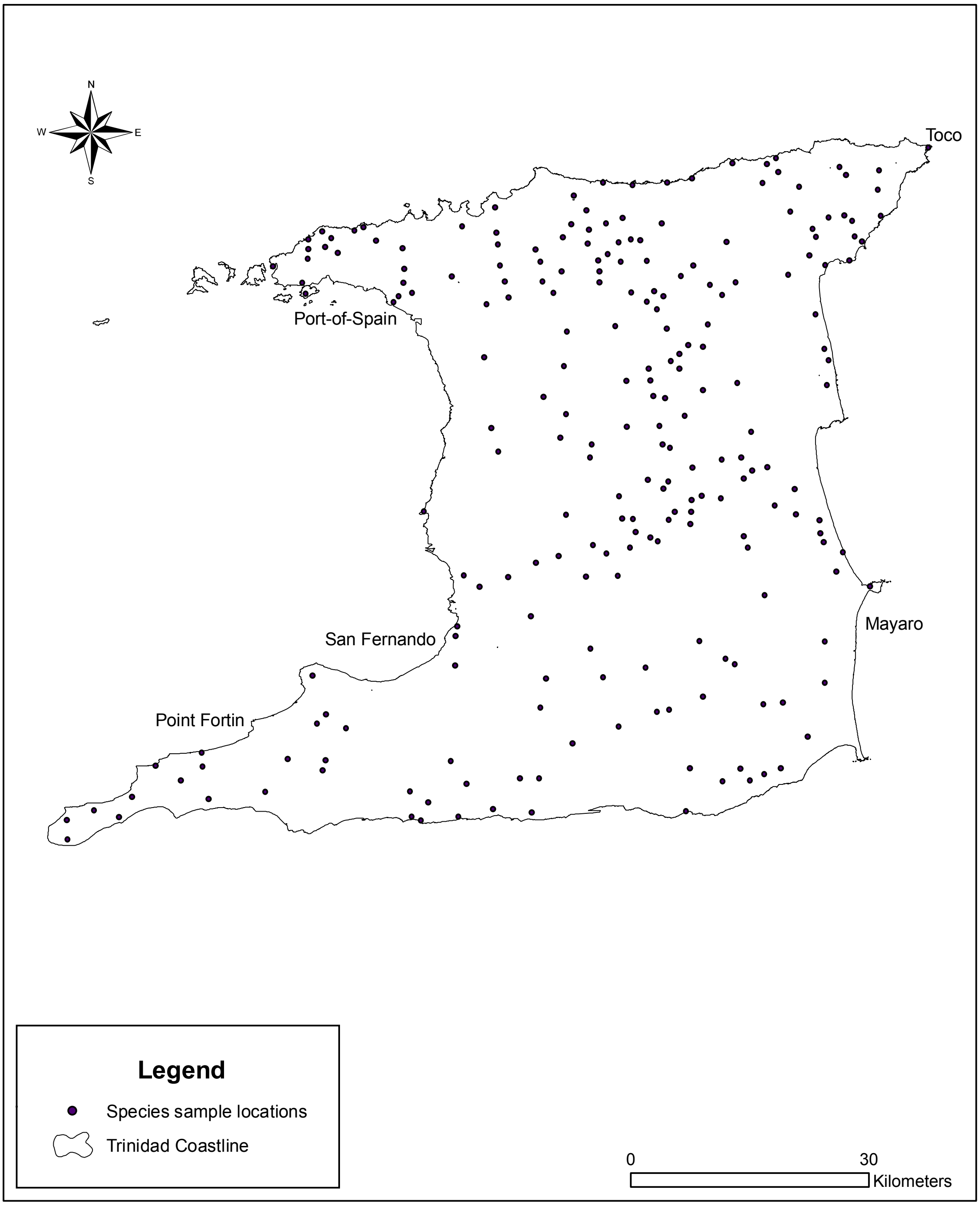
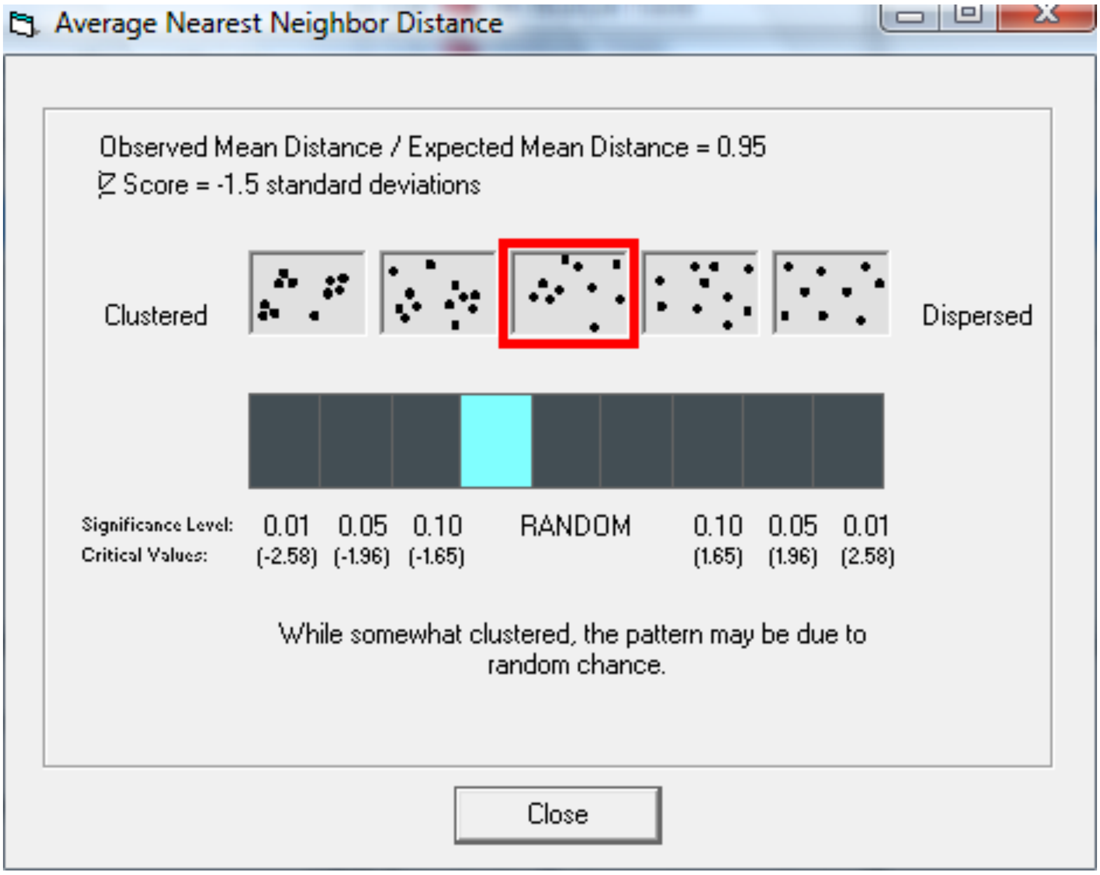


Figure 4.1: Global set of species location points used for Species Distribution Modelling.



Observed Mean Distance / Expected Mean Distance = 0.95
Z Score = -1.5 standard deviations

While somewhat clustered, the pattern may be due to random chance.

```
Observed Mean Distance:   2342.550572
Expected Mean Distance:   2429.293990
Nearest Neighbour Ratio:  0.950990
Z Score:                  -1.500162
p-value:                  0.133573
```

Z score (standard deviation)	p-value (probability)	Confidence interval
< -1.65 OR > 1.65	< 0.10	90.00%
< -1.96 OR > 1.96	< 0.05	95.00%
< -2.58 OR > 2.58	< 0.01	99.00%

Figure 4.2: Average Nearest Neighbour Summary for global set of species locations used for the species distribution modelling.
Based on the values in the above table, the z and p values obtained from the Average Nearest Neighbour Index test of the global set of species locations used for the species distribution modelling indicate that while there was a small degree of clustering, this pattern is more than likely due to random chance.

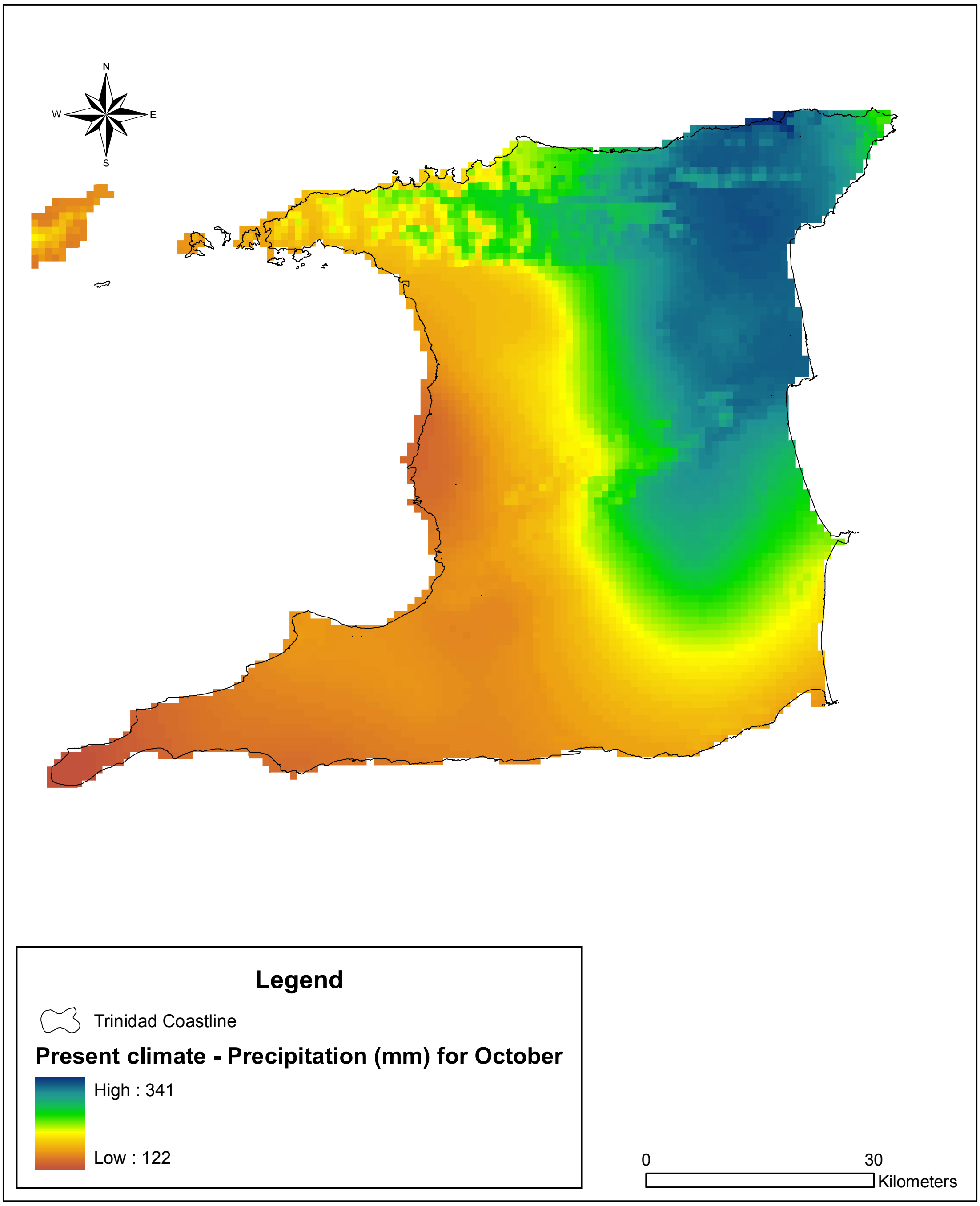


Figure 4.3: Precipitation during October for the present climate (WorldClim) (at a 1 km^2 resolution).

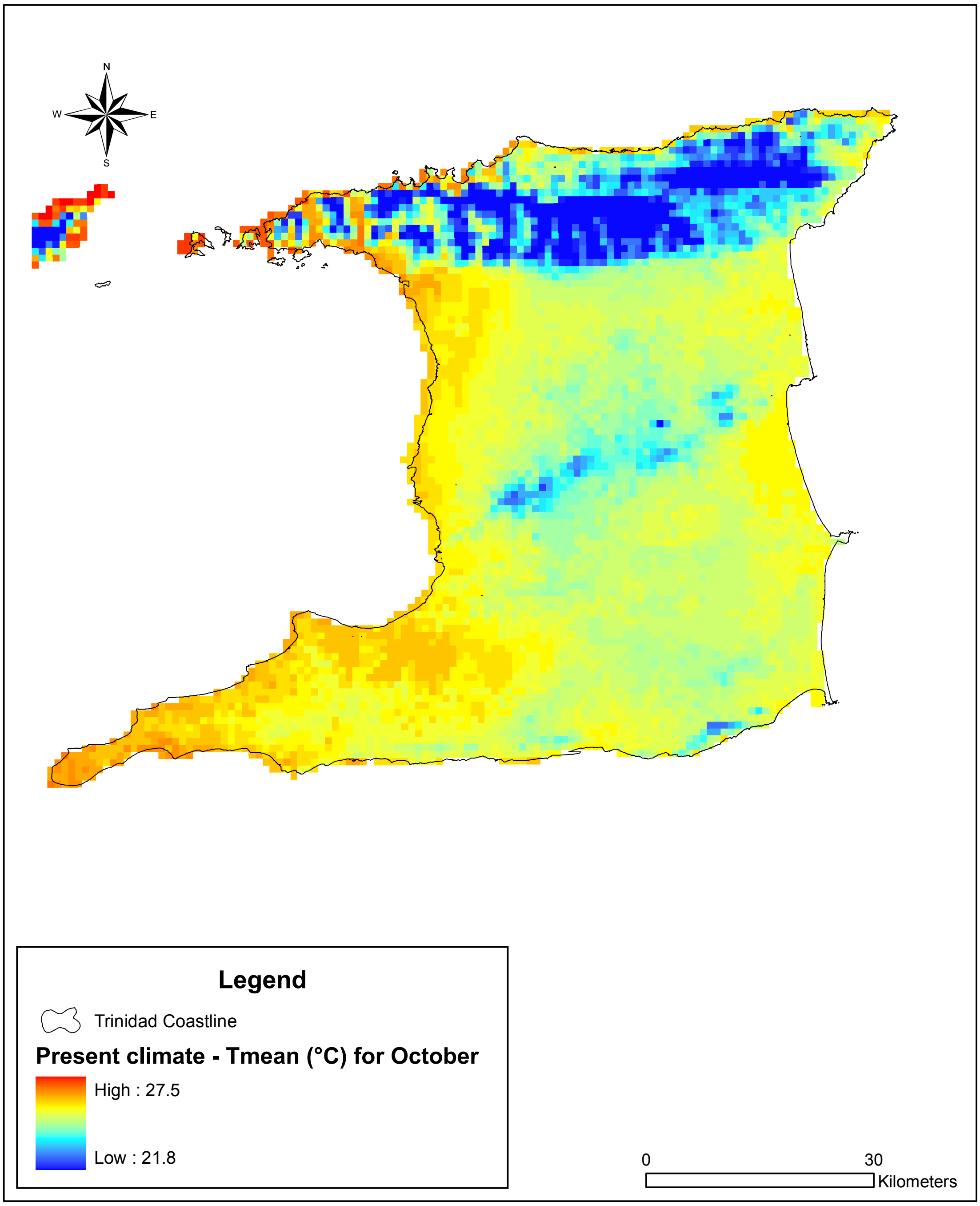


Figure 4.4: Tmean during October for the present climate (WorldClim) (at a 1 km^2 resolution).

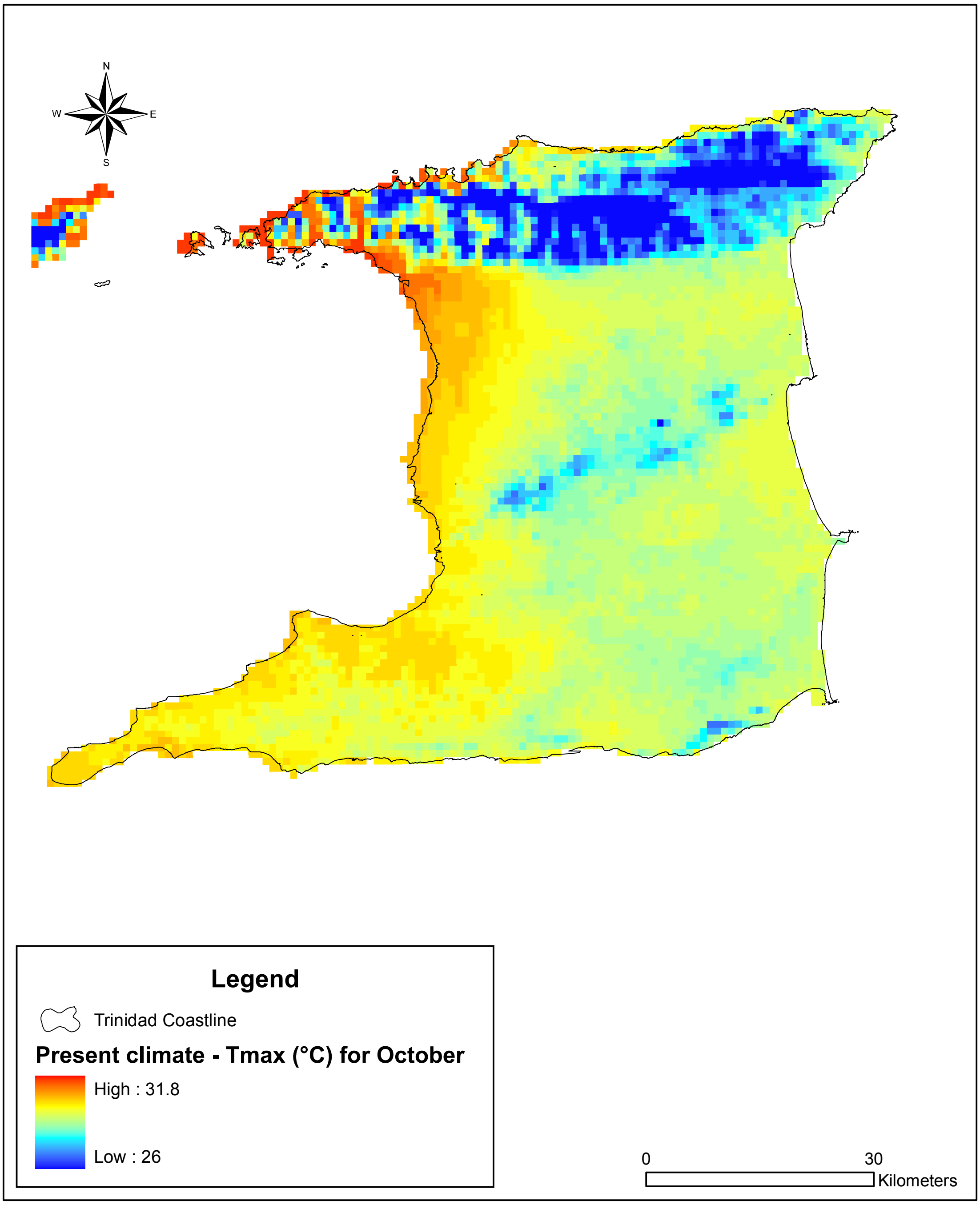


Figure 4.5: Tmax during October for the present climate (WorldClim) (at a 1 km^2 resolution).

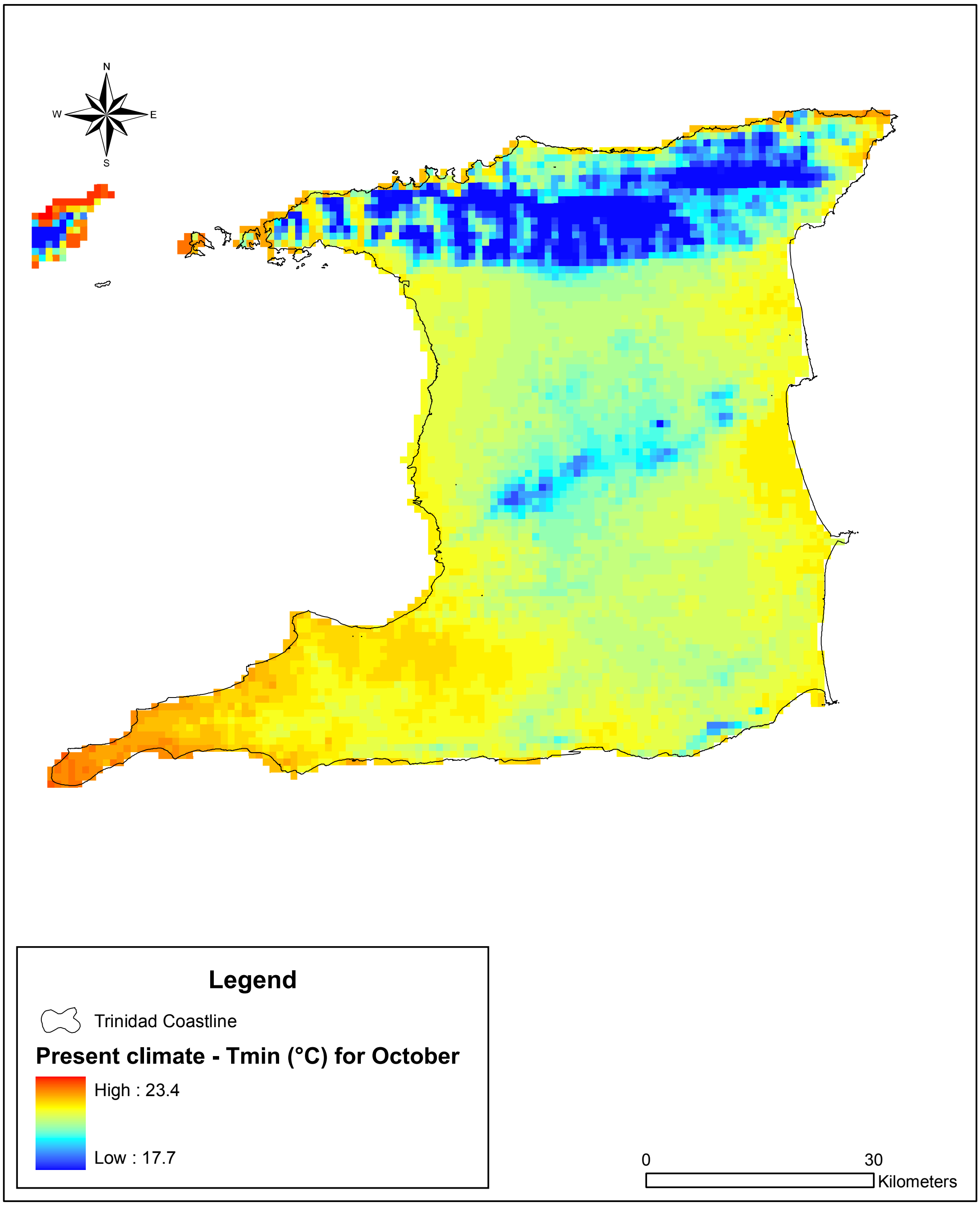


Figure 4.6: Tmin during October for the present climate (WorldClim) (at a 1 km^2 resolution).

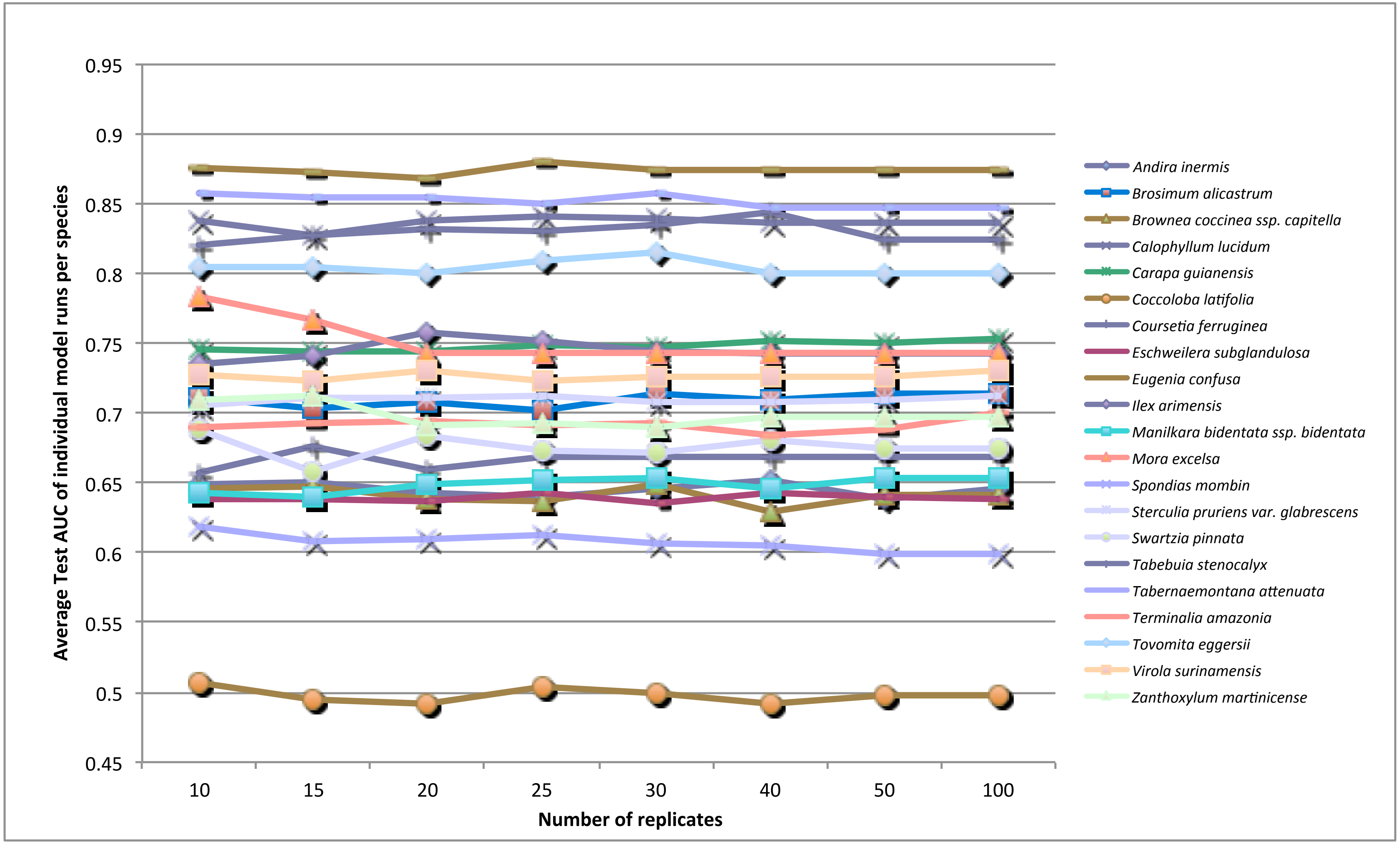


Figure 4.7: Variation of species models strength (Test AUC) with number of cross-validation replicates.

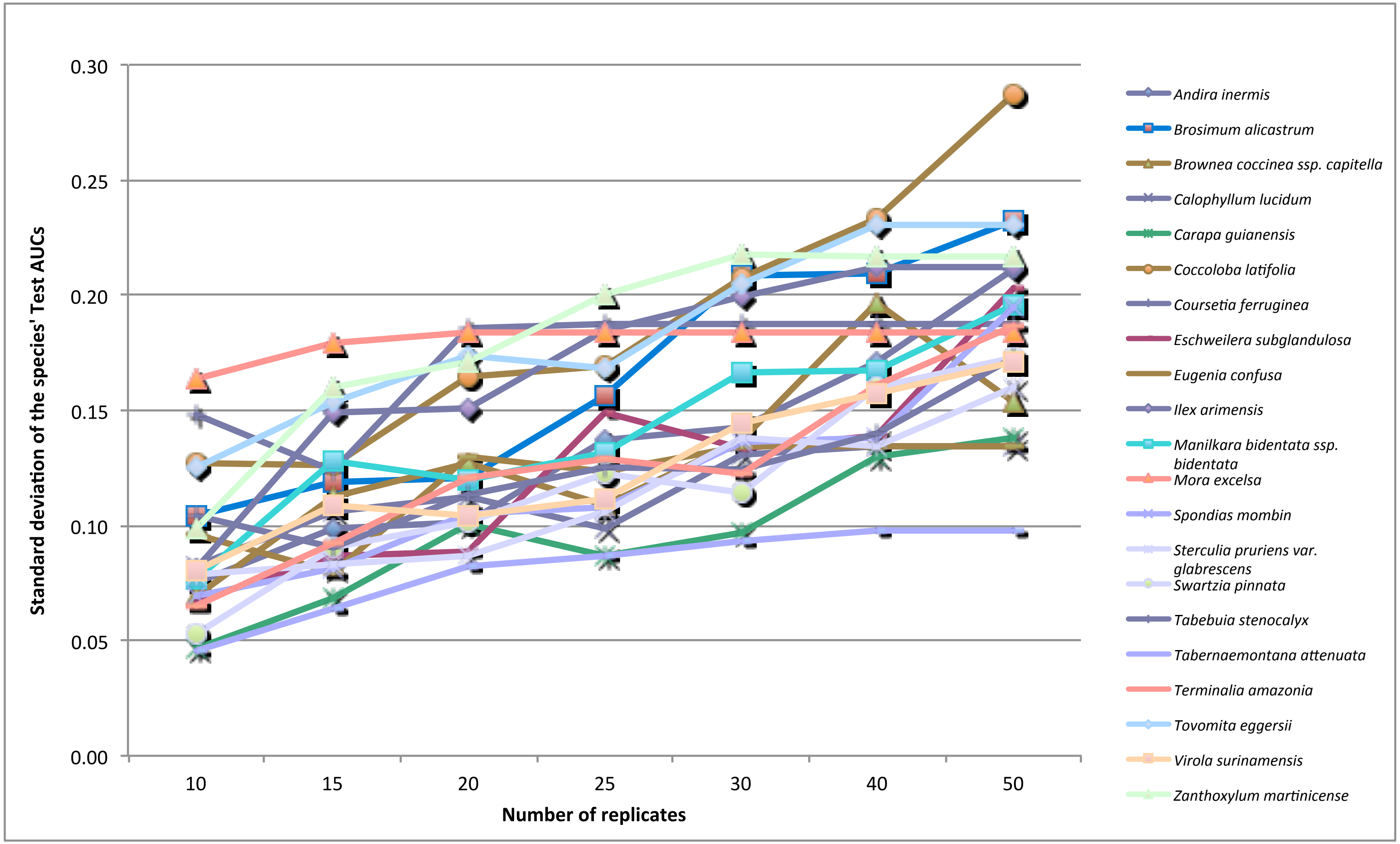


Figure 4.8: Standard deviation of species models strength (Test AUC) with number of cross-validation replicates.

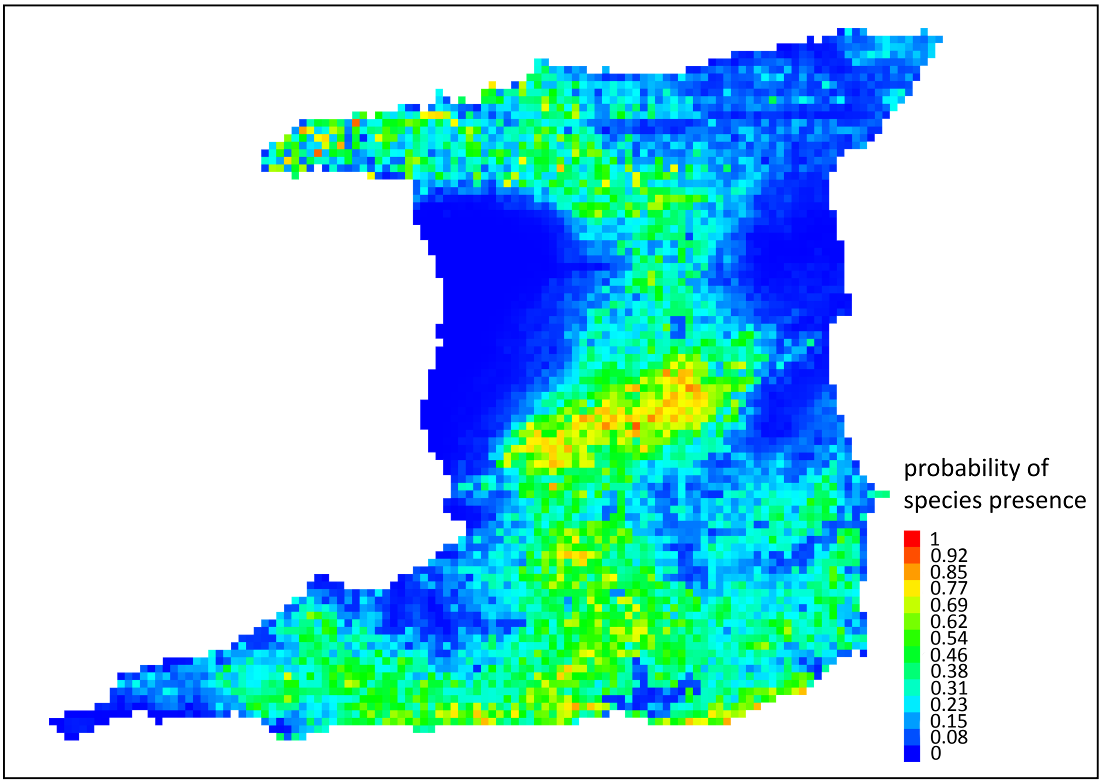


Figure 4.9: Raw MaxEnt logistic output grid for *Brosimum alicastrum* (present climate).

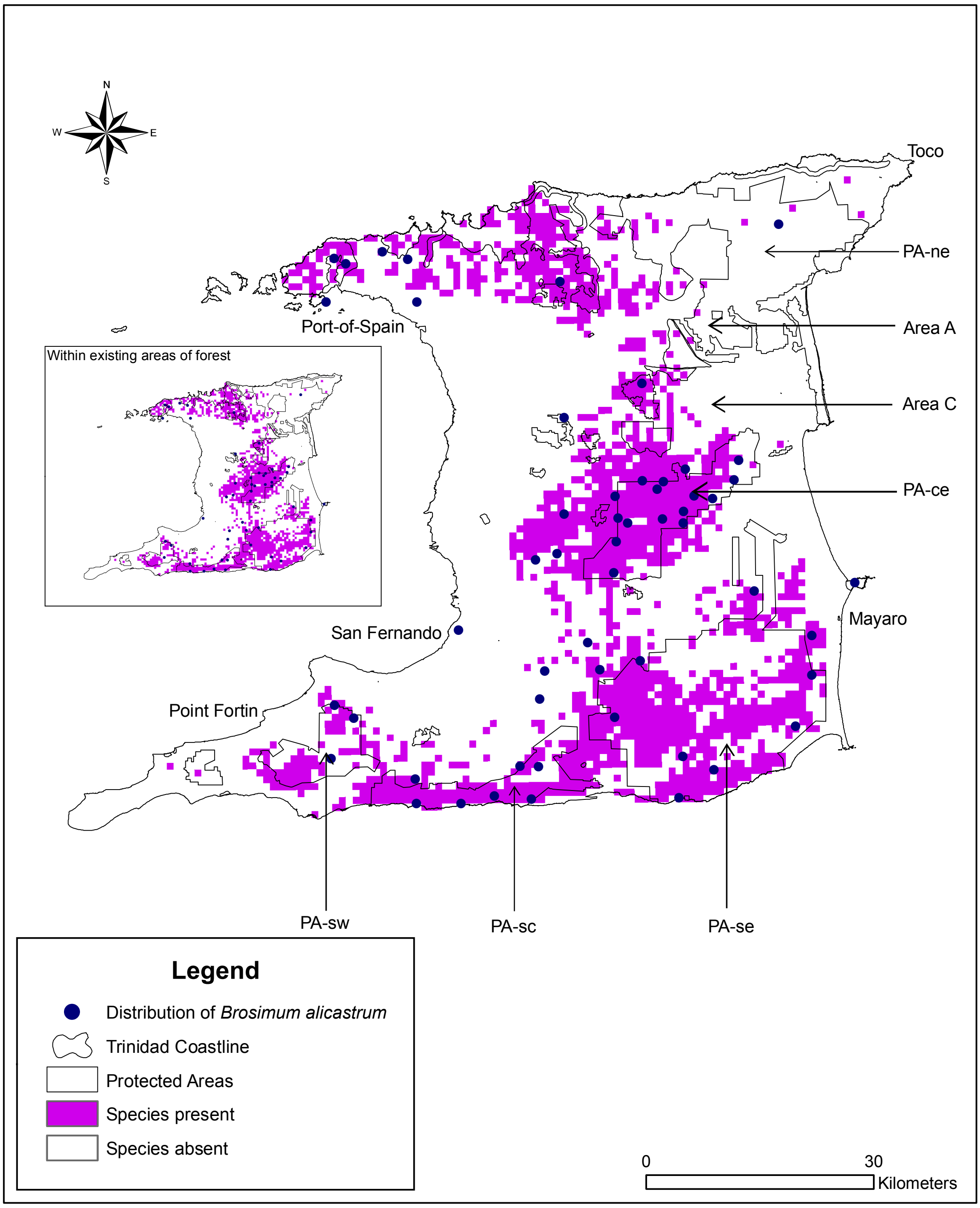


Figure 4.10: Potential climatically suitable areas within Trinidad for the distribution of *Brosimum alicastrum* under present climate conditions.

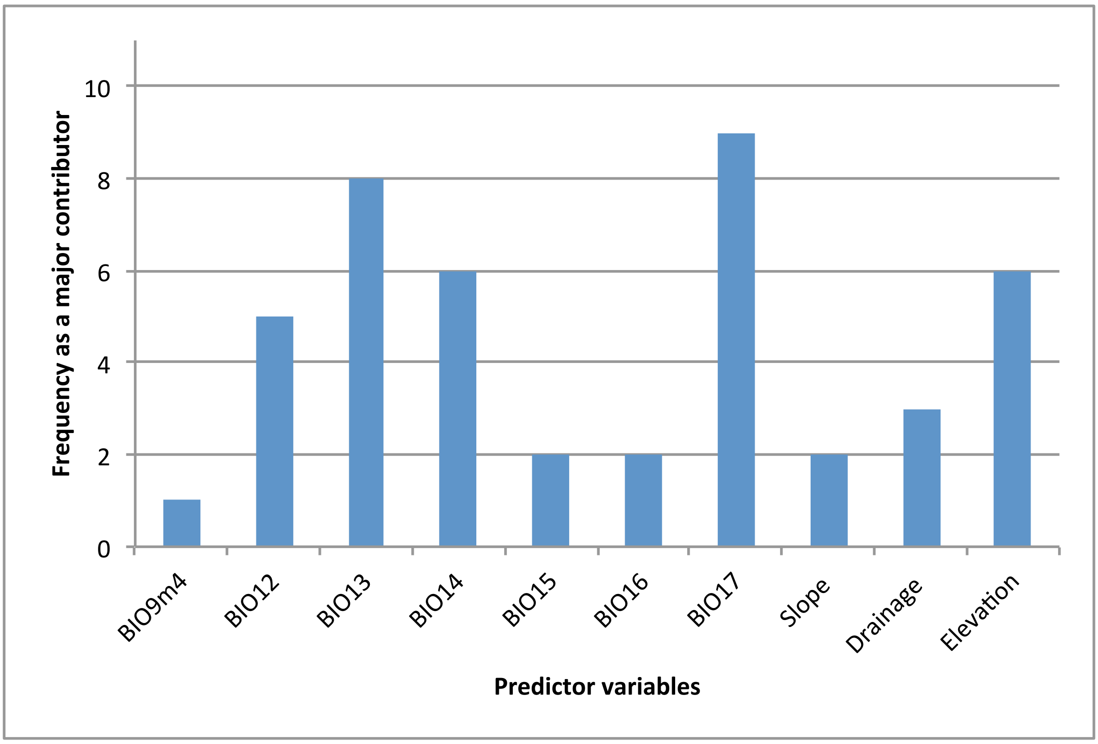


Figure 4.11: Predictor variables that were consistently main contributors to the species models.

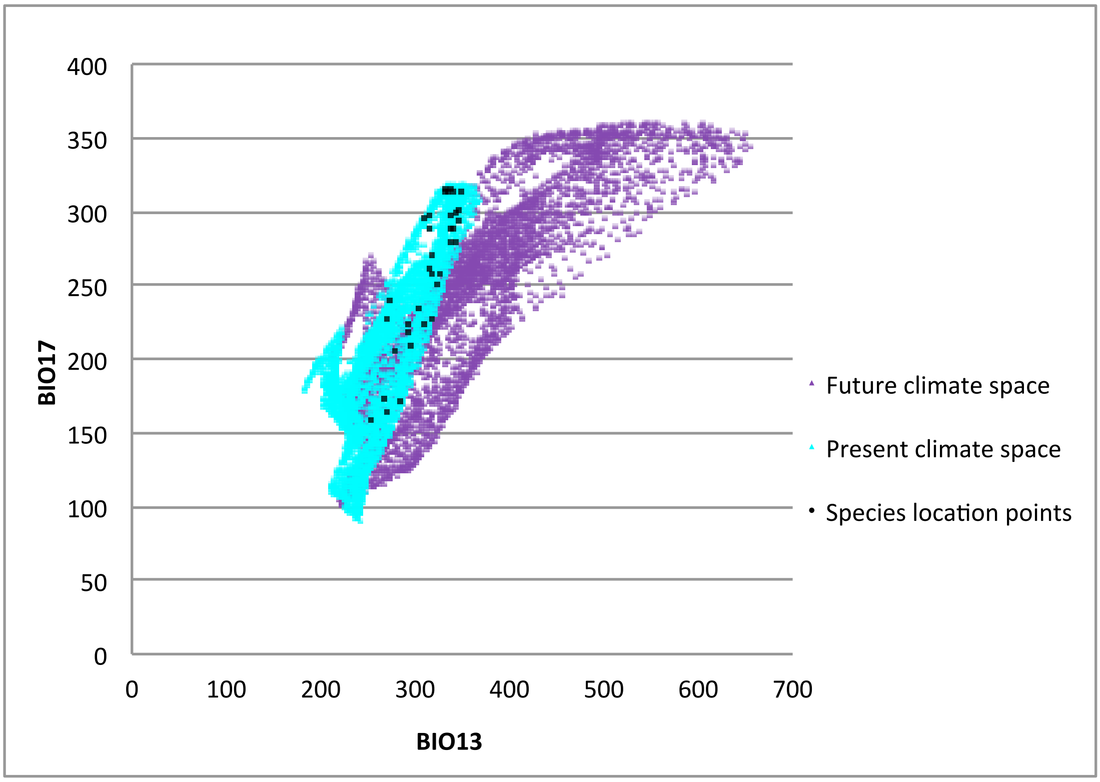


Figure 4.12: Climate space graph: the present distribution of *Tabernaemontana attenuata* in relation to its present and projected future climate spaces.

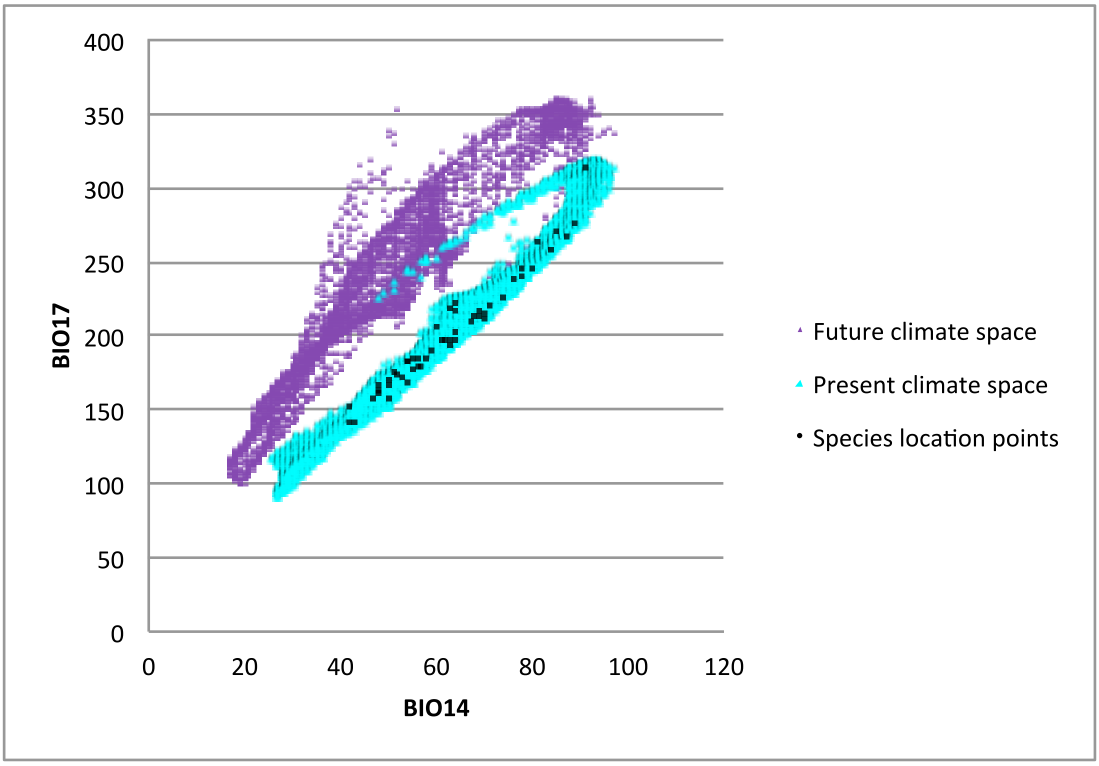


Figure 4.13: Climate space graph: the present distribution of *Brosimum alicastrum* in relation to its present and projected future climate spaces.

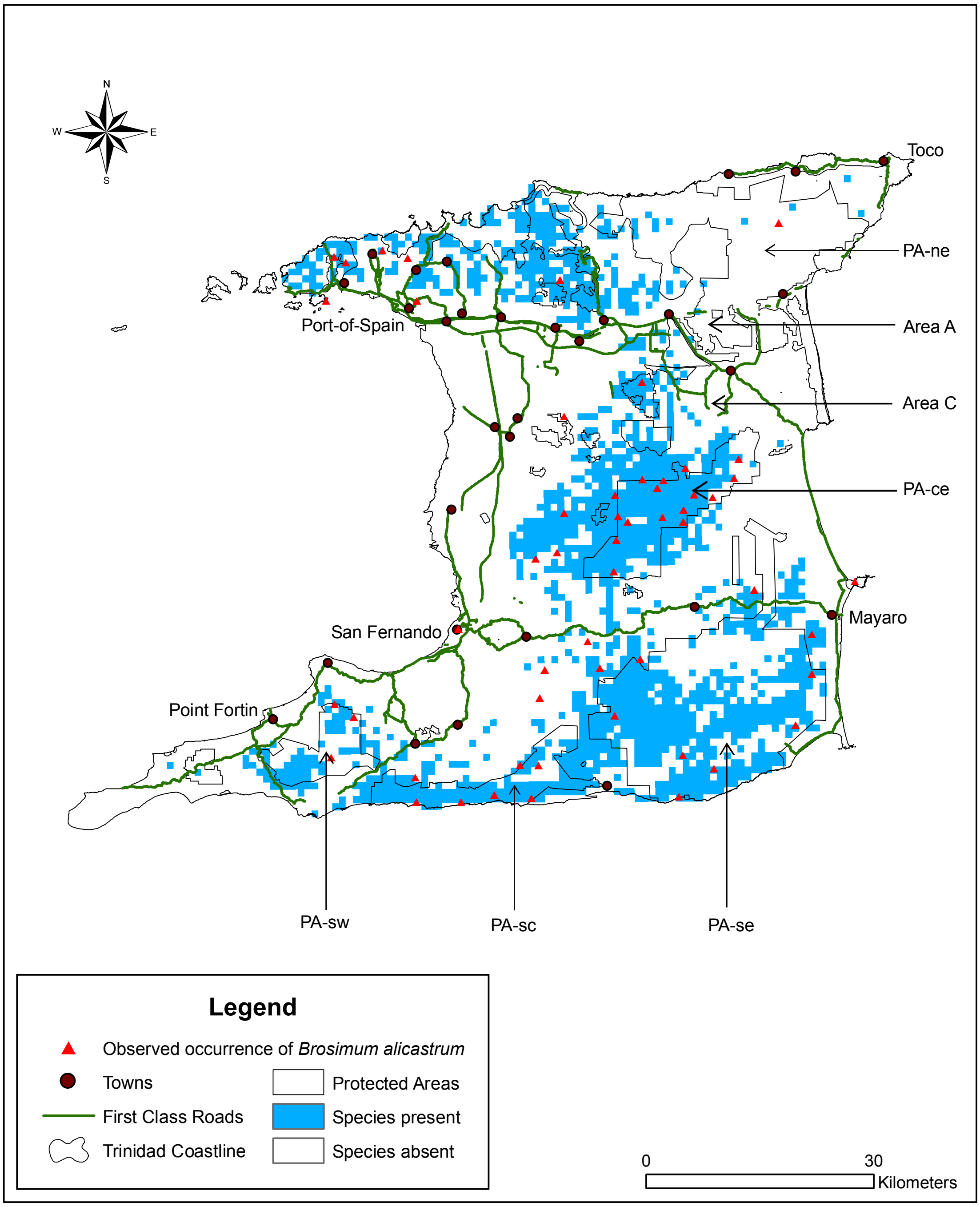


Figure 4.14: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Brosimum alicastrum* (Moussara) under present climate conditions.

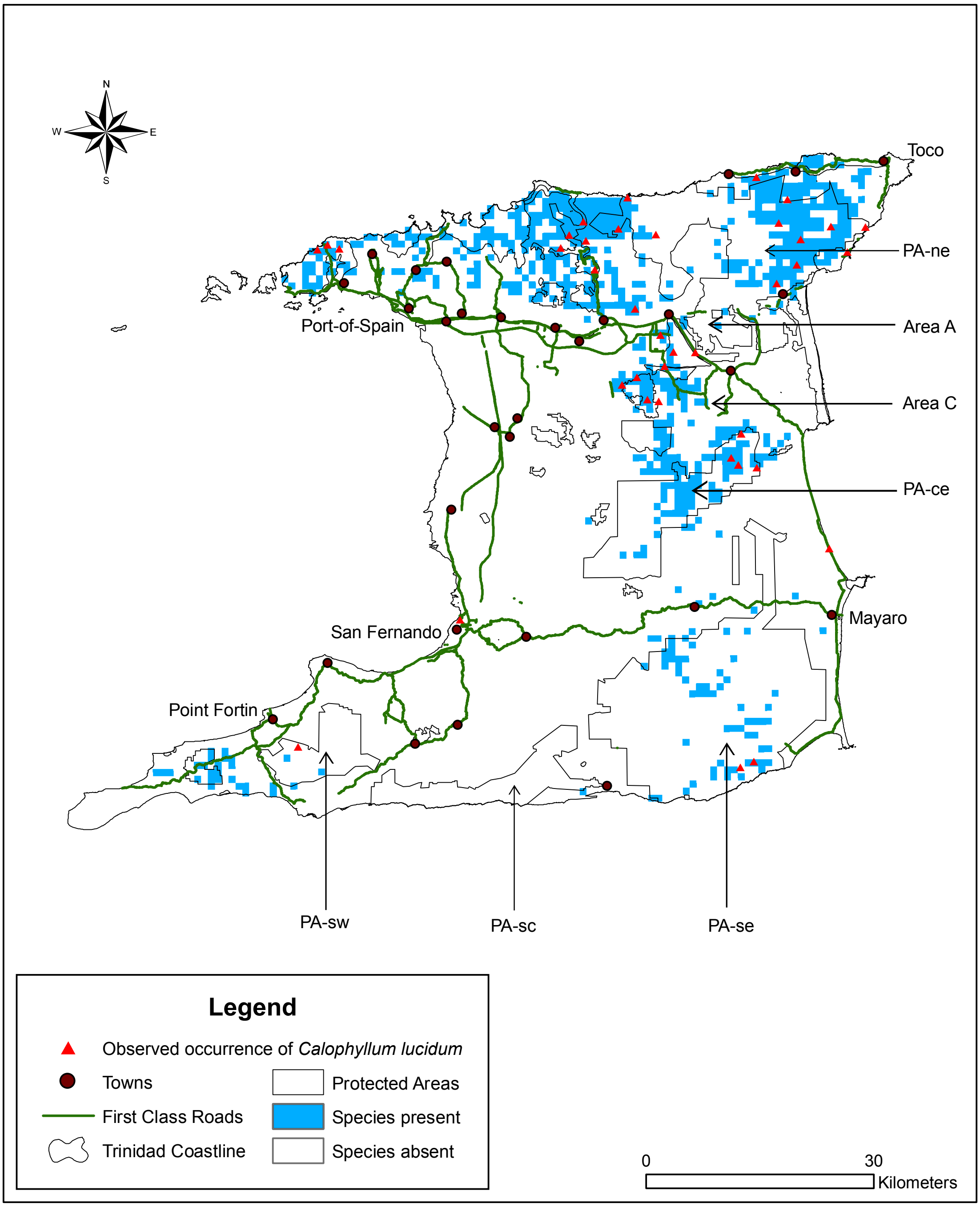


Figure 4.15: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Calophyllum lucidum* (Galba) under present climate conditions.

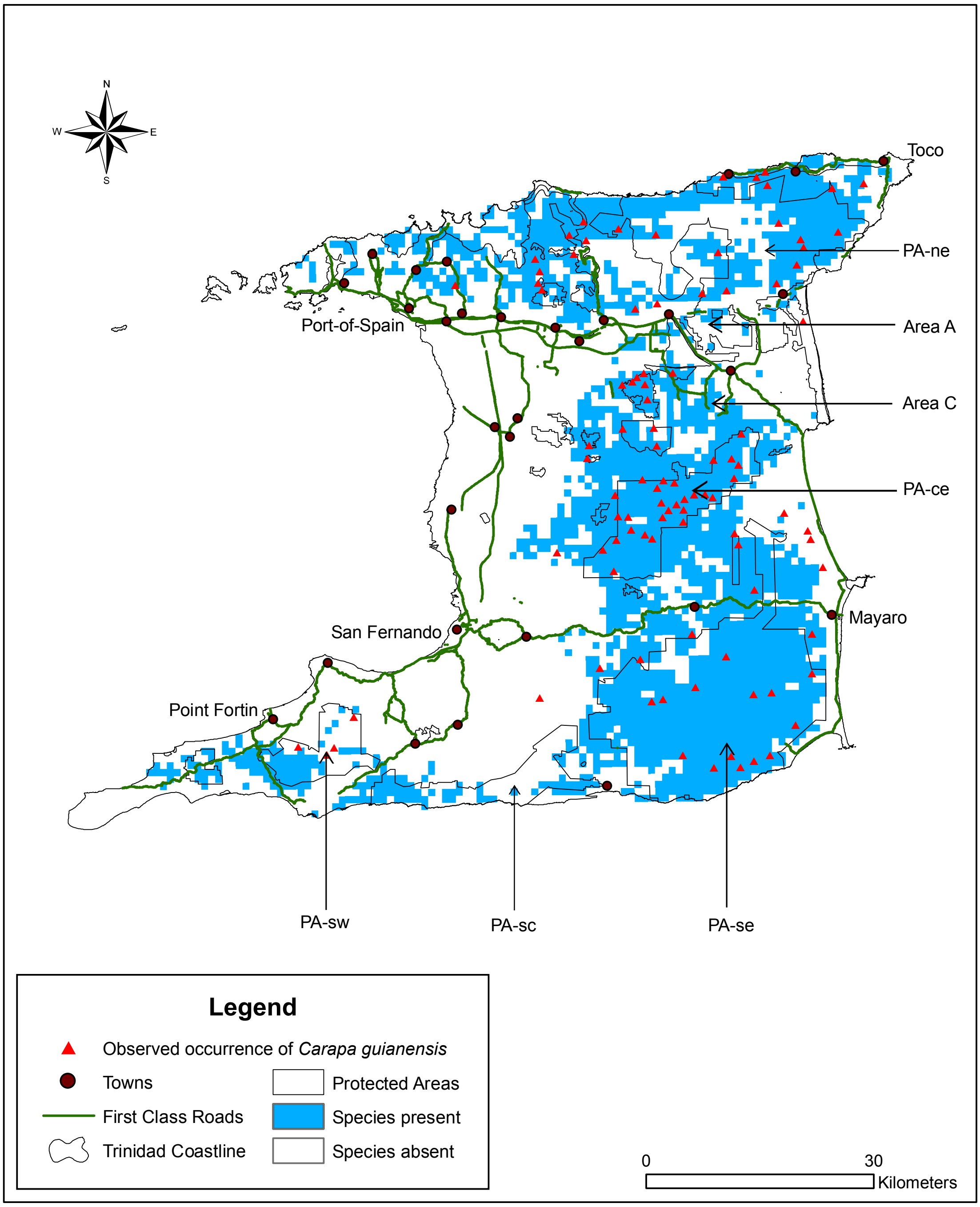


Figure 4.16: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Carapa guianensis* (Crappo) under present climate conditions.

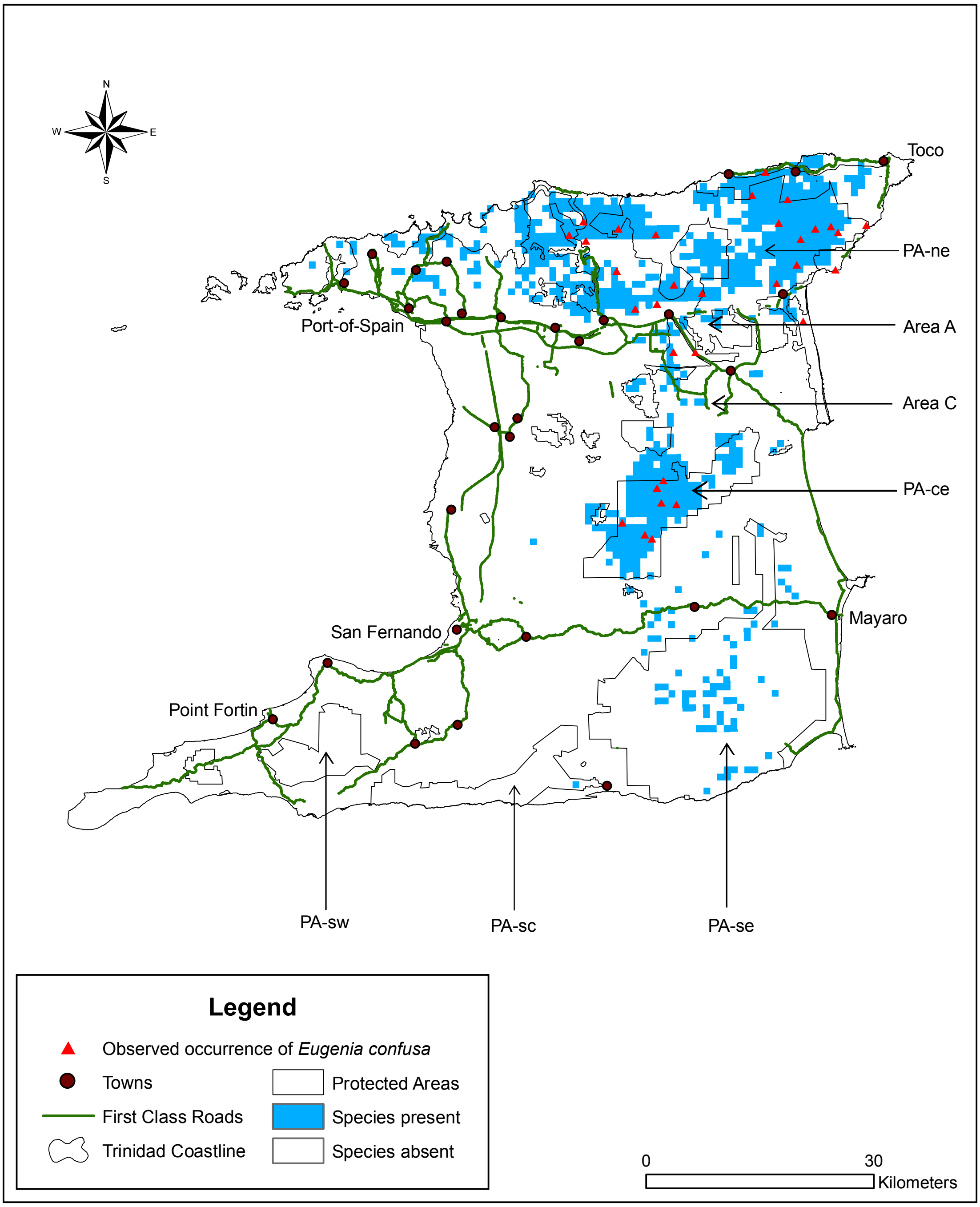


Figure 4.17: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Eugenia confusa* (Wild coffee) under present climate conditions.

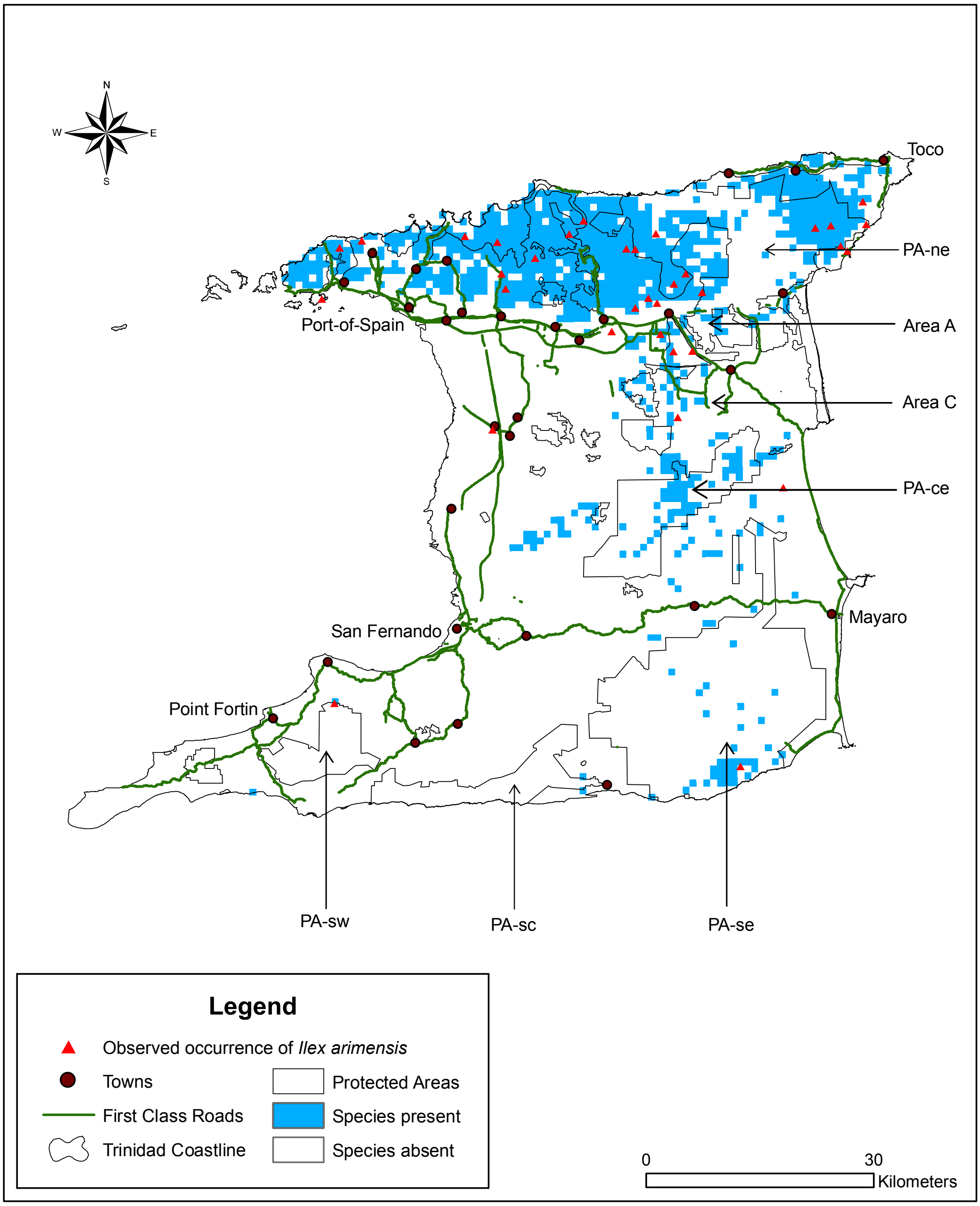


Figure 4.18: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Ilex arimensis* (Biscuitwood) under present climate conditions.

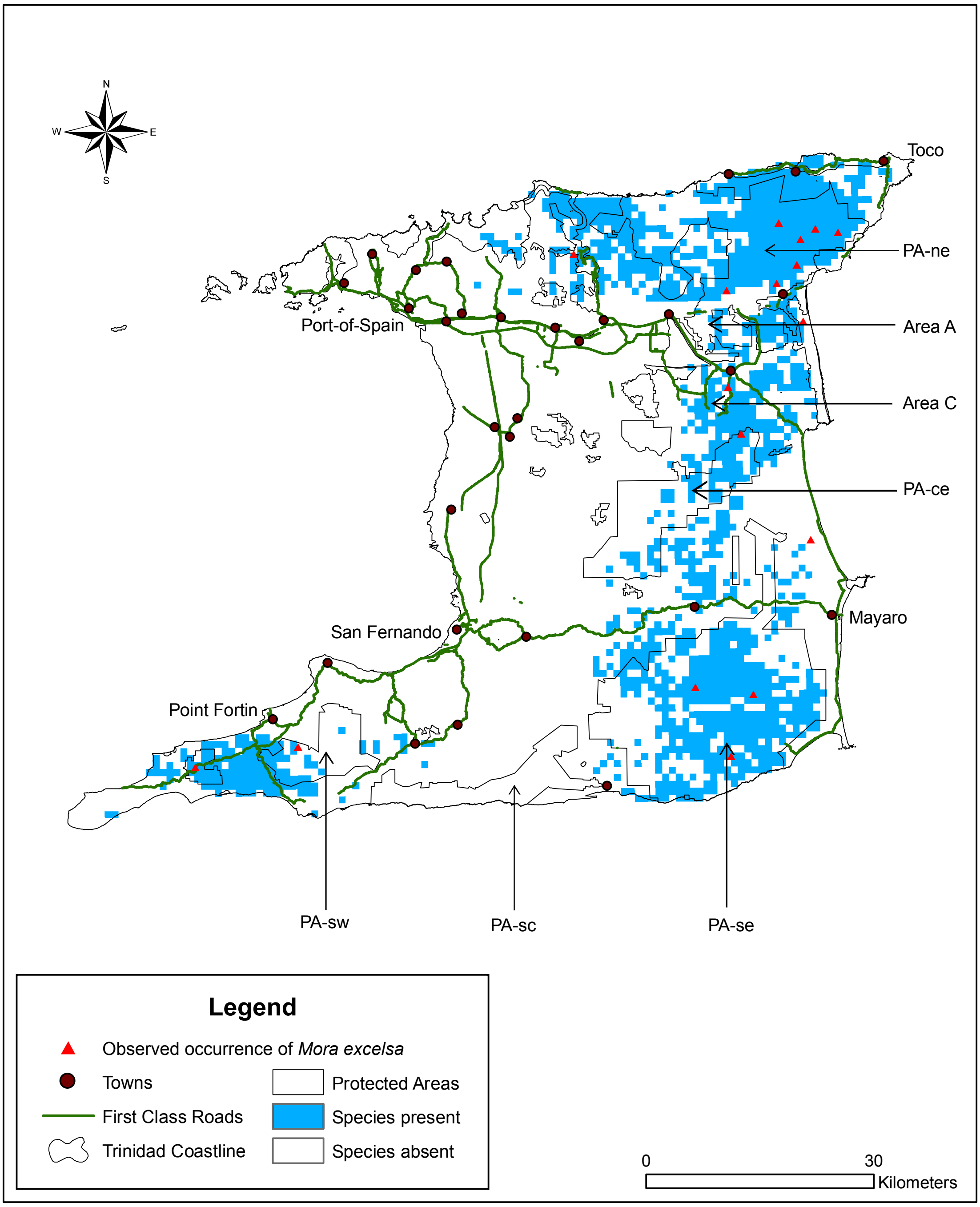


Figure 4.19: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Mora excelsa* (Mora) under present climate conditions.

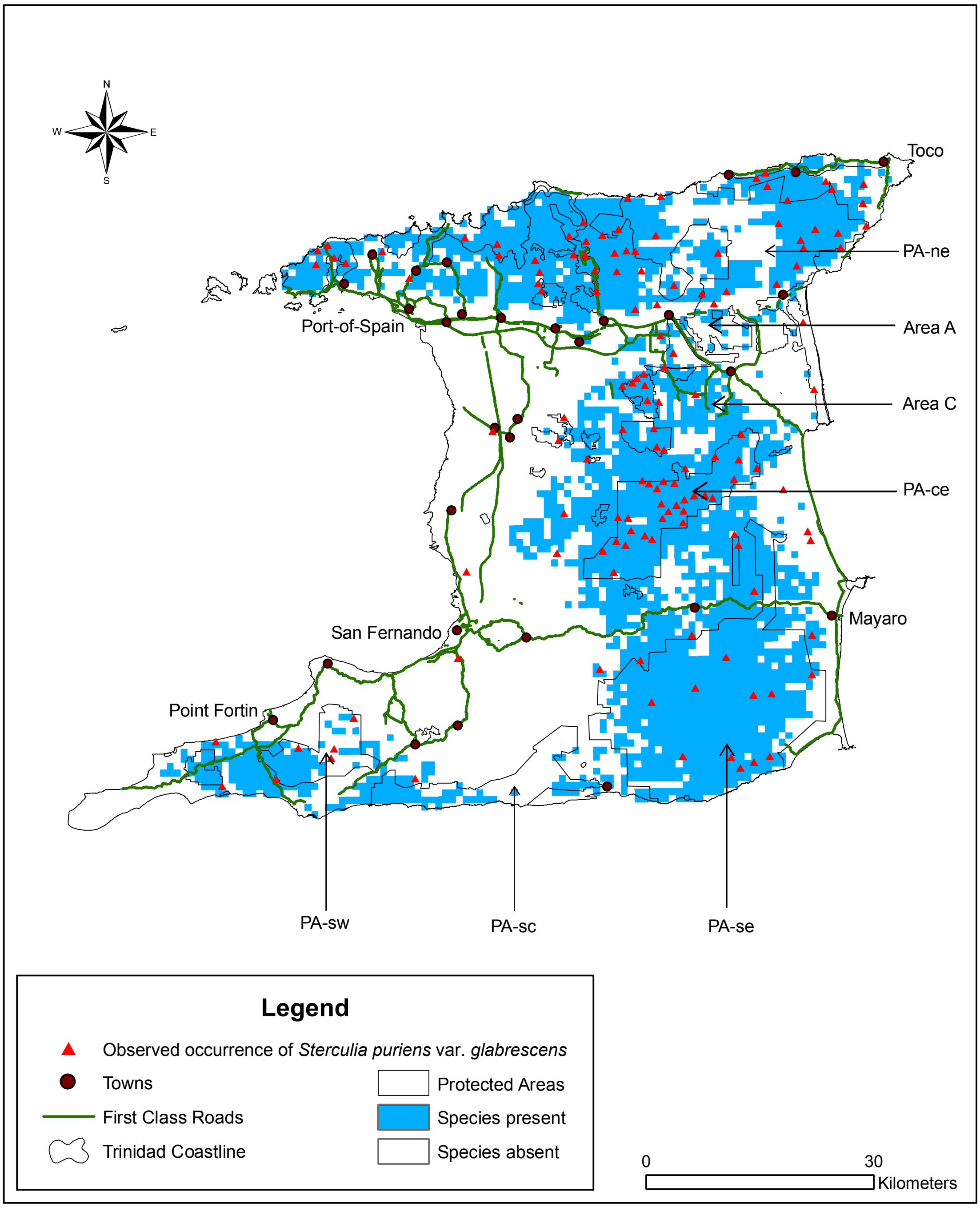


Figure 4.20: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Sterculia puriens* var. *glabrescens* (Mahoe) under present climate conditions.

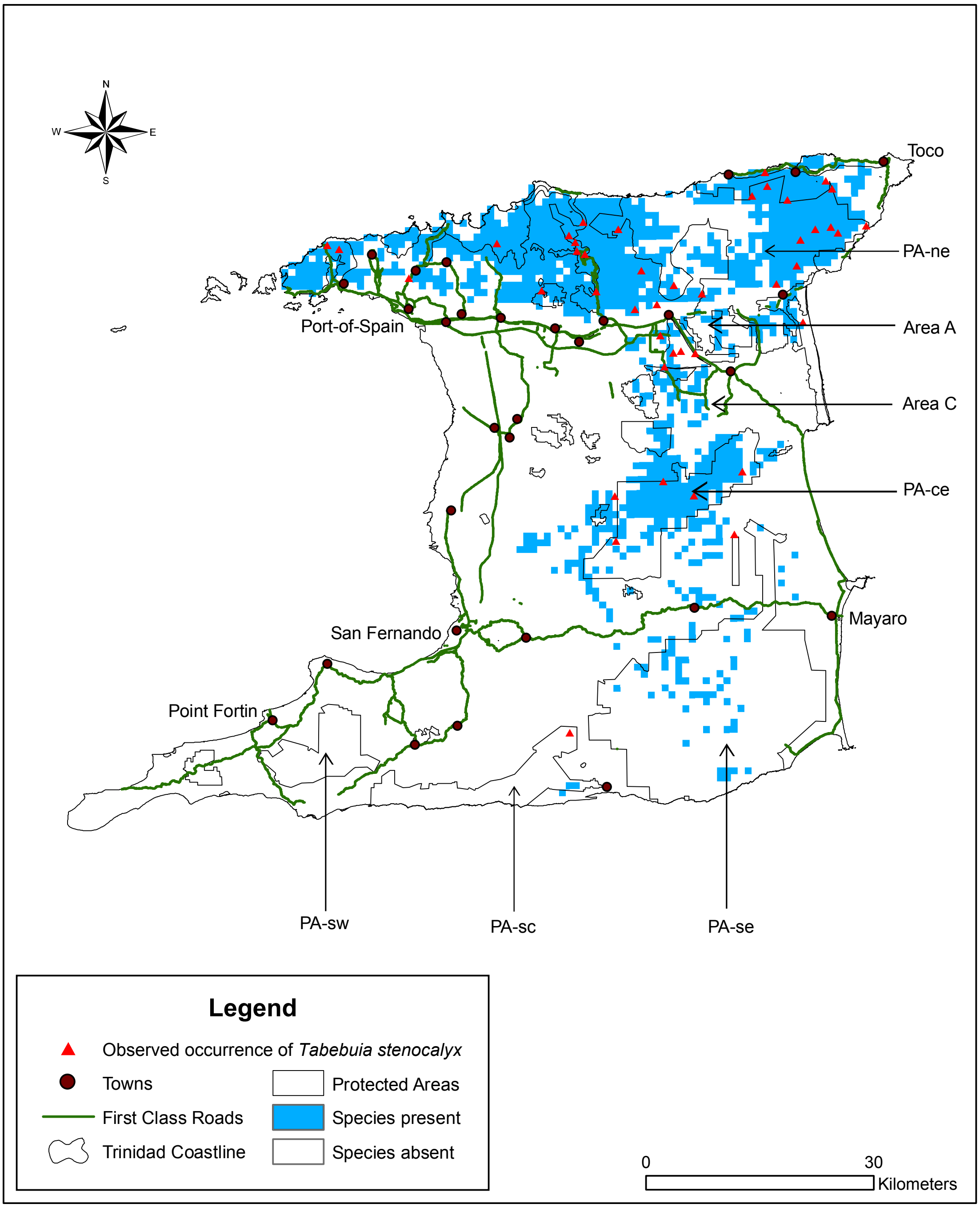


Figure 4.21: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Tabebuia stenocalyx* (Wild Calabash) under present climate conditions.

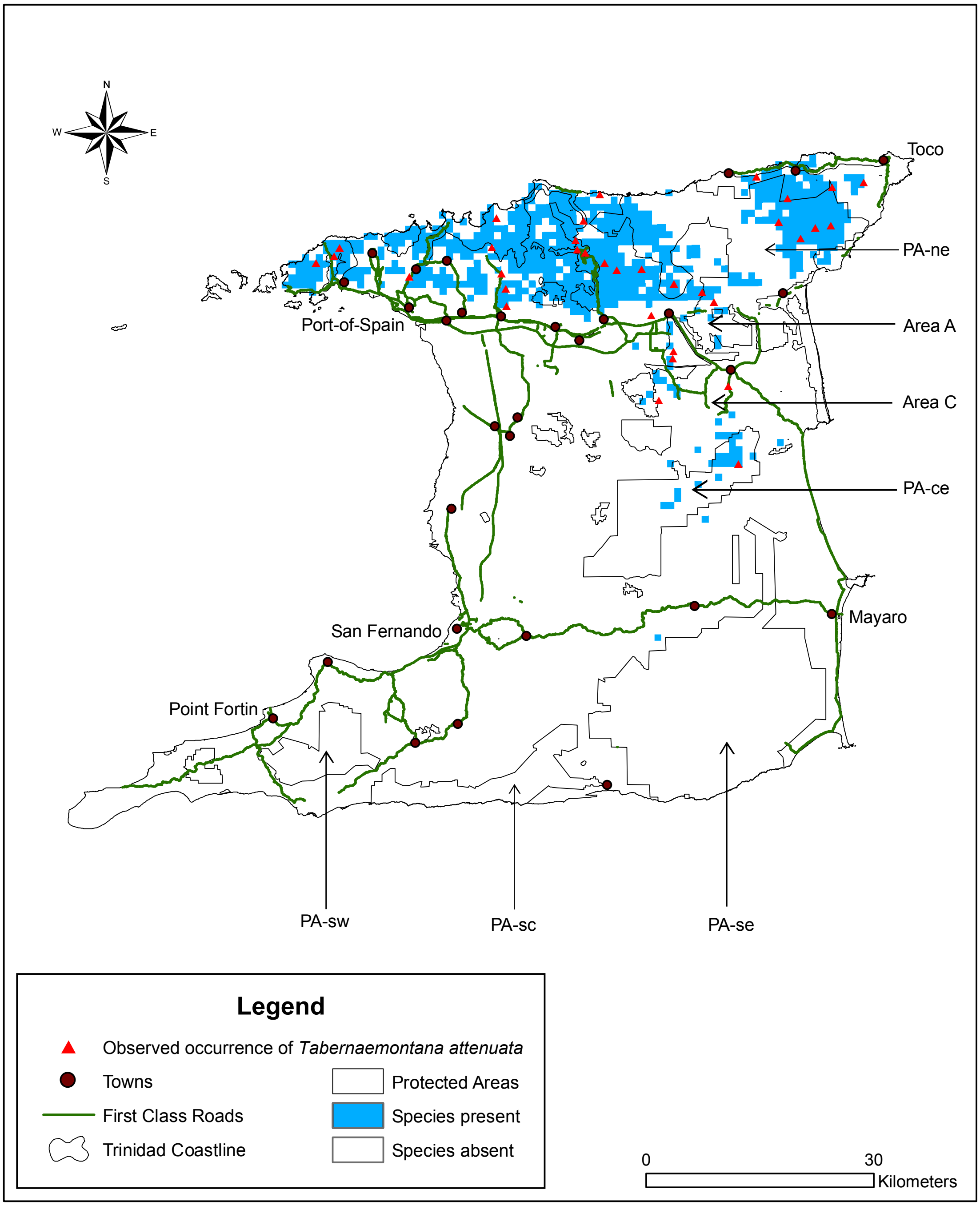


Figure 4.22: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Tabernaemontana attenuata* (Wild Jasmine) under present climate conditions.

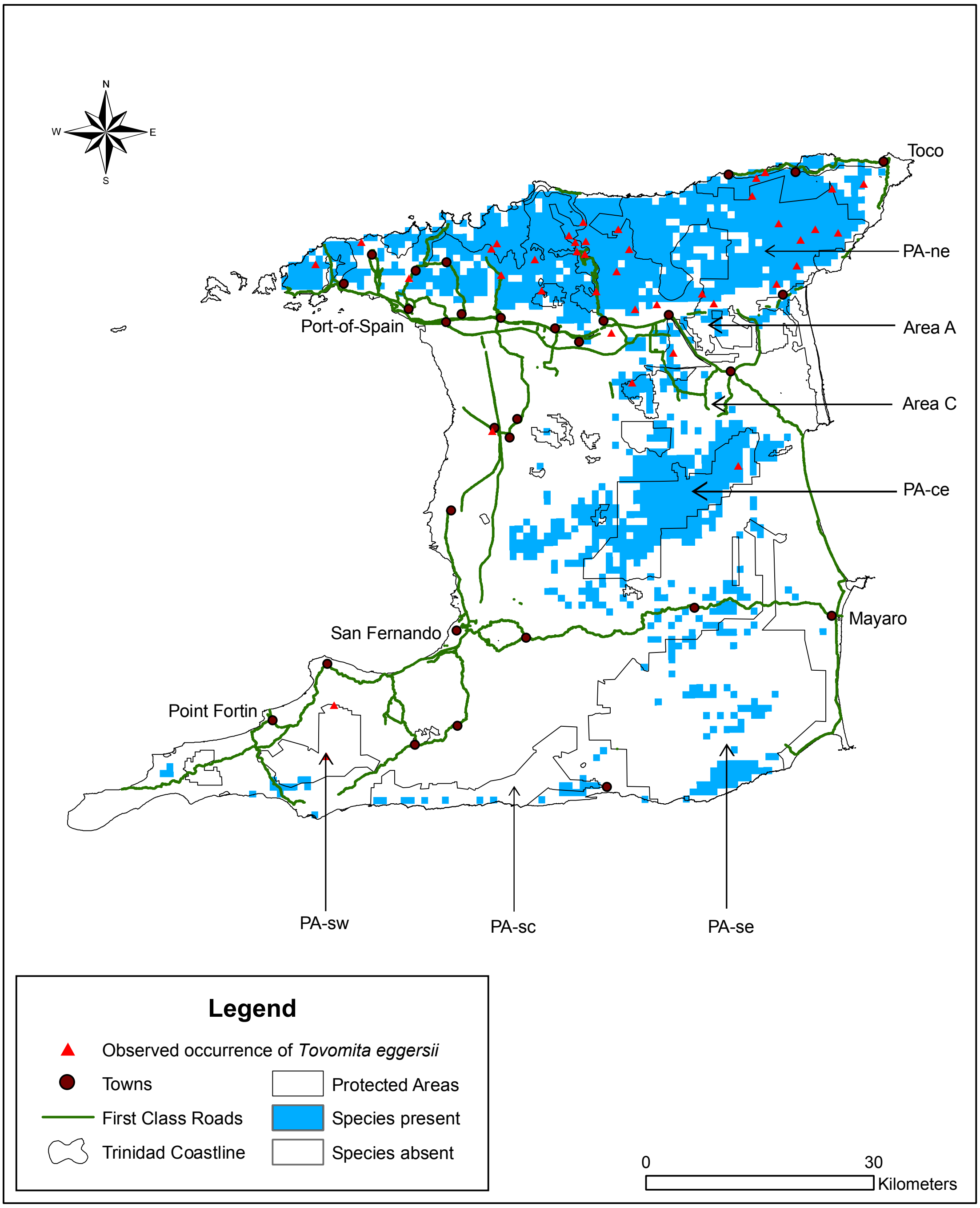


Figure 4.23: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Tovomita eggersii* (Cocoa Mangue) under present climate conditions.

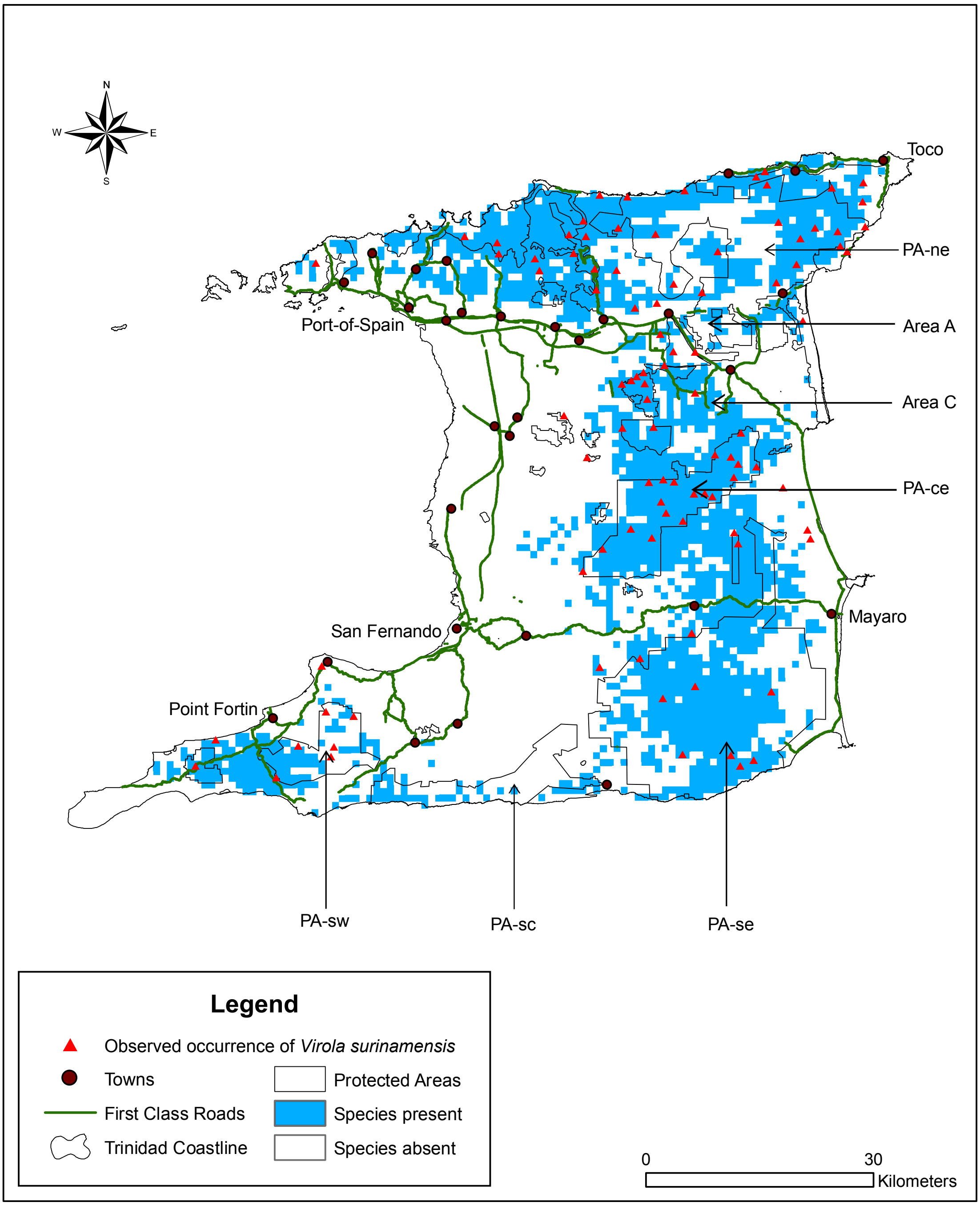


Figure 4.24: Potential climatically suitable areas within the forested regions of Trinidad for the distribution of *Virola surinamensis* (Cajuca) under present climate conditions.

Chapter 5

Projecting future distributions of selected tree species within Trinidad and its protected areas network

5.1 Introduction

This chapter is the second of this thesis' two part investigation into the use of SDM as a potential tool for integrating climate change into conservation planning within a Caribbean SIDS. It involves the projection of the present potential distributions of the eleven selected tree species (generated in Chapter 4) to the climate conditions projected for an SRES A2 future. For each species, the SMs for both present and future climates are then combined to create a 'change map' which illustrates areas of suitable climate space gain, loss or no change from the present to the future scenario. Change maps for the eleven species are combined to create a collective change map which portrays areas of anticipated gains, losses or no change in suitable climate space for the collective rather than individual species. These change maps are used to assess the ability and effectiveness of the PAN within the island to cope with projected changes in collective species distribution into the future. Finally, suggestions are made towards the use of SDM for conservation initiatives at a regional rather than the island scale in order to enhance the potential of species survival.

5.1.1 Projected species response to an already changing climate

An accumulating body of observations indicate anthropogenic climate change is having impacts on the natural world. These include climate-related extinctions, phenological alterations and shifting of geographic distributions across a range of taxonomic and functional groups (Hickling et al. 2006; Jonzén et al. 2006; Lenoir et al. 2008; Parmesan and Yohe 2003; Pounds et al. 2006; Root et al. 2003). Furthermore, paleoecological records (Graham and Grimm 1990), and modelled simulations of future range shifts, indicate greater changes within the coming century, with the potential that future species assemblages will be substantially different from those that exist today (Huntley et al. 2006; Pereira et al. 2010; Thuiller et al. 2011).

Some of these studies suggest that the net effect of these range shifts will be a general reduction in species distribution ranges and hence, an increased risk of extinction for species which migrate in upslope or poleward directions within continents (Hickling et al. 2006; Lenoir et al. 2008; Thomas et al. 2004). This is because the upslope migration of species will meet with progressively smaller areas of suitable habitat (due to montane geometry) resulting in the isolation and eventual extinction of the species (Lenoir et al. 2008). Additionally, poleward shifting species are projected to meet with either decreasing continental areas (southern hemisphere) or lower levels of endemism and species richness (continents of the northern hemisphere) (Walther et al. 2002). This combination of the shifting and reduction of species distribution ranges is expected to challenge severely the effectiveness and relevance of present-day biodiversity conservation planning and management strategies.

However, there are no clear indications as to whether the projected effects mentioned above will be of the same intensity and direction within terrestrial ecosystems of small islands; despite the much publicised concern that SIDS will be among the first areas affected by climate change (Chapter 1). This is because the increasingly rich literature on the use of SDM to predict species distributions (present and future), and for use in conservation planning, has been based within continental settings (where space is not a critical limiting factor and where competition for alternative uses of large areas of land is much less than in islands). Indeed, a thorough literature search yielded no SDM studies that were based upon predicting the shifts of terrestrial species (and the resulting consequences for conservation strategies) within small islands and/or their PAs. Instead, the vast majority of the very few SDM-based studies were focused upon the expected impacts upon coral reefs and other coastal ecosystems, in addition to economic and infrastructural impacts (Hoegh-Guldberg et al. 2007; Tompkins and Adger 2005). The analyses of this chapter attempt to project the potential distributions of the eleven selected tree species (Chapter 4) within a future SRES A2 scenario, and in the process highlight the main uncertainties that were encountered as a result of no available guidance in the literature for SDM analyses at this scale.

5.1.2 Difference between modelling present-day and future species climate space

A key distinction between the modelling applications used in Chapter 4 and those used to predict species distributions under climate change is that the former generates predictions within the period matching the training data. This contrasts with the latter which uses models generated for the potential present species distribution to forecast (or hindcast) distributions at another point in time – during which some environmental predictors may extend beyond the current climate. Forecasting is inherently uncertain as no observations of species occurrence can be used from the training data to support directly or test these predictions (Elith and Leathwick 2009). MaxEnt addresses this problem by 'clamping', in which variables outside the training range are treated as if they were instead, at the limit of the corresponding training range (Phillips et al. 2006, 2009). A clamping image is produced which illustrates the absolute difference in predictions between a clamped versus a non-clamped output, in effect showing where clamping has had large effects on the projected output. While this does not remove forecasting uncertainties, it aids in pointing out areas where extreme caution should be exercised during interpretation.

Many authors believe that ignoring the future because of these uncertainties is not an option (Wiens and Bachelet 2010), hence a rich literature attempts to integrate climate change into conservation management and planning. SDM is increasingly being used to facilitate this integration by projecting how the distributions of species may change under different climate change scenarios (Akçakaya et al. 2006; Botkin et al. 2007; Lawler et al. 2009; Thuiller 2004). These SMs are based on the premise that species respond to climate change by: (i) adapting to changing conditions or remaining in isolated pockets of unchanged refugia, (ii) shifting their distribution ranges to follow their required environmental conditions or (iii) becoming extinct (Holt 1990). Much literature has focused on (ii) in which SMs are used to project future potential species distributions (Botkin et al. 2007; Franklin et al. 2009).

A great many of these SMs utilise environmental variables which characterize the places that a given species is known to occur to develop correlative models. These models are then extrapolated to project potential future distributions based upon the expected future locations of required environmental features. Additionally, correlative models do not require detailed (and usually scarce) physiological data about individual species; therefore they can easily be applied to a large number of species. This enables conservation planners to assess potential impacts of climate change upon a wide range of species and hence habitat assemblages (Berry et al. 2002).

5.1.3 Assumptions and uncertainties of SDM

As with all models, SMs are based on assumptions and hence incorporate accompanying uncertainties (Thuiller 2004). One assumption is that species are able to disperse to suitable locations under a changing climate (Jeschke and Strayer 2008; Pearson and Dawson 2003). However, species' dispersal capacity may be compromised if environmental conditions change more rapidly than a species' ability to disperse (McLachlan et al. 2007). Additionally, landscapes through which species move may be fragmented by anthropogenic activity, introducing dispersal barriers as well as creating mosaics of habitat patches with varying degrees of suitability (Araújo et al. 2006; Midgley et al. 2006; Thuiller et al. 2006). Some authors believe the impacts of this phenomenon may exceed those of climate change (Hof et al. 2011; Jetz et al. 2007; Pyke 2004). However, conservation strategies involving the 'assisted migration' of species show potential for addressing many of these problems associated with disrupted habitat connectivity, especially with respect to 'slow-moving' species such as plants (Collingham and Huntley 2000; McLachlan et al. 2007). Further, as mentioned in Chapter 4, this thesis treats the results of its SM analyses as representations of the potential distribution range of the species being modelled. It does not attempt to infer whether or not these species will be able to migrate to new areas that are suitable for their survival.

Correlative SDM also assumes that natural communities are Gleasonian in nature (after Gleason 1926) and hence do not account for species interactions (Guisan et al. 2006). Some authors argue that the contribution of biotic interactions to the distribution of a given species at the macro-scale may have been under-estimated (Araújo and Luoto 2007; Gutiérrez et al. 2005); however it should not be forgotten that attempts to resolve the vast array of direct and indirect interactions within even a small subset of a community is an overwhelming challenge. This is particularly because the nature of these interactions, species presence and abundance can be dynamic and prone to constant change in space and time (Franklin et al. 2009; Pearson and Dawson 2003). However, it has been shown that application of SMs at macro-scales (at which climatic influences on species distributions are dominant) can reduce the impact of biotic interactions (Luoto et al. 2006; Pearson and Dawson 2003; Pearson et al. 2004). Further, the reality that many SMs have been highly successful at simulating potential present species distributions fundamentally conflicts with the notion that species distributions cannot be adequately defined (Pearson and Dawson 2003).

Several studies argue that despite the rate of current and future environmental change exceeding the capacity of most species to adapt genetically (e.g., long-lived species with limited dispersal) (Etterson and Shaw 2001; Williams and Jackson 2007), there have been documented cases of some species that are capable of rapid evolutionary change (Franks et al. 2007). Additionally, some species have exhibited rapid behavioural adjustments to changing environmental conditions which demonstrate their capacity to adapt to changing conditions without shifting distributions (Root et al. 2003). For example Root et al. (2003) noted that some bird species have advanced their timing of breeding activity in association with warmer temperatures. However, it still remains to be seen if such adaptations will remain viable as climate and other interacting species continue to change.

5.1.4 Climate scenarios

In order to forecast the potential impacts of twenty-first century climate change upon species distributions, climate scenarios with sufficient spatial resolution are required to represent potential changes across heterogeneous biological and physical landscapes. According to Beaumont et al. (2008), 'climate scenarios are plausible future climates that have been constructed to determine the impacts of climate change on resources and the environment'. For the purpose of impacts modelling, future climate scenarios are of two types: (i) idealised scenarios; or (ii) simulated scenarios derived from climate models incorporating assumptions about future concentrations of greenhouse gas emissions (Beaumont et al. 2008).

5.1.4.1 Idealised scenarios

Idealised scenarios represent specified *a priori* changes in climatic variables across a region, for example, precipitation changes of ±5%, ±10%, ±15% and temperature changes of 1 °C, 2 °C, 3 °C, 4 °C. These scenarios allow sensitivity analyses to be conducted over a range of change possibilities to explore species responses as well as to identify thresholds above which species may be adversely affected by changing conditions (Williams et al. 2003). There are disadvantages attached to idealised scenarios. Relationships between climate variables are assumed to be linear. Additionally, apart from implying uniform change in climate across regions of interest, they do not facilitate the estimation of a temporal scale of species response. However, despite these disadvantages, idealised scenarios that consider a range of possible future climates can be an effective intermediate step in assessing species response to this range of conditions – which can then be refined further with the use of simulated scenarios (Beaumont et al. 2008).

5.1.4.2 Simulated scenarios

The simulated climate scenario used for the analyses in this thesis was derived from one of the climate models within the Fourth Assessment Report (AR4) of the IPCC. The climate models from the AR4 are fully coupled models that incorporate oceanic, atmospheric, land surface, seasonal snow cover and ice dynamics. These provide credible climate simulations at continental scales that range from seasonal to decadal time scales (Randall et al. 2007). Additionally, some of these models have been shown to perform well regionally at daily time scales (Perkins et al. 2007).

These climate models also incorporate emissions scenarios by first using biogeochemical models to convert estimates of future greenhouse gas emissions to changes in greenhouse gas concentrations. These concentrations are then incorporated into the future based on four narrative storylines developed by the IPCC. These storylines (A1, A2, B1, B2) are set along two orthogonal axes: (i) Global vs Regional and (ii) Economic vs Environmental; they represent estimations of projected emission, environmental, social, technological and demographic developments over several decades (Nakićenović et al. 2000). All scenarios derived from the same storyline constitute a scenario family and forty scenarios have been defined by the Special Report on Emissions Scenarios (SRES). Together these scenarios are considered to account for the current uncertainty range of future greenhouse gas emissions (Nakićenović et al. 2000). While these were initially believed to represent emissions scenarios that are both plausible and pertinent, it should be noted that alternative futures are possible(Nakićenović et al. 2000). Indeed, recent studies have shown present rates of increase in carbon dioxide emissions are surpassing the highest of the SRES scenarios (Canadell et al. 2007; Raupach et al. 2007; Sokolov et al. 2009), and there is now the expectation that projections summarised by the IPCC may underestimate future change. Consequently, some authors have suggested that conservative B1 and B2 emission scenarios should be replaced by the more extreme A1 and A2 scenarios for analyses involving SDM (Beaumont et al. 2008).

Indeed, a new generation of scenarios are being developed to incorporate and reflect (i) advances in climate models and (ii) almost a decade of data on emerging technologies, environmental observations (e.g., land cover change) and economic data (Moss et al. 2010). The development of these new scenarios involves three (preparatory, parallel and integration) phases. The preparatory phase involved the selection of four existing scenarios [(i) 8.5 Wm^{-2} – very high emission scenario, (ii) 6 Wm^{-2} – high stabilisation scenario, (iii) 4.5 Wm^{-2} – intermediate stabilisation scenario, (iv) 2.6 Wm^{-2} – very low mitigation scenario] from the literature. The associated concentration and emission pathways of these are referred to as Representative Concentration Pathways (RCPs). The following parallel stage involves: use of these RCPs to generate climate model runs while other research groups simultaneously develop new socio-economic scenarios and appropriate storylines that are consistent with the RCPs. As the name suggests, the integration phase involves the amalgamation of the socio-economic pathways with the results from the climate model runs to develop a final set of integrated scenarios. These new scenarios will facilitate and link research on the impacts, adaptation and mitigation of climate change (Moss et al. 2010).

These new scenarios were unavailable for this study and hence analyses were conducted using the SRES A2 scenario (Section 5.2.1). The latter is consistent with the scenario mentioned above – which is characterised by the assumption of minimal international cooperation and hence little technology development, in conjunction with the high dependence of Asian economies on domestic coal resources (Moss et al. 2010).

5.1.5 Climate model uncertainties

SMs can project potential shifts in a species' distribution due to changes in climate by incorporating the future projections based on GCMs with the correlative relationship between the species being modelled and its required environmental conditions. The GCM grids consist of ten to twenty vertical layers of the atmosphere and up to thirty ocean layers across horizontal distances that range from approximately 250 km to 600 km (Jones et al. 2004; Wiens and Bachelet 2010). Different GCMs rely on and incorporate different parameters and functions in an effort to describe the dynamics of atmospheric circulation, ocean effects and feedbacks between land surfaces and the atmosphere. Hence different future climate projections may exist for a given level of greenhouse gas emissions – depending on the GCM being used (Jones et al. 2004).

Although GCMs may provide realistic representations of the large-scale aspects of climate, they generally do not facilitate good descriptions of climate at the regional and local scales (Hawkins and Sutton 2009, 2011) which are necessary for the assessment of potential impacts of climate change upon species distributions (Benestad 2004). Further, GCMs also assume homogeneous cloud cover and elevation within each grid cell, hence the complexity and climate patterns of heterogeneous landscapes, peninsulas and small islands which occupy only a small portion of a given grid may be overlooked and assumed to be ocean (Jones et al. 2004; Wiens and Bachelet 2010).

This coarse resolution is a problem for most conservation and impact assessment as many of these studies have documented cases in which the species that are most vulnerable to climate change are at present already confined to small areas (Kremen et al. 2008). Additionally, the planning of PAs tends to occur at a fine scale, with approximately 75% of internationally recognised PAs being approximately 300 km^2 in area or less (Tabor and Williams 2010). There is therefore an urgent need for high resolution future climate scenarios, which can be derived by the downscaling of GCMs (Jones et al. 2004).

5.1.6 Downscaling GCMs

The coarse resolution of GCMs can be refined to capture sub-grid cell heterogeneity by downscaling to the regional scale (Wilby et al. 1998). Two main types of downscaling exist: statistical downscaling and dynamical downscaling; both of which aim to incorporate the effects of land cover and topography. Importantly, both these methods are constrained by the coarse-scale output of the GCM from which they are derived. They are therefore not GCM substitutes but tools which, when used in combination with a GCM, add high resolution detail to broader projections (Jones et al. 2004). The former involves interpolations from empirical relationships among variables derived from GCM data or weather station observations in order to incorporate greater spatial variability into the climate change scenarios (Wilby et al. 2004). Common techniques include weather classification schemes, weather generators and regression models (Wilby et al. 2004). While computationally less demanding, statistical downscaling depends heavily upon the availability of sufficient weather observation data and also assumes that past relationships between regional climate and local weather persist into the future.

Dynamical downscaling involves the use of RCMs which are nested within a GCM (Fowler et al. 2007; Spak et al. 2007). RCMs explicitly represent the atmospheric processes operating at sub-grid scales and are resolved to simulate climate patterns at a fine scale (approximately 10 to 50 km). This allows for more detailed, realistic representation of climate features including regional scale anomalies, orographic precipitation and extreme climate events (Fowler et al. 2007; Spak et al. 2007). Although computationally demanding, an RCM is able to simulate most of the processes, interactions and feedbacks among climate components represented in the GCM (Daly et al. 2007; Jones et al. 2004). They are also better at representing the incidence of extreme weather events such as hurricanes (Jones et al. 2004), which is particularly useful for forecasting within Caribbean SIDS. A consequence of computational intensity is that for many regions (including the Caribbean) limited numbers of RCM simulations are presently available. This, in turn, prevents sufficient characterisation of uncertainty for these climate projections within SDM analyses (Diffenbaugh et al. 2008).

5.1.7 RCMs for the Caribbean region

Most small islands, including those in the Caribbean, have strong concerns about the potential impacts of climate change, which are very different to those of their continental neighbours. The close proximity of the small islands of the Caribbean to the large land masses of northern South America and Central America implies that some islands may partly share the climate features of one or the other of these land masses. However, these islands also share other climate features that are more important in defining their individual climates such as the strong relationship of their climate to sea surface temperatures (Jones et al. 2004). The coarse resolutions of GCMs do not distinguish the climate of these islands from the surrounding ocean. Additionally, many of the islands have areas of complex topography, such as mountains and uplands, which may substantially influence precipitation patterns, as well as overall climate heterogeneity across the island.

The Hadley Centre of the United Kingdom's Met Office has generated an RCM (HadRM3P) which is based on an the HadAM3H, an improved version of atmospheric component of the most recent Hadley Centre's coupled Atmosphere-Ocean General Circulation Model (AOGCM), the HadCM3 (Jones et al. 2004). Referred to as the Providing REgional Climates for Impacts Studies (PRECIS) RCM, it has been defined at horizontal resolutions of 50 km and 25 km and includes 19 atmospheric levels (reaching up to 30 km in the stratosphere) as well as four soil levels. It describes and diagnoses dynamical flow, clouds, precipitation, the atmospheric sulphur cycle, radiative processes, the land surface and deep soils, while maintaining the same formulation of the climate system as that of the GCM. This aids in ensuring that the model provides high-resolution regional projections of climate change that are considered consistent with changes projected at the continental scale by the GCM (Jones et al. 2004). This RCM is freely available for use by non-Annex I Parties to the United Nations Framework Convention on Climate Change and can be applied to many area of the world for generation of high-resolution climate change projections. It was used by the Cuban Meterological Institute to simulate the SRES A2 Greenhouse Gas emission scenario at resolutions of 50 km^2 and 25 km^2.

When applied to generating future climate scenarios of the Caribbean the PRECIS RCM was shown to 'reasonably' represent the current climate of the region with respect to the (wet and dry) seasonal rainfall, as well as annual and seasonal temperature patterns. It was also able to show an improvement in detail (compared to the GCM), particularly with respect to changes in topography, relief and surface type (Campbell et al. 2011).

5.1.8 Other issues of uncertainty

Climate change is believed to operate differently at different scales; being driven mainly by dynamics that operate at global and continental scales, its effects descend to alter climate and weather at the regional and local scales (Pearson and Dawson 2003). Hence its impacts may affect biological systems in different ways at different scales. The choice of spatial scale for SDM depends on the scales of the available species distribution data as well as the environmental/climate data. A common dilemma of the choice with respect to the spatial scale to be used in SDM modelling is based upon the fact that at a fine scale species distributions may be more influenced by biotic interactions, while environmental and climate factors appear to be more pertinent at coarse resolutions of broad geographic scales (Pulliam 2000). According to Wiens et al. 2009 some of the uncertainties associated with the discrepancy between climate and species occurrence data can be averaged out if the scale of the projected distribution is large, although this approach is prone to substantial over-estimations of suitable areas (Jetz et al. 2009; Seo et al. 2009). Additionally, while SMs that model fine-scale features are more likely to capture the factors that determine the realised distribution of a species, sufficiently fine-scale data may not be available for the region of interest.

SMs, like all other models, are sensitive to the quantity and quality of the data with which they operate. Apart from the uncertainty related to the degree of spatial auto-correlation and other factors related to the reliability of species occurrence records (Chapter 4), uncertainties also exist regarding the characteristics of the GCM used for projection of the potential future distribution of a given species. The spatial and temporal resolution of the climate data used to construct a GCM also affects its downscaling. Further, the uncertainties associated with the downscaling become important for conservation planning and management at the eco-regional and local scales.

Incoherence in scale between the species occurrence data and the grain-size of the climate model (and other environmental data) used to generate an SM can amplify the uncertainties related to the analyses (Root and Schneider 1993; Wiens and Bachelet 2010). When considering the distribution of target species in order to identify suitable areas for survival, it has been recommended that the climate change projections should correspond at least approximately to the scales of the species occurrence data (e.g., 25 km x 25 km pixels) (Wiens and Bachelet 2010). This matching of the scales of conservation management with climate change projections can be more problematic within the Caribbean SIDS (e.g., unavailability of sufficiently downscaled climate data); and care should be taken to acknowledge the uncertainties associated with these downscaled products (Wiens and Bachelet 2010). For example, some islands of the Caribbean can be encompassed within just one 50 km x 50 km pixel of an RCM; this makes matching of species occurrence data with climate change projections impractical for SDM.

Finally, there is little guidance on how to go about selecting the most appropriate climate model for a given application, with the final decision usually being influenced by data access (Beaumont et al. 2008). A good example of this is the paucity of data for the Caribbean region. SDM within the Caribbean using RCM data was impossible until the recent publication of the PRECIS RCM simulations for the region by the Caribbean Community Climate Change Centre (CCCCC) in Belize during 2010. Hence, SDM analyses are, at present, limited to the PRECIS RCM simulations at 50 km^2 and 25 km^2 resolutions and it is therefore not possible attempt to characterize the uncertainty with respect to other climate projections (from alternative climate projections of other GCMs) within SDM analyses at this point in time.

5.1.9 The way forward

The limitations of SDM that use a correlative approach to forecast species distributions are well documented in the literature, yet SMs remain an important tool for the estimation of the first-order effects of a changing climate upon species distributions (Pearson and Dawson 2003). Despite all the uncertainties mentioned above, SDM and in particular, correlative models are currently the only practical options for exploring the future responses of a wide range of species to an already changing climate. Some authors believe that the results of SMs can effectively contribute to conservation planning once their results are assessed and interpreted in conjunction with the uncertainties and limitations of the SM and climate model used for projection (Elith and Leathwick 2009).

Several authors have observed that this area of research is constantly being modified, improved and updated in its applications (Elith and Leathwick 2009; Franklin 2009). They believe that future efforts to incorporate dispersal, demography and the mechanistic constructs of species' responses to biogeo-physical factors will enhance the ecological realism of SMs (Lawler et al. 2009; Pearson et al. 2006; Thuiller et al. 2006). At present, there are several means that can be used to improve the use of SMs for extrapolation as well as reduce or expose sources of errors. For example, the use of ensemble forecasting (Araújo and New 2007), the retrospective testing of predictions (Araújo et al. 2005) or the reduction of differences between models by consensus (Pearson et al. 2006). Alternatively, where available, SMs can be linked with estimates of evolutionary change or with dispersal, physiological, landscape and/or population models in order to represent potential processes of change (Kearney and Porter 2009; Keith et al. 2008). However, considerable challenges still remain, especially with respect to how to model the likely change in biotic interactions as climate changes (Elith and Graham 2009). Nevertheless this is a work in progress which must be sustained, as the one thing that ecologists do seem to agree upon in the literature is that assessing the consequences of anthropogenic climate change for biodiversity is an essential task which must not be ignored (Thuiller 2007).

5.1.10 The effectiveness of PANs challenged

One area of improvement and development is the incorporation of SDM within reserve selection algorithms to determine the most suitable areas for: (i) the establishment of future conservation areas and/or (ii) identifying sensitive areas within existing PANs. Despite the dynamic nature of expected species distribution changes in response to climate change (Section 5.1.1), PANs (and the PAs that comprise them) remain at the centre of modern conservation efforts (Rodrigues et al. 2004). The establishment of current PANs have been based upon the implicit assumption of a relatively stable climate and takes no account of the dynamic nature of species' geographic ranges in response to climate change (Hannah et al. 2002).

Indeed, since the early 1800s conservation strategies involved the establishment of PAs – based on the assumption that individual species and their biological attributes are inextricably linked to location (Hannah 2010). Over the last two to three decades, these conservation strategies have expanded to also encompass the maintenance of biological diversity. However, this new goal was still often linked to a paradigm of place, with each region having its unique suite of species, genetic characteristics and ecosystems that required conservation. This 'paradigm of place' has continued to persist because the core of our conservation tools consists of networks of Protected Areas, which are also location focused. Furthermore, spatially fixed PANs within many countries are becoming increasingly isolated as a result of habitat destruction and are hence believed by many to be unsuitable (in their present state) for sustaining biodiversity conservation targets into the future (Hannah 2008, 2010; Pressey et al. 2007).

Some authors have surmised that the already occurring shifting of species geographic range to new areas will result in many species moving out of already established PANs (Araújo et al. 2004; Hannah et al. 2005). In addition, other research has demonstrated that the expected overall trend of a reduction of species range with climate change will also serve to contribute to net loss of representation within existing PANs (Hannah et al. 2005, 2007; Thomas et al. 2004). Such species range dynamics are therefore expected to reduce the effectiveness and relevance of the present PANs within a region with respect to future conservation strategies and objectives. These authors argue that much more research is required in order to develop mechanisms for the planning and management of PANs to cope effectively with these changes (Hannah et al. 2002; Scott and Lemieux 2005; Scott et al. 2002). This call for further research is not an isolated one, indeed the IPCC's special report, Climate Change and Biodiversity (Gitay et al. 2002, page 41) has highlighted that

> "the placement and management of reserves and protected areas will need to take into account potential climate change if the reserve systems are to continue to achieve their full potential".

Additionally, institutions such as the World Wildlife Fund (Hansen et al. 2003) have gone further by stating that in light of the limited defence that current PANs offer against the already occurring rapid environmental changes, they need to be

> "changed and adapted if they are to meet the challenges posed by global warming".

5.1.11 Analyses for improving the effectiveness of PAN within a changing climate

In an effort to address this need, some studies have examined the impact of climate change upon PAs (Coetzee et al. 2009; Hole et al. 2009), usually focusing on mechanisms to facilitate range shifts such as the enhancement of connectivity and dispersal (Hodgson et al. 2009). However, this study (assumes perfect dispersal) will not focus upon these areas in this discussion except to briefly mention that it has been found that long-distance connectivity between PAs is more costly and less feasible than attempts to establish connectivity within and adjacent to PAs (Hannah 2008). Additionally, the effectiveness of such connectivity is heavily dependent upon the degree and extent of anticipated species range shifts (Hodgson et al. 2009).

Empirical studies have shown that SDM, if carefully implemented are able to forecast successfully broad-scale directional changes of species range under climate change scenarios (Araújo et al. 2005; Dobrowski et al. 2011; Kearney et al. 2010; Rodríguez-Sánchez and Arroyo 2008). SDM has however been less effective in estimating the magnitude of these changes as this is contingent on unmeasured factors, such as dispersal capacity and availability of refugia (Araújo et al. 2005). However, it has been demonstrated that SMs are able to indicate range increase or decrease with reasonable accuracy. Hence it is possible to provide conservative interpretation of model projections by indicating direction, as well as increase/decrease in range (as with the winners, losers, shifters and grounded used in Section 5.2.7 below) without quantitative inference of unmeasured factors, such as extinction risk, population parameters or abundance (Brook et al. 2009).

Taking the potential of SDM further in an attempt to address this need, other researchers have argued that the creation of new reserves to supplement already existing PANs is the most logical way to curtail the expected future loss of species representation (and habitat) mentioned above (Anderson and Martínez-Meyer 2004; Coulston and Riitters 2005; Hannah et al. 2007; Hossell et al. 2003). Two main methods have been discussed in the literature for the identification of such new reserves, these focus upon either achieving ample species or climatic representation within PANs.

The former involves the coupling of SDM with reserve selection algorithms (which reflect suitability of habitat inside and outside the PAN). SDM simulations are used to facilitate the calculation of hundreds to thousands of species range gains or losses within existing PANs. The reserve selection algorithms are then used to add systematically potential reserves in order to compensate for anticipated lost representation, to the point where no further improvement can be obtained for future climate scenarios. The maximum achievable improvement in species representation is then measured and gauged against pre-defined target levels of species representation (which varies place to place depending on conservation objectives) (Araújo et al. 2004; Pressey and Cowling 2001; Pressey et al. 2007; Williams et al. 2005).

The latter method involves the adding of areas which contain climates that are poorly represented within a given PAN. Again, new areas are added incrementally until climatic representation targets are achieved. These climatic representation targets are determined by the climatic tolerance ranges of target species which are being protected. Hence, as with the species representation method, the climatic representation targets ultimately depend upon the number of species whose ranges are modelled and incorporated into the prevailing conservation strategies (Pyke and Fischer 2005; Pyke et al. 2005).

While both these approaches are believed to increase the chances of maximising species representation within PANs as climate changes, the species representation method has the advantage of being the only one which can meet specific targets regarding the area under protection for a given species (Hannah 2008). Because species survival into the future depends on having ample area available to support viable populations, this option has been explored to a greater depth. Hence based on the premise that species representation objectives are the most relevant means of determining whether a PAN will be able to conserve effectively into the future; a PAN is considered to remain effective as a conservation tool if it alone, or in conjunction with additional areas, is able to capture the expected climate driven shifts of targeted species. However, if, even with additional areas, a PAN is unable to sustain species representations, then it is considered to be of limited use for future conservation efforts (Hannah 2008; Hannah et al. 2007).

In several areas of the globe PANs can still be used as important tools for substantially augmenting the chances of species conservation into the future (Alagador et al. 2011; Araújo et al. 2011). This can be done by (i) incorporating climate change into conservation planning and (ii) creating new PAs which, together with current PAs, satisfy biodiversity targets for both the present and future climates simultaneously. Authors such as Hannah et al. (2007) go as far as inferring that such investment in new PAs is likely to be necessary in all parts of the world where the conservation of biodiversity into the future is sought.

5.1.12 Climate change needs to be constrained

Several of the main goals within the Protected Areas Policy of Trinidad and Tobago (GOTT 2009b) have incorporated species conservation within their descriptions. These include:

> “ (i) Preserve genetic materials as elements of natural communities, prevent the loss of any plant or animal species, maintain biological diversity,

> and protect natural ecological patterns and processes
>
> (ii) Protect and restore populations of rare, endangered, and endemic species and the habitats on which they depend for survival
>
> (iii) Manage populations of species and areas of ecosystems that are used for extraction of goods (e.g. timber harvesting, wildlife hunting, harvesting of craft materials)."

Hence, a naturally occurring question is whether the addition of new PAs will be sufficient to sustain successfully species representation targets into the future. Analyses of this nature are difficult to justify if taken from the perspective that storylines of anthropogenic development are likely to be very different between trajectories that exist at present and those that will be formulated in fifty years from now. One study was found which directly addressed this question (assuming that storylines will remain unchanged) (Hannah et al. 2007). It was able to demonstrate that while the addition of new PAs within three varied regions of the world (the Cape Floristic Region in South Africa, Europe and Mexico) were able to restore substantially species representations that are projected to be lost by 2050 due to climate change, complete restoration was impossible (restored species representation varied between 78% to 94%). Further, despite a strong performance up to 2050, these findings did not imply that representation will be maintained later on, especially if climate change becomes more severe (Hannah 2008).

Efforts to conserve biodiversity into the future are expected to achieve little success unless the international community finds a way to constrain and stabilise the concentration of greenhouse gases in the atmosphere (Franklin 2009; Hannah et al. 2007). Today, as greenhouse gas emissions continue to increase, strong and rapid climate change, in conjunction with other anthropogenic disturbance (e.g., deforestation), have created an urgent need to adapt traditional conservation techniques, such as the establishment of PAs. It has become clear that apart from providing sustainable management of ecosystems and habitats, in order to be effective, conservation strategies require simultaneous mitigation of the impacts of climate change. For example, the above study (Hannah et al. 2007) indicates that greenhouse gas levels of only double that of pre-industrial carbon dioxide levels would already decrease the capacity of many improved PANs (new PAs added) to maintain their biodiversity targets. Hence, despite the postulation that these additional PAs, if adequately sized and placed can compensate for the projected shifts in species range outside of existing PAs; this is based on the assumptions that climate change will be limited to the lower range (2 °C) of current international objectives and that range dynamics can be constrained to scales that can be captured by PAs (Hannah et al. 2005).

5.1.13 Plight of the Small Island Developing States

In addition to the above requirements, the level of climate change experienced, the physical and biotic geography, the existing PAN and the taxa which are targeted by conservation efforts within any two areas in the world will be unique. Hence there is great variation in the area of additional PAs that will be required to facilitate this conservation of biodiversity into the future. But what are the options for countries or regions which may not be able to allocate substantial amounts of land to the creation of new PAs? For many regions of the world such as many of the Caribbean SIDS, the creation of new PAs will be difficult if not impossible due to limited survival of undisturbed natural habitat, increasing levels of habitat destruction and intense competition for alternative uses of land within such small, fixed geographic spaces. Yet, according to the discussion above, it is more than likely that the current fixed PANs of these islands will be insufficient to preserve the biodiversity of these islands.

The potential of this problem is further exacerbated by the fact that the establishment of the majority of PAs within many developing countries including many of the Caribbean SIDs has been carried out on an ad-hoc basis, with PAs being established in areas that are considered unsuitable for development and agriculture (Section 2.1.5). Also, the few PAs that were not established on the basis of such convenience were however based on conservation planning strategies which effectively ignored the dynamic nature of species' geographic range as they respond to climate change. Additionally, in the case of Trinidad, the opaque nature of jurisdiction, legislation and policy governing different PAs (Section 2.2) which together comprise the PAN poses a further impediment to the application of any strategy which may seek to add and manage new PAs to the existing PAN. Furthermore, while some recent research has reported results which can be viewed as potential analogues to SDM within SIDS [e.g., the limitation and potential isolation and extinction of cold-adapted and higher elevation species within Scotland and western Europe (Berry et al. 2007; Lenoir et al. 2008; Walmsley et al. 2007)]; no literature was found on examples of assessment of future species representation within the terrestrial PANs of small islands in the Caribbean, nor any suggestions for adaptation measures at such a small scale. What is to become of species representation within the PANs of these islands as climate continues to change? The answers will remain elusive until steps are taken to begin the process of assessment at this scale.

It is beyond the scope of this chapter and even this thesis to replicate analyses involving the use of reserve selection algorithms described above. However it does seek to take the first steps of (i) forecasting the potential future distributions (suitable climate space) of the selected eleven species (from Chapter 4) and (ii) combining these eleven future projections to create a 'collective model' in order to highlight areas across Trinidad and its PAN which are projected to lose, maintain and gain representation of suitable climate space for these species forty years into an SRES A2 scenario.

5.2 Methods

5.2.1 Regional Climate Models

For these analyses, simulated monthly averages (P, Tmax, Tmin and Tmean) based on the PRECIS Caribe RCM (generated for the Central America, Mexico and the Caribbean region) were obtained from the Department of Computer Science, Mathematics and Physics at the Cave Hill campus of the UWI in Barbados. These data were originally derived from the HADRM3P RCM which was generated from the HadAm3H GCM (an improved version of the HadCM3 GCM). Simulations based on the SRES A2 greenhouse gas emission scenario at a resolution of 25 km^2 were used for these analyses.

From the SRES collection of storylines mentioned in Section 5.1.4.2 (Figure 5.1), the SRES A2 storyline describes a very heterogeneous world which is based on a theme of self-reliance and the preservation of local identities. It describes a continuously increasing population (due to slow convergence of fertility patterns across regions) in conjunction with economic development that is regionally focused. Additionally, it incorporates fragmented and relatively slower (compared to the other SRES storylines) per capita economic growth and technological change. This scenario also predicts an increase in global carbon dioxide concentrations from 380 ppm in 2000 to 700 ppm in 2080 that is accompanied by rises in temperature of 2.8 K (Nakićenović et al. 2000).

5.2.2 Preparation of Future Climate Data

5.2.2.1 Time frame of study

As the SDM analyses for this study focused on the potential impacts of changes in climate within the next 40 years; ‘future climate data’ was derived (below) to represent simulations of the SRES A2 scenario for changes in climate over the island of Trinidad between the present (2000–2010) and the 2035–2065 periods.

5.2.2.2 Preparation of future climate data from the RCM’s simulated monthly averages

Several steps were involved in the derivation of the future climate data. The RCM data obtained consisted of simulated monthly averages for P, Tmax, Tmin and Tmean from the year 2000 to 2099. For each year the data consisted of a total of 48 ASCII grids [12 grids per parameter (one for each month)] each with a resolution of 25 km^2 (e.g., Figures 5.2 to 5.5).

5.2.2.3 Calculation of a ‘climate signal’ between present and future climates

The first stage required the calculation of the simulated ‘climate signal’ between the present and the future period of interest (2035–2065). The following steps were involved:

1. Monthly averages for P, Tmax, Tmin and Tmean were calculated for the periods representative of the present (2000 to 2010) and future (2035 to 2065) climates (e.g., Figures 5.6 to 5.9). The unavailability of simulations for years prior to 2000 prevented the present time period from spanning more than 10 years. Ideally, the present average should have been calculated from 1960 to 1990 to match the period from which WorldClim used

observation data to generate its present climate surfaces.

2. For P, the climate signal was calculated by dividing the future precipitation values by those of the present (e.g., Figure 5.10).
3. For Tmax, Tmin and Tmean, the difference in climate simulations between present and future periods were calculated by subtracting the present parameter values from the future values (e.g., Figure 5.11).
4. The result consisted of 48 ‘climate signal grids’ – comprising of 12 (monthly) climate signal grids for each parameter.

5.2.2.4 Interpolation of climate signal grids to a resolution of 1 km^2

The resolution of these climate signal grids was 25 km^2 which contrasted with the WorldClim present climate dataset of 1 km^2 resolution. In order to proceed further, the resolution of both datasets needed to be the same. This was achieved by interpolating the simulated climate signal data from 25 km^2 to 1 km^2 using the Inverse Distance Weighted (IDW) interpolation technique.

IDW interpolation is based on the premise that points within the interpolating surface that are close to one another are more similar than those which are far apart. Therefore in order to predict the value of an unmeasured point, the IDW uses the known values of surrounding locations – with the closest having more weight than those which are further away. The final interpolated surface is a weighted average of scatter points with the weight assigned to each scatter point inversely related to the distance from the unmeasured point (Kennedy 2004).

The IDW was seen as the most suitable interpolation method for the purpose of this study as, apart from being intuitive and efficient, it is ideally suited to evenly spaced points (as with the 25 km^2 simulated climate grids) and is sensitive to outliers. Furthermore, unlike some other interpolation techniques, it does not extrapolate values beyond the value limits of known location points (Kennedy 2004).

The 48 ASCII climate signal grids generated in Section 5.2.2.3 above were imported as raster images into ArcGIS 9.3 and interpolated to a spatial resolution of 1 km^2 using the IDW function of the Spatial Analyst Tools within the ArcToolbox. These 1 km^2 raster images were then converted to and ASCII format using the 'Raster to ASCII' function of the Conversion Tools within the ArcToolbox (e.g., Figures 5.12 and 5.13).

5.2.2.5 Future climate data

These 48 interpolated climate signal ASCII grids were then combined with corresponding ASCII grids of WorldClim's present data for the P, Tmax, Tmin and Tmean data described in Section 4.2.3.1. This combination represented the 'future climate scenario data' for the monthly averages of P, Tmax, Tmin and Tmean to be used in the generation of the future Bioclim variables for the SDM analyses.

Combination of these data involved:

1. Finding the product of the interpolated climate signal and WorldClim present ASCII grids for Precipitation (e.g., Figure 5.14).
2. Adding the interpolated climate signal ASCII grids for Tmax, Tmin and Tmean to their respective WorldClim present data counterparts (e.g., Figure 5.15).

5.2.3 Creation of future Bioclim variables

This future climate scenario data generated for P, Tmax, Tmin and Tmean were used to generate Bioclim variables following the same procedure outlined in Table 4.1 of Chapter 4. These were limited to the Bioclim variables that were selected for further SDM analyses in Section 4.2.3.3 (Table 4.1).

Differences between future and present grids of (i) these Bioclim variables (Figures C.1 to C.30), (ii) mean annual temperature (BIO1) (Figures C.31 to C.33), (iii) mean annual precipitation (BIO12) (Figures C.7 to C.9), (iv) mean seasonal temperature (BIO1 split into dry and wet seasons) (Figures C.34 to C.39) and (v) mean seasonal precipitation (BIO12 split into dry and wet seasons) (Figures C.40 to C.45) (Appendix C) were also generated to assist in the explanation of the species distribution patterns analysed below.

5.2.4 Projecting future distributions of species using MaxEnt

5.2.4.1 MaxEnt requirements

The potential distribution model of each species under the SRES A2 scenario was generated within MaxEnt by taking the model trained on the suite of predictor variables for the present climate (Chapter 4) and ‘projecting’ it by applying it to a new suite of corresponding predictor variables for the SRES A2 scenario.

In addition to the species location data and directory of predictor variables for the present climate (as used in Chapter 4), the input requirements into MaxEnt also included a directory of corresponding predictor variables for the future SRES A2 scenario.

Apart from this single modification, the procedure and settings configuration in MaxEnt was identical to those used for the generation of the potential present distribution models in Chapter 4 (Section 4.2.8).

5.2.4.2 Future projection output

As with the potential distribution models built in Chapter 4, the projected future distribution of each species was expressed as a probability distribution grid map – with each pixel illustrating the probability of occurrence of suitable climate space for the species of interest (e.g., Figure 5.16). There was also another accompanying grid map which showed the effects of 'clamping' upon the projected future distribution (e.g., Figure 5.17).

Additionally, for each Bioclim variable used in the construction of the SMs, the MATLAB software (The MathWorks Inc. 2009) was used to locate and compute the number of pixels for which future conditions extended beyond the range of the present. These were used to calculate the proportion (%) of Trinidad that was projected to experience novel climate conditions for each Bioclim variable. These data were also mapped in ArcGIS 9.3 to show the location of these novel climate conditions across the island (Table 5.2).

5.2.5 Presence/absence maps for the SRES A2 scenario

Species presence/absence maps for the SRES A2 scenario (e.g., Figure 5.18) were then created in the same manner as the presence/absence maps for present climatic conditions described in Sections 4.2.11.2 and 4.2.11.3.

Each of these presence/absence maps was then clipped with the GIS forest cover polygon for 2007 (Chapter 2) in order to discern the net loss of each species' potential future (SRES A2 scenario) distribution due to limitations in forest cover during this year (Table 5.3).

5.2.6 Change maps

The presence/absence ASCII grids of each species for both the present climate (generated in Section 4.2.11.3) and the future SRES A2 scenario (generated in Section 5.2.5) were both combined to create a 'change map' within a MATLAB environment. These change maps illustrated the anticipated changes in each species' distribution range (across the entire island) from its potential present distribution to its projected distribution forty years into the future under the SRES A2 scenario. The following steps were involved in the construction of these change maps:

1. The presence/absence ASCII grids – consisted of pixel values: 0 (absent) and 1 (present).
2. For each pixel within the ASCII grids, a binary chronological sequence of pixel values was developed by combining corresponding values from the present and future grids in the format (present future). For example, if at a given pixel, species A was absent during the present climate but present during the future climate scenario, this would be depicted by the sequence (0 1).
3. There were four possible chronological sequences which could occur:
    (i) (0 0) = species does not occur now and may not occur in the future
    (ii) (0 1) = species does not occur at present but could occur in future
    (iii) (1 0) = species occurs at present but may not occur in the future
    (iv) (1 1) = species occurs now and could occur in the future

4. The resulting ASCII grid contained pixels labelled with the decimal values derived in step 4 above. It expressed the change status of each pixel within the grid.
5. These species ‘change’ ASCII files were then imported into ArcGIS 9.3 as raster images – where they were referred to as ‘change maps’ (Figures 5.19 to 5.29) which depicted the projected change in species range across the entire island.
6. Insets for these change maps were then created (see insets within Figures 5.19 to 5.29) which limited the change maps (described in point 5 above) to the areas of existing forest within the island, effectively excluding all other areas within Trinidad which had been cleared for development. These were created by overlaying and clipping the change maps above with the Dissolved Forest Cover polygon for 2007 (Section 2.3.2) within ArcGIS 9.3.

5.2.7 ‘Winners’, ‘losers’, ‘shifters’ and ‘grounded’

Inspired by a concept used in the MONARCH report (Walmsley et al. 2007) the change maps of the eleven species were used to categorise the species as ‘winners’ , ‘losers’, ‘shifters’ and ‘grounded’. These categories were all based upon anticipated changes in the distribution range of a given species compared to the size of the area of its potential present distribution range (Chapter 4). As the names suggest, a ‘winner’ refers to a species which is projected to experience an overall increase in the total area of its distribution range while a ‘loser’ refers to a species which is projected to experience a decrease of 50% or more of the area occupied by its present distribution range. Additionally, a ‘shifter’ was defined as a species whose distribution range is anticipated to experience (i) less than a 50% decrease in area compared to its potential present range (inclusive of new areas of expansion) and (ii) a noticeable expansion into previously unoccupied areas (see summary table below). Finally, a 'grounded' species referred to one which is projected to experience no change in its entire potential present distribution under the SRES A2 scenario.

5.2.8 RCM sensitivity analysis

Because only the SRES A2 Greenhouse Gas emission was available for use in this study, it was desirable to explore the projected response of the 11 species to slight climate deviations from this scenario.

This involved the following steps:

1. Within a MATLAB environment, the ASCII grids of the future climate scenario monthly averages for P, Tmax, Tmin and Tmean generated in Section 5.2.2.5 were modified by changing the precipitation values of each pixel by ±10% and/or the temperature values (Tmax, Tmin and Tmean) by ±1 °C. This effectively created a range of alternate scenarios which fell either within the SRES A1F1 marker scenario range (least optimistic SRES scenario) or the lower edge of the SRES B1 marker scenario range (most optimistic SRES scenario) (Figure 5.1).
2. These changes allowed for a total of 9 possible scenarios (Table 5.4) inclusive of the original SRES A2 scenario.
3. The Bioclim variables selected for further analyses in Section 4.2.3.3 were generated for all 8 modified scenarios following the same procedure outlined in Table 4.1 of Chapter 4.
4. MaxEnt was then used to generate future projections of all eleven species – for each of the modified scenarios.

5. Species presence/absence maps for all modified scenarios were created in the same manner as were the presence/absence maps for present climatic conditions described in Sections 4.2.11.2 and 4.2.11.3.
6. For each species, the number of pixels categorised as ‘present’ were tabulated and compared across all 9 scenarios.
7. The effects of changes in temperature and precipitation upon each species were then calculated and expressed as the anticipated change the area of a species’ distribution compared to the original SRES A2 scenario (Table 5.5).

5.2.9 Total maps – Present and Future

The set of eleven binary presence/absence ASCII grids generated in Chapters 4 (Sections 4.2.11.2 and 4.2.11.3) and this Chapter’s Section 5.2.5 for the selected tree species were summed within a MATLAB environment to create a ‘total count grid’ for the present and the future (SRES A2) climates. Within both of these total count grids, each pixel value represented the total number of species present within that pixel. Each of these total count grids was then mapped in ArcGIS 9.3 to create a ‘total count map’ which illustrates the distribution of species density for the present and the future climates (Figures 5.30 and 5.31).

5.2.10 Choosing a threshold for the creation of collective presence/absence maps

From each of the total count grids (Figures 5.30 and 5.31), the number of species present at each pixel was tallied (Figure 5.32). Frequency distribution curves (for present and future) of the number of species versus number of pixels were then plotted – from which an inflexion point on each curve was discerned (Figure 5.32). The number of species at this inflection point was used as a guide to determine a threshold (equal to 3 for both present and future) from which the ‘collective species presence/absence map’ for (i) the present and (ii) the future climates were created (Figures 5.33 and 5.34). Within the ASCII grids of these maps, all pixels with species numbers up to and excluding this threshold was mapped as ‘absent’ and all pixels with species totals more than or equal to the threshold was labelled ‘present’. For the purposes of this study, these collective species presence/absence maps represent the areas of Trinidad within which a general rather than individual species presence are projected to occur during the present and future climates.

5.2.11 Collective change map

Using the method described in Section 5.2.6, the (binary) ASCII grids for the collective species presence/absence maps of the present and future climates were then combined to create a ‘collective species change map’ (Figure 5.35). This map illustrates the anticipated changes (range contractions, expansions and stable areas) in the ‘collective’ species presence from the present to forty years into the future under the SRES A2 scenario.

The creation of such a map represents a method of analysing projected changes in suitable climate space for any set of species – such as those comprising a particular community of interest or other sets of concern.

5.2.12 Connection between the collective change map and projected changes in climate

This collective species change map (Figure 5.35) was then compared – both visually and statistically to the Bioclim difference maps (Section 5.2.3) in order to discern whether the anticipated changes in collective species distribution was related to anticipated changes in climate. The Bioclim maps used for this comparison were all located within Appendix C.

The statistical component of this comparison was done using the Band Collection Statistics tool within ArcGIS 9.3. This tool was used to generate a correlation matrix within which the correlation coefficients represented the ratio of the covariance between both maps – divided by the product of their standard deviations. Ranging from +1 to -1, these correlation coefficients represented a measure of dependency between (the cell values of) both maps. Positive correlations represented a direct relationship between the contents of both maps, while negative correlations indicated an inverse relationship. A correlation coefficient of 0 implies that the contents of both maps were independent of each other (Snedecor and Cochran 1968).

5.3 Results

The results described in this section refer specifically to patterns or trends observed with respect to the set of eleven tree species that were selected for the SDM analyses in Chapter 4 (Section 4.2.9). Hence care should be taken not to confuse species-related terminology with inferences regarding all of the vegetation present within a given area. For example, the terms 'species richness' and 'densities' refer only to the density within this set of eleven species and not to the density of all species within a given area.

Furthermore, it should be remembered that the term 'potential future distribution' of a given species refers specifically to the availability of suitable climate space for that species (thereby indicating areas which will be favourable for its future distribution). It does not take into account the species ability to disperse to these areas and the availability of suitable habitat nor does it predict where that species will actually occur in the future.

5.3.1 Loss of species' potential future distributions due to limitations in forest cover during 2007

Net losses in the potential future distributions for this group of eleven species as a result of restrictions in forest cover availability ranged between 0% and 40.3% during 2007 (Table 5.3), with five out of eleven species expected to experience net losses greater than 25% of their potential future distributions.

5.3.2 Anticipated changes in Bioclim variables from present to an SRES A2 future

This section begins by discussing projected changes in BIO1 (mean annual temperature) and BIO12 (mean annual precipitation) – on both an annual (Table 5.6) and seasonal (Table 5.7) basis. This is in order to provide context regarding the general picture of changes in overall 'climate' (i.e., precipitation and temperature) to be expected from the RCM data. It is against this general picture that changes in the Bioclim variables (specific, biologically meaningful) used to build the SMs are discussed (Table 5.8).

5.3.2.1 Annual differences

Some general patterns were discerned from the maps that illustrated the change between present and future Bioclim conditions across the island (Figures C.1 to C.33 in Appendix C) under a SRES A2 scenario. Details of the annual differences between BIO12 (Annual Precipitation) (Figure C.9) and BIO1 (Annual Mean Temperature) (Figure C.33) are given in Table 5.6

5.3.2.2 Seasonal differences

Trinidad experiences two seasons per year, the dry season (January to June) and the wet season (July to December). Details of the seasonal differences between the present and SRES A2 scenario for BIO12 (Figures C.42 and C.45) and BIO1 (Figures C.36 and C.39) are described in Table 5.7.

5.3.2.3 Remainder of Bioclim variables

A description of the differences between the present and SRES A2 scenario for the remaining Bioclim variables [BIO13 to BIO19 (Figures C.10 to C.30), BIO9m4 (Figure C.6) and BIO4 (Figure C.3)] employed within these analyses is provided in Table 5.8.

Additionally, as can be seen from Table 5.2, the novel climate conditions (outside the range of present climate) projected for Trinidad within a SRES A2 scenario ranged from 0.1% (BIO19) to 36% (BIO13) of the island's area. It is also clear that six (BIO9m4, BIO12, BIO13, BIO16, BIO17 and BIO18) of the ten Bioclim variables were projected to experience novel climate conditions – to varying extents, within the north-eastern 'quarter' of the island. In contrast, the novel climate conditions for BIO14, BIO15 and BIO19 were located along the central region of Trinidad's western coast. BIO4 was the only exception – for which novel climate conditions were projected to be scattered across the island.

5.3.3 Species change maps and the winner, losers and shifters

The change maps generated in Section 5.2.6 illustrated individual changes between the potential present and future distributions (with respect to the SRES A2 scenario) for all eleven species that were modelled in these analyses (Figures 5.19 to 5.29). A loss in distribution range was anticipated for all species, with the proportion and location of these losses varying dramatically. It was also very noticeable that these areas of projected range contractions were generally large and contiguous in nature. In a contrasting manner, while proportions of stable distribution ranges of all species were projected for all species, these areas were generally much smaller and less contiguous than the projected areas of range contractions. Areas of range expansion occurred for all species, except *Sterculia puriens* var. *glabrescens* and *Calophyllum lucidum* (Figures 5.25 and 5.21). These areas of expansion were generally smaller than areas of stable and contracting range, and varied in terms of both location and contiguity.

The majority (eight) of the 11 species were categorised as losers, and are projected to lose more than 50% of their potential distribution range under the SRES A2 scenario (Table 5.1). Particularly noteworthy are *Calophyllum lucidum* and *Sterculia puriens* var. *glabrescens*, *Tabebuia stenocalyx*, *Eugenia confusa*, *Carapa guianensis*, and *Tovomita eggersii* – all of which were projected to lose more than 90% of their present distributions. The remaining area (relative to the size of their present potential distributions) ranged from 49.9% (Figure 5.23) to 0.9% (Figure 5.21), with *Calophyllum lucidum* and *Sterculia puriens* var. *glabrescens* projected to suffer the greatest loss of distribution range, bordering on almost complete disappearance (Figures 5.21 and 5.25).

Two species *Brosimum alicastrum* (Figure 5.19) and *Virola surinamensis* (Figure 5.29) were categorised as shifters. These were forecasted to maintain areas equivalent to 64.8% and 52.4% respectively of their potential present distribution range. When the change maps of both these species were compared, a striking, contiguous concurrence of projected presence (categories 1 and 3 in change maps) was noticed within the south-western and south-central region of the island.

The lone winner, *Mora excelsa* (Figure 5.24), was projected to experience a 22.7% increase in range size compared to that of its potential present distribution. Again, forecasted presence of this species indicated a strong, fairly contiguous presence across the south of the island.

However, interpretation of these patterns should also take into consideration that the SMs generated for these analyses do not include other factors (e.g., dispersal ability and habitat availability) which may influence the actual distribution of a given species – especially at finer scales (Berry et al. 2005, 2007; Pearson and Dawson 2003). Hence, these change maps may portray an optimistic impression of what may actually occur relative to, and should not be mistaken for, the realised niche of a given species.

Species	**Percentage of current distribution range projected to:** **(i) occur** **(ii) be lost** **(iii) expand (new)**	**Anticipated change in species distribution (Winner/Loser/Stable/Shifter)**
Brosimum alicastrim	(i) 65 (ii) 51 (iii) 16	**Shifter** – Expansion within north-eastern region of island; maintains distribution within south-central Trinidad
Calophyllum lucidum	(i) 1 (ii) 99 (iii) 0	**Loser** – almost entire range lost
Carapa guianensis	(i) 11 (ii) 91 (iii) 2	**Loser** – most of range lost – with pockets of distribution remaining intact within the south-central region of the island
Eugenia confusa	(i) 10 (ii) 92 (iii) 2	**Loser** – most of range lost with small pockets remaining intact within North and Central Trinidad
Ilex arimensis	(i) 50 (ii) 65 (iii) 15	**Loser** – At least half of range lost, with new pockets of climate space scattered within central and southern Trinidad
Mora excelsa	(i) 123 (ii) 55 (iii) 78	**Winner** – despite contracting within the NE part of its distribution range – this species gains about 1/5 area – expanding westwards – especially within southern Trinidad
Sterculia puriens var. *glabrescens*	(i) 1 (ii) 99 (iii) 0	**Loser** – Majority of climate space lost
Tabebuia stenocalyx	(i) 2 (ii) 98 (iii) 0	**Loser** – Majority of climate space lost
Tabernaemontana attenuata	(i) 39 (ii) 81 (iii) 20	**Loser** – Over 70% of climate space lost – with new pockets of suitable climate space occurring in scattered locations across Trinidad – but concentrated in the NE, NW, SW and SE regions of the island
Tovomita eggersii	(i) 11 (ii) 91 (iii) 2	**Loser** – Majority of climate space lost with stable or new range located along the western coast of central Trinidad as well as the NE, north-central, NW regions of the island.
Virola surinamensis	(i) 52 (ii) 77 (iii) 29	**Shifter** – despite contracting within the northern and eastern parts of island – this species gains about significant climate space within southern Trinidad

Table 5.1: Anticipated changes in species distribution range based on the SRES A2 scenario.

5.3.4 RCM sensitivity analysis

It is noteworthy that when the range of change in annual temperature values (+0.2 °C to +2.7 °C) and annual precipitation levels (-21.4% to 34.4%) used for these RCM sensitivity analyses were compared to the range of local warming and changes in precipitation projected for Trinidad from the A2, A1B and B1 (no data available for A1F1) scenarios (available at `http://country-profiles.geog.ox.ac.uk/`); both temperature and precipitation ranges of the former effectively encompassed the combined projection range of the latter (A2, A1B and B1 scenarios) which spanned from +0.7 °C to +2.6 °C and -21% to 1% in precipitation. This therefore achieved the purpose of the sensitivity analyses (Section 5.2.8) which was to compensate for the use of only one SRES scenario for the SDM.

Change in the projected area occupied by a given species in response to deviations of ±10% precipitation and/or ±1 °C varied among the eleven species – with the response of each species to all four scenarios being unique (Table 5.5). The future distributions of seven out of the eleven species were projected to decrease in size in response to an increase in temperature relative to the SRES A2 scenario; while three species (*Virola surinamensis*, *Tabernaemontana attenuata* and *Mora excelsa*) were projected to increase. The inverse trend was observed for scenarios where there was a decrease in temperature relative to the SRES A2 scenario, with the same sub-set of seven species showing an increase in expected range size while *Virola surinamensis*, *Tabernaemontana attenuata* and *Mora excelsa* were shown to decrease. *Brosimum alicastrum* was the only species which showed no projected change in range size in response to deviations of temperature from the SRES A2 scenario.

However, changes in the size of forecasted future species distributions in response to deviations of precipitation (relative to the SRES A2 scenario) were not as uniform as the species response to deviations in temperature. Seven of the eleven species exhibited decreases in their relative areas in response to an increase in precipitation, while *Carapa guianensis*, *Eugenia confusa*, *Tabebuia stenocalyx* and *Tovomita eggersii* were seen to increase. A more obvious trend was observed in response to a decrease in precipitation, with ten of the eleven species showing increases in area, while only *Brosimum alicastrum* was projected to suffer a decrease in area.

From these observations generalised inferences can be made about species response to deviations of precipitation and temperature from the SRES A2 scenario. The strongest inference derived was that species tended to favour conditions of relatively lower precipitation; while greater precipitation resulted in a general decrease in the size of projected future species distributions. Species also appeared to favour relatively lower temperatures, with general decreases in species distribution size observed for scenarios with higher temperatures. Hence the general response to deviations of precipitation and temperature seemed to indicate that the size of the forecasted future distributions increased under drier, cooler conditions than those of the SRES A2 scenario.

This is unsurprising as, despite tropical forests being generally portrayed as consisting of a collection of plant species which thrive in humid, moist conditions, this applies only to some types of tropical forests – such as tropical rainforest. There are other types of tropical forests which do not exist under such humid, moist conditions (Richards 1996). Indeed consultation with local experts from Trinidad confirmed that many tree species within the island require drier conditions during important phases of their reproductive cycles and are known to be limited by too much moisture availability (Baksh-Comeau, pers. comm. 2010). Hence, it is not at all strange that the distributions of most of the species modelled for these analyses increased under drier conditions simulated by the sensitivity analyses.

5.3.5 Total Map – Present

From the analyses described in Section 5.2.9, species richness across Trinidad for the present climate was observed to vary, with certain regions having low species richness (0 to 2 species) while other parts of the island were projected to have medium (3 to 5 species) and high richness (6 to 11 species) (Figure 5.30). Based on these subjectively selected thresholds, three clearly defined zones of medium-to-high species richness were defined within the island (Figure 5.36). These zones were used purely for illustrative purposes and do not have a functional value. The largest of these (containing 3 to 11 species) was observed along a horizontal zone that stretches across the Northern Range (the Northern Horizontal Zone (NHZ)). The majority of this NHZ was considered to have a high density of species, with medium and low species densities (1 to 5 species) occurring mainly between the eastern and central regions of this zone.

A zone of medium-to-high species richness also extends longitudinally from the east-central part of the NHZ in a southerly direction towards the southern coastline (the Longitudinal Zone (LZ)). Species richness was observed to gradually decrease in a southerly direction within the LZ, with relatively higher density levels occurring within its northern and central regions (4 to 9 species) compared to that of its southern region (2 to 7 species). A third zone of mainly medium species richness was observed to occur horizontally along the southern edge of the island (the Southern Horizontal Zone (SHZ)), especially within its south-western (2 to 6 species) and south-eastern (2 to 7 species) portions. The central region of this zone was characterised mainly by low species richness (1 to 3 species).

Areas with mainly low species richness included the area between the central and eastern regions of the Northern Range (1 to 4 species) and the western region of the island (0 to 2 species). Finally, visual inspection of Figures 5.19 to 5.29 revealed that with the exception of *Tabernaemontana attenuata* (the potential distribution range of which was confined to the NHZ and the LZ); the remaining ten species were distributed within all three of these zones of higher species richness.

5.3.5.1 Species richness within the PAN

The existing PAN within the island was observed to contain projected medium and/or high levels of species richness for the present climate. All of the PAs within the Northern Range as well as all of the large PAs within the central region of the island were encompassed within the NHZ and the LZ. The PAs along the southern edge of the island were also, for the most part, included within the SHZ. The main exception to this was the PA-sc, half of which coincided with the relatively lower species densities projected to occur within the central portion of the SHZ (Figure 5.30).

When limited to areas of existing forest on the island, most of the PAs were also projected to contain medium and/or high levels of species richness. The two main exceptions to this were the PA-sw and the PA-se which have been recently deforested (see Chapter 2).

5.3.6 Collective Species presence/absence Map – Present

The map produced from Section 5.2.10 (Figure 5.33) mirrors the trends described for the present total map (Figure 5.30) in Section 5.2.9. Collective species presence was found to exist across the majority of the Northern Range as well as within the LZ. Additionally, collective species presence occurred along the SHZ, except for the central region of this zone.

Similarly, collective species presence is projected to occur throughout most of the existing PAN of the island – with the exception of approximately half of the PA-sc, and a quarter of the PA-sw (due to the harvesting of *T. grandis* and agriculture (Section 2.4.2) (Figure 5.33).

5.3.7 Total Map – Future

A big contrast was observed between projected species richness across the island for the future SRES A2 climate (Figure 5.31) compared to that of the present climate. Low species richness is projected to pervade the island, with the medium-to-high species densities across the majority of the NHZ and LZ (for the present period) being greatly reduced (0 to 2 species).

A single zone of mainly medium species richness (3 to 6 species) for the future is projected to be located within the central and western portions of the SHZ. Further, unlike the present total map, the central region of the SHZ is projected to contain medium (instead of low) density levels which extend northward in a narrow band that tapers off at the central part of the island (within the LZ).

There are also small pockets of medium-to-high species richness within the south-eastern and north-eastern corners of the island (3 to 7 species) as well as scattered along the western half of the island's northern edge.

Unlike the present climate, visual inspection of Figures 5.19 to 5.29 revealed that within an SRES A2 future, just five species (*Brosimum alicastrum*, *Carapa guianensis*, *Ilex arimensis*, *Mora excelsa* and *Virola surinamensis*) were distributed within all three of these zones (NHZ, LZ and SHZ). Further, these areas of future distribution were much smaller and less continuous compared to those of present climatic conditions.

5.3.7.1 Species richness within the PAN

The PAs located within the Northern Range as well as those within Area A are not expected to contain high species richness during the SRES A2 scenario. However large portions of the PA-ce, PA-se as well the entire PA-sc and PA-sw are encompassed within this zone of mainly medium species richness (Figure 5.34). Further, when limited to areas of existing forest on the island, large portions of the PA-sw and the PA-sc are excluded due to recent deforestation described in Section 2.4.2.

5.3.8 Collective Species presence/absence Map – Future

The collective species presence projected for the future SRES A2 scenario (Figure 5.34) also followed the trends illustrated within the total map for the future (Figure 5.31).

It is projected to be limited to only a few PAs within the southern part of the island, with no PA completely containing this presence. Of these, the PA-sw and PA-sc are expected to contain the highest proportions of collective presence, with the majority of their areas being encompassed. The PA-se and PA-ce are also expected to contain part of the collective species range, although these areas are less contiguous (compared to the PA-sw and PA-sc) and do not represent very large portions of these PAs. The PA-ne is projected to completely lack collective species presence, while the smaller PAs along the north-western coast are projected to contain scattered fragments of the collective species range.

When limited to the areas of existing forest within the island, the two PAs (PA-sw and PA-sc) containing the highest proportions of collective species presence were observed to lose large areas of this presence due to deforestation (Chapter 2). However, in light of the fact that almost 50% of the island has been forested since 1969 (Section 2.4.4.1), there are several means by which these PAs can be reforested to eventually represent long-term reserves. These are highlighted in Sections 5.4.8 and 6.2.1.

5.3.9 Collective change map

The anticipated change in collective species presence between the present and future climates (Figure 5.35) follows a similar pattern to the collective species map for the future (Figure 5.34). It shows that a greater part of the collective species range is projected to contract in the future to less than half its present size, with stable collective species presence occurring mainly along the central and south-western regions of the SHZ and extending northward into the LZ up to the central part of the island. Additionally, pockets of stable collective species range are also projected to occur within the south-eastern and north-eastern corners of the island as well as being scattered across the western part of the island's northern coast.

Areas of collective species expansion were in total, much less than the total area of anticipated stable collective species presence. These areas of expansion were also limited to the central and south-western parts of the SHZ – again extending northward in a tapering manner towards the central region of the island. As with the stable collective range, small areas of expansion are projected within the south-eastern and north-eastern corners of the island.

5.3.9.1 Collective presence within the PAN

Similar to the distribution of the collective species presence for the future, the majority of the stable collective species range is expected to be limited to the majority of the PA-sw and PA-sc, and to lesser extents within the PA-se and PA-ce. Additionally, smaller, less contiguous areas of future collective species presence are also projected to be scattered within small areas of the PAs along the north-western and north central coast of the island.

Areas of collective species expansion are however limited to the PA-sw, PA-sc and the western edge of the PA-se as well as their external peripheries. In particular, the area between the PA-sc and the PA-se appears to be the most contiguous part of this collective species expansion range. Scattered areas of collective species range expansion are also projected to occur along the southern external periphery of the PA-ce.

These areas of projected stable and expanding collective species range represent areas of conservation interest. However, when limited to areas of existing forest within the island, the majority of the area projected to be suitable for collective range expansion both inside and outside the boundaries of the PAs is eliminated due to deforestation. This occurs particularly along the eastern periphery of the PA-sw (settlement, industry and agriculture) (Figure 2.13) and within the PA-sc and its northern periphery (harvesting of *T. grandis*) (Figure 2.14). The remaining areas of projected collective range expansion are confined to mainly within the PA-sc and the edges of the PA-se as well as the noticeably contiguous area between both these PAs. In a similar manner, large sections the projected collective stable range have been removed due to deforestation within the PA-sw and PA-sc, the non-protected region between the PA-se and the PA-ce and the north-eastern corner of the island. The major areas of collective stable range which remain, and hence which represent areas of interest for conservation purposes – are now limited to the southern edge of the island, parts of the PA-se and PA-ce as well as the western half of the island's northern edge.

5.3.10 Correlation of collective species presence to changes in Bioclim variables

From the correlation coefficients derived by comparing the collective change map with the Bioclim difference maps (Section 5.2.12), correlation coefficients ranged from 0.08 (BIO1 – dry season) to 0.74 (BIO17) (Table 5.9). Bioclim variables with coefficients greater than an arbitrary 0.65 (BIO12, BIO13, BIO14 and BIO17) were then visually compared in greater detail.

Visual patterns within the collective change map (Figure 5.35) also appeared to concur most strongly to the maps that illustrated the projected difference between present and future conditions for BIO17 (Figure C.24), and to lesser extents, for BIO12 (Figure C.9), BIO13 (Figure C.12) and BIO14 (Figure C.15) in decreasing order.

From Figures 5.35 and C.24, it was observed that the majority of the projected areas of collective species presence (both stable and expanding range) during the future strongly concurred with areas where the change in precipitation of the driest quarter (BIO17) was anticipated to be between 0% and a 20% increase. This included areas within the SHZ, the south-eastern and north-eastern ends of the island as well as western half of the island's north coast. Additionally, the majority of projected zone of collective species contraction in Figure 5.35 concurred with areas in Figure C.24 that are projected to experience a decrease in precipitation within the driest quarter.

A similar, though less pronounced and detailed concurrence was observed between

Figure 5.35 and the difference patterns for BIO12 and BIO13 (Figures C.9 and C.12). Areas of future collective species presence within the SHZ and southern regions of the LZ were observed to concur within areas that are projected to experience between approximately 0% and 20% increases in both mean annual precipitation (Figure C.9) and precipitation of the wettest month (Figure C.12). However future collective species presence within the western half of the island's north coast were observed to concur with relatively lower increases of between 7% to 10% in mean annual precipitation and -5% to 10% in precipitation of the wettest month. This difference between the SHZ (and southern LZ) and the NHZ is thought to be associated with areas of higher elevations within the latter and the accompanying atmospheric lapse rate which occurs with increases in altitude. The influence of elevation upon collective species change within the NHZ is discussed further within Section 5.4.6.

The concurrence of collective species presence with the difference pattern projected for BIO14 (Figure C.15) was less pronounced than those of BIO12 and BIO13. Within the SHZ this ranged from no change in precipitation of the driest month to increases of up to 40%. However, the most noticeable concurrence with projected collective species presence in the future was observed for the south-eastern and north-eastern corners of the island where increases of between 40% to 48% are projected to occur.

The seasonal difference maps for BIO12 were also observed to be concurrent with the collective future species presence. While the difference map for the wet season (Figure C.45) showed almost the same concurrence and relationship as BIO12 (Figure C.9), the difference map for the dry season (Figure C.42) indicated that there is projected to be an approximate increase of about 10% to 12% in precipitation within the area that contains the tapering band of collective future species presence which extends from the SHZ into the LZ towards the central region of the island. This increase in range was noticeably less than the areas on either side of this band, which are projected to experience increases in precipitation that are greater than 20% precipitation and were characterised by no future collective presence.

5.4 Discussion

These analyses were based upon several assumptions and hence careful data interpretation is required for this discussion. This study was focused upon projecting where suitable climate space (both present and future) may occur for selected species with no attempt to predict actual distributions as a result of climate change. In addition to the uncertainties discussed in Chapter 4 and this chapter, there are seven key caveats which need to be considered. Firstly, climate was assumed to be the dominant factor influencing present distribution of the eleven study-species. An equilibrium of present species distributions with climate was assumed, but other factors, e.g., biotic interactions, species dispersal ability (assumed to be perfect) and habitat suitability, were assumed to be temporally stable and were not incorporated. The study focused on a species' Trinidadian climate space and did not consider whether its entire climate space existed within the Caribbean region or beyond. Climatic extremes were also ignored which may have a profound effect on the distribution of a species at its range margins. Finally, only one GCM (HadAM3H) under only one climate scenario (SRES A2) was used, hence the full range of uncertainty may not be illustrated.

In particular, it should be noted that these analyses did not incorporate species dispersal because, apart from no information being available on the dispersal potential of the species modelled within Trinidad; there is also a lack of congruence within the literature regarding the importance of animals as agents of plant species dispersal to and within insular environments. For example, studies such as Whittaker and Jones (1994) report the important role played by birds in facilitating inter-island dispersal of some plant species; as well as the importance of frugivorous bats in the endogenous dispersal of already established plant species within islands such as Krakatau. However, dispersal does not guarantee establishment – as seen with several legumes which make it to the shores of Hawaii, but seldom become established Carlquist (Carlquist 1980). There are other studies such as Cody and Overton (1996) and Carlquist (1966a) which report decreased dispersal potential of many taxa – both plants and animals within insular environments. Additionally, authors such as Hansen et al. (2008) have reported that the already few frugivorous taxa (e.g., birds, bats, tortoises and lizards) which facilitate plant dispersal within islands may be limited in doing so due to drastic reductions in native habitat within many islands (e.g., the Caribbean SIDS). Such reduced habitat may not be able to support viable populations of some plants as seedlings may not be dispersed far enough to escape natural enemies (Janzen-Connell model). This situation is further compounded by reports of increases in invasive species due to increasing temperatures and human visitor frequency – which may lead to these invasive species successfully out-competing other establishing species that have been dispersed by bats, birds or other frugivores (Bergstrom and Chown 1999).

5.4.1 Conceptual challenges regarding scale

Modelling the potential species distributions within Trinidad presented conceptual challenges that were distinctive when compared to the majority of SDM studies conducted over larger landmasses. It has been well described in the literature that different factors influence species distribution at different scales; with climate exerting a greater influence at the macro-scale, while biotic interactions are believed to be a more dominant driving force at local scales (Pearson and Dawson 2003; Wiens and Bachelet 2010). However, this hierarchical concept was derived from SDM studies carried out in much larger areas within continental settings. Within small islands, there is no available guidance with respect to the dimensions of such a hierarchical system. For example, are these hierarchical scales fixed and absolute (at a continental scale) or do fractal alternatives exist at the small island scale (Halley et al. 2004)? If yes, then at what dimensions does a 'macro-scale' or 'local-scale' exist within this island? If no, then is it justified using climate data to generate SMs at the small island scale?

These questions became particularly important when considering the validity of the resolution of the climate data that were used for these analyses. In the absence of relevant answers in the literature, the results of Chapter 3 were referred to; where it was observed that precipitation (climate) at the island-wide/ 'macro-scale' and elevation (topography) within the Northern Range/ 'intermediate-scale', appeared to influence the location of ecologically similar groups of vegetation within the island. This was used as a guide to infer that the use of 25 km^2 climate data could contribute in a meaningful way to the SDM analyses of this chapter.

5.4.2 Discrepancy between present and future climate data

A resolution of 1 km^2 (WorldClim's climate grids) was selected to represent the present climate instead of a more coarse-grained climate grid (e.g., a 5 km^2 or 10 km^2 resolution) as the former would be able to capture the way that climate is affected by the complex topography of the Northern Range more clearly than the latter. While some authors have pointed out that the representation of climate at such fine resolutions could lead to misleading interpretation of results (Wiens and Bachelet 2010), it can also be argued that choosing slightly coarser girds such as 5 km^2 or 10 km^2 would not change the general patterns depicted in the model output. This is in keeping with the prevailing recommendation which dictates that uncertainties related to the use of SDM for forecasting require that interpretation be limited to this general pattern rather than emphasis on details (Franklin 2009). Adherence to this recommendation would to help to ensure that the results generated from 1 km^2 data were not misinterpreted.

There was also an obvious discrepancy between the resolutions of the present and future climate data used for the analyses with the future climate data being of a 25 km^2 resolution. Future climate projections were also available on the WorldClim website at a 1 km^2 resolution. Despite these data being of the same resolution as the present climate data, they were not chosen for these analyses because they were generated using a ‘change factor technique’ which involved the interpolation of changes from a GCM. This study used the same ‘change factor technique’ (Sections 5.2.2.2 to 5.2.2.5) to generate the future climate data that were input into MaxEnt – but made use of the added resolution and detail from the PRECIS RCM instead of a GCM. These WorldClim data were therefore not as representative of regional climate details as simulations from the PRECIS RCM, especially since there were much fewer observation points on the island that were used to generate the WorldClim climate grids. In contrast, while the 25 km^2 simulations of the PRECIS RCM were coarser, its dynamical downscaling allowed for a more realistic representation of climate features in response to the complex topography of the Northern Range, regional scale anomalies, orographic precipitation and extreme climate events.

Additionally, the 25 km^2 climate grids used for this interpolation consisted only of twelve data points, which led to some pixels having three or fewer adjacent pixels (e.g., Figure 5.2). However, this issue regarding resolution of climate change projections is not unique to these analyses. Nevertheless, there are a number of limitations to the interpolation of these climate change surfaces which arose – and which should be taken into consideration. These include:

(i) The RCM data were derived from only one model, hence even if the resolution was perfect, this would still be a snapshot of a plausible climate change future.

(ii) The 25 km^2 data used for these analyses is the highest resolution projection data that currently exists for this region, hence these analyses used the best data available (compared to GCM data at 250 km^2 – which does not even 'recognise' the island as land).

(iii) Interpolation is a conservative method of superimposing these RCM data onto the higher resolution baseline (WorldClim) data (and WorldClim is by no means considered realistic for the Caribbean region)

(iv) The 25 km^2 data (12 points) adds regional variation to the projection compared to alternative GCM data (1 point). These 12 points were able to show contrasting changes between the northern and southern regions of the island, and also 'recognised' regions of higher elevation within the island's interior.

(v) Nonetheless the interpolation process only projected the 25 km^2 response in the RCM onto the higher resolution baseline; it is assuredly the case that the RCM missed higher resolution local responses that are additional to those simulated at 25 km^2, and this is a fundamental limitation that should be borne in mind.

(vi) Statistical downscaling could be used to take the RCM data and estimate point or high resolution, but this requires time-series of observed data at the point or WorldClim gridded resolution. However, these were/are not available for the island. Therefore, these analyses did the maximum that was possible with the available climate change data.

5.4.3 The losers prevail

One of the main points emerging from these analyses (Table 5.1) is that none of the species modelled were projected to maintain entirely stable distributions (‘grounded’ species) under the SRES A2 scenario, with large contractions in potential distribution range being projected for the majority of species under such future conditions (Figures 5.19 to 5.29). A noteworthy example of this trend in range reduction is that of the loser *Stercilua puriens* var. *glabrescens* (Table 5.1). As outlined in Section 3.2.6, this species was included in the list of tree species chosen for the SDM analyses because it was identified as the most ubiquitous of the ecologically important species within the island. As shown in Figure 5.25, its potential present range which encompassed the majority of remaining forested regions on the island is projected to almost completely disappear.

Such contraction of these species’ potential distribution range is likely to be exacerbated in the future if forest cover across the island decreases as a result of the increasing deforestation rates and anthropogenic encroachment of forested areas reported in Section 2.5.3. As seen in Table 5.3, the already contracted potential future distributions of almost half of the species within this group would automatically suffer net losses of 25% or more in area if forest cover remains as it was during 2007. Should forest cover decrease beyond that of 2007, then the already small potential distributions of these species (under SRES A2 conditions) would contract further – and hence further lowering their chances of survival within the island into the future.

Many authors have suggested that species response to a changing climate may be individualistic and that the composition of communities which exist today is likely to be different to those of a future, changed climate (Milly et al. 2008; Pearson et al. 2004; Thuiller et al. 2008). It is now generally accepted that the drivers which lead to these distribution changes are varied and interdependent. These include, but are not limited to, climate, biotic interactions such as dispersal and competition, physiological requirements and genetic properties of the species (Hampe 2004; Pearson and Dawson 2003; Pearson and Dawson 2004). However, as in many other studies, very little, if any of such information exists for the species modelled in these analyses. This scarcity of data is one of the main reasons that SDM, for all of the uncertainties associated with it, is still the only method which allows for the forecasting of species response to climate change.

A good example of this paucity of data is that of a well-studied species within the island, the sole winner of this study, *Mora excelsa*. These analyses show that its distribution range is projected to change from a range-limited potential present distribution to one which expands to encompass an area almost 20% greater than the size of its potential present distribution range (Figure 5.24). *Mora excelsa* is an enigmatic mono-dominant species which can form up to 85–95% of the canopy trees within a forest (Beard 1946a). This is in contrast to most other tropical forests within which the dominant tree species seldom rises to more than 10% of the canopy trees. The reason behind this mono-dominance and hence its distribution range has been a source of mystery to ecologists over the years (Beard 1946a; Huston 1994; Richards 1996); and while this has been hypothesised to be linked to its prolific reproductive ability which results in an unusually large amount of seedlings carpeting the forest floor (Beard 1946a; Janzen 1970), the factors responsible for its distribution and mono-dominance are yet to be discovered.

5.4.4 Species response to an SRES A2 future

The results of the RCM sensitivity analyses revealed that the majority of the eleven species modelled generally appeared to favour cooler, drier conditions than those projected for the SRES A2 scenario. The maps that illustrate the difference between present and projected SRES A2 conditions for BIO12 and BIO1 (Figures C.9 and C.33 from Appendix C) indicate that these conditions occur within 'transition zones' between the hotter, drier western and central regions of the island and its cooler wetter southern and eastern edges. This transition zone along the southern periphery as well as north-eastern and south-eastern ends of the island also coincides with large portions of the anticipated areas within which both shifters as well as the lone winner are projected to exist and expand in the future (Figures 5.19, 5.29 and 5.24).

However, the transition zone along the (central) eastern periphery of the island neither concurred with the projected future distribution ranges of the shifters and winner nor with those of any of the other species modelled (Figures 5.19 to 5.29). This is likely to be at least partially as a result of edaphic factors, with a large part of this region consisting of the Nariva Swamp, one of the major wetlands of the island. Forests within this area tend to be categorised as swamp-forests and were excluded from the ecological analyses in Chapter 3 which determined the species that were selected for these SDM analyses. If swamp-forest species were included as part of these analyses, it is likely that the RCM sensitivity analyses would not have indicated such a strong tendency of the set of species towards cooler, drier conditions – as species within these forests are generally believed to prefer moist/humid, warmer conditions. In such a situation, a less acute preference for cooler, drier conditions together with the lower elevation of such areas – and hence a lack of additional cooling from an atmospheric lapse rate (Section 5.4.6) may contribute to an increased probability that the collective species presence would extend to include the transition zone within the eastern region of the island.

Further, none of the eleven species were observed to exist or expand within the central Northern Range, which is anticipated to experience the highest increases in precipitation (Figures 5.19 to 5.29). A similar pattern was observed for the western periphery of the island, which, with the exception of *Mora excelsa* and *Virola surinamensis*, is not anticipated to contain suitable climate space for any of the other species during an SRES A2 scenario (Figures 5.19 to 5.29). Some may view this as a lucky co-incidence because as outlined in Chapter 2, this western region also represents the portion of the island that has been most converted to irreversible forms of development.

5.4.5 The influence of precipitation-based climate parameters

When compared to the maps which illustrate the anticipated difference in the highlighted Bioclim variables (Section 5.3.10) across the island between the present and SRES A2 climates (Appendix C), it was observed that collective species presence is projected to be maintained and/or expand in areas which experience between stable to moderate increases in precipitation, during not just the dry, but also the wet season (BIO13). It was also clear that areas which are projected to (i) continue to experience large amounts of precipitation in spite of, or as a result of projected changes between the present and future climates (e.g., the region between the central and eastern parts of the NHZ) or (ii) areas which expect decreases in precipitation (e.g., the western region of the island) will not be expected to support collective species presence in the future.

Taking these local variations in ‘climate’ conditions into consideration, it is feasible that these results (distribution of collective species presence) do not contradict – but actually conform to the results of the RCM sensitivity analyses (species preference of drier and cooler conditions – Section 5.3.4). The collective species presence is anticipated to occur within regions of the island that are projected to experience a combination of zero to moderate increases in precipitation in conjunction with temperature change zones that range from stable to the lowest available increases within the island (Figure C.33). It is possible that the congruence of collective species presence with areas of stable to moderate increase in precipitation instead of areas projected to experience a decrease in precipitation may simply be a response to the condition that there are no areas within the island that are projected to experience a decrease in temperature. Hence, hotter conditions are ‘physiologically compensated’ by mild increases in precipitation (Figure C.33). Conditions which deviate from this combination such as (i) high levels of, or increases in precipitation, (ii) decreases in precipitation – together with /or greater than minimal increases in temperature would result in conditions which do not lead to the physiological equivalent of cooler, drier conditions – hence a loss of collective presence occurs. Additionally, that the pattern of collective species presence for the future appeared more crafted to the details of projected changes in precipitation parameters rather than temperature patterns is not unexpected; as the findings of Chapter 3 (Section 3.3.2.3) which were based on independent (non-modelling based) analyses, highlighted precipitation as a major influence upon the community composition within the island.

This explanation highlights a potential difference with respect to the interpretation and explanation of SDM conducted at the small scale of a Caribbean SIDS compared to large, continental scale analyses. It demonstrates the need for details of local climate conditions at a finer than 25 km^2 resolution within islands of this size. However, the paucity of published work on such finer-scaled climate conditions may lead to the requirement of greater access to 'expert' knowledge.

5.4.6 Influence of elevation within the NHZ

However, apart from the influence of precipitation-based parameters mentioned in Section 5.4.5, elevation was also perceived to influence areas of both future collective species stable and contracting range within the NHZ. A comparison of altitude above sea level (Figure 3.22) with the collective change map (Figure 5.35) revealed that regions within the NHZ which were projected to support stable collective species range belonged to one of two elevation categories. Firstly, areas within the NHZ ranging from 0 to 304 m above sea level which were also projected to experience (i) between 1 °C and 1.2 °C increases in annual temperature (Figure C.33) and (ii) annual precipitation increases of between 8% to 12% (Figure C.9). Secondly areas within fringes of the north-western peninsula which were greater than 304m above sea level and which were projected to experience (i) increases in annual temperature between 1 °C and 1.3 °C and (ii) 7% to 10% increases in annual precipitation.

In the case of the former, the final outcome of incorporating temperature decreases due to an atmospheric lapse rate of 1.66 °C per 309 m with projected changes in annual temperature (Figure C.36) led to an anticipated final temperature range increase of between 0.3 °C to 1.2 °C – within areas of projected mild increases in precipitation. As suggested in Section 5.4.5 such projected small increases in temperature may be 'compensated' for by stable to moderate increases in precipitation – and hence conform to the cooler, drier conditions required to sustain species range survival as indicated by the RCM analyses. Also, incorporation of the same atmospheric lapse rate in the latter situation would result in overall decreases in temperature (compared to the present BIO1 map – which does not incorporate the effect of an atmospheric lapse rate) combined with very small projected increases in precipitation within the already naturally arid north-western peninsula. Such conditions would again create cooler, dry conditions which conform to the findings of the RCM analyses.

In contrast, the majority of the NHZ which was projected to experience collective species range contraction belonged to an altitude above sea level range of 179 m to 968 m. Incorporation of temperature decreases due to the atmospheric lapse rate with projected increases in annual temperature resulted in overall temperature decreases ranging from approximately 0 °C to 4 °C (compared to the BIO1 map for the present climate). When combined with projected increases in annual precipitation in excess of 20%, such cooler, more moist conditions are likely to lead to collective species range contraction due to non-conformance with the cooler, drier conditions that are required to sustain future species survival.

5.4.7 Caution with respect to interpretation

Firstly, based on the patterns of novel climate conditions projected for the Bioclim variables used in these analyses (Table 5.2), there was a greater uncertainty associated with (i) the north-eastern quarter and (ii) the central region of the western coast of Trinidad within the SMs that were generated by MaxEnt. When compared to the collective change map, these areas of greater uncertainty also coincide with the regions within which collective range contraction is projected. From a simplified perspective, if one considers that these novel climate conditions do not correlate with the present climate conditions that were used to construct these models, then it is likely that such areas would not be projected as suitable climate space for these species in the future. However, because the MaxEnt clamping was invoked for these analyses, these novel climate conditions were not incorporated in the construction of the SMs. This is because, as mentioned in Section 5.1.2, the MaxEnt clamping treats variables outside the training range as if they are instead, at the limit of their training range. This is likely to be the reason for small areas within the north-eastern corner of the island being projected as suitable for the future survival of the individual species within this group (Figures 5.19 to 5.29). Additionally, it is noteworthy that, for the most part, the collective presence projected for the future does not coincide with these areas of novel climate conditions, but instead occur within areas that are projected to experience climate conditions within the present climate range. Such areas of collective presence are therefore associated with relatively less uncertainty. Therefore, apart from the small area of collective presence projected to occur at the north-eastern corner of the island, the collective change map concurs with areas of less uncertainty within the SMs that were generated by MaxEnt.

Secondly, the pattern of collective species range response is contrary to the trends that have been reported in the literature which describe the movement of species either pole-ward or upward (in altitude) in search of pre-existing climatic conditions as the climate changes (Hickling et al. 2006; Lenoir et al. 2008). This is perhaps because as demonstrated by these analyses and those of Chapter 3, the distribution of these eleven species appears to be mainly driven by suitable combinations of precipitation-based climate variables and elevation. Hence it is unsurprising that the collective species presence was observed to follow areas within the island that are projected to experience suitable precipitation and elevation levels rather than simply migrating northwards towards the poles.

However, all of the eleven species modelled during these analyses, are anticipated to experience at least partial range contraction within the NHZ. It could be therefore be inferred that the species which live in the moist, cooler conditions of the NHZ but may not be able to 'adapt' to the projected increases in temperature within this region (e.g., Figures 5.21 and 5.22) when compared to the species which are able to live within the hotter, drier conditions of the SHZ. Hence it may require less effort on the part of the SHZ species to adjust to increases in temperature (and mild increases in precipitation) compared to those which are found within the NHZ.

However, this argument does not hold as there are more examples (Figures 5.19, 5.20, 5.23, 5.24 and 5.29) which have potential distribution ranges that span the length of the island from the NHZ to the SHZ. While all of these are projected to maintain a stable presence within the SHZ and contract from the NHZ, this cannot be attributed to the loss of specialised temperature conditions (within the NHZ) because of the wide range of environments within which these 'generalists' are known to exist. Indeed the only inference that can be made from the results of these analyses is that the 'climate space' of these species are projected to shift to the SHZ and its environs, which is anticipated to result in the contraction of the collective presence range to the southern part of the island.

5.4.8 Potential of incorporating Trinidad's PAN into future conservation strategies

There are several foreseeable problems that such a contraction of the collective presence is likely to pose for the development of any future conservation strategies which seek to incorporate the future survival of these species within the PAN of the island. It can be seen from Figure 5.35, that apart from a small scattering of areas within the small PAs along the north-western coast of the island (which occur within the difficult terrain of the Northern Range – and are hence not threatened by deforestation); the future collective survival of these species is projected to be limited, for the most part, to (i) the smaller PAs within the SHZ and its environs and (ii) the northeastern corner of the island – which is situated mostly outside of the PA-ne. Hence the largest PA within the island (PA-ne) is not projected to contribute towards the future collective survival of these species, in addition to which, the second and third largest PAs, the PA-se and the PA-ce are only anticipated to contribute partially towards collective presence in the future.

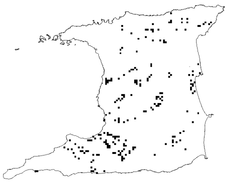
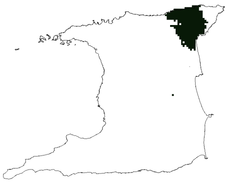
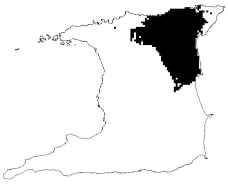
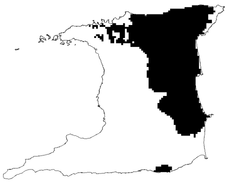
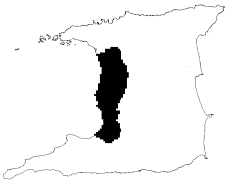
At first glance, it may be considered that (i) the merging of the PAs within the SHZ as well as (ii) the expansion of these PAs to encompass their present external peripheries (which are important for future collective species expansion) could enhance the potential of ensuring the future collective survival of these species. However, while the PA-sw and PA-sc are almost completely encompassed within the projected collective range, as mentioned in Section 5.3.9.1, forest within the PA-sw and its periphery have been cleared to make way for irreversible forms of development such as settlement and industry. Additionally, a large part of the PA-sc has been have been converted to teak (*Tectona grandis*) and Caribbean pine (*Pinus caribea*) plantations by the Forestry Division of Trinidad and Tobago. Further, approximately 50% of the projected range of collective expansion is expected to lie at the external peripheries of these PAs, particularly noteworthy is the contiguous region of projected expansion between the PA-sc and the PA-se. However, these areas are known to be under private ownership and apart from being eroded due to deforestation (Figures 2.21, 2.22 and inset of Figure 5.35), could also prove difficult to acquire due to the widespread squatting upon these lands (Section 1.1.5). Likewise, the majority of the area within the north-eastern corner of the island that is projected to sustain stable collective presence is privately owned and has been deforested to make way for settlement and agriculture.

This brings almost to a full circle the issues discussed in Chapter 2, which highlight the need to ensure adequate allocation of natural areas for the conservation of the island's flora and fauna. There are some means by which some of the above impediments to the expansion and merging of the PAs within the SHZ may be addressed. Firstly, legislation within the National Protected Areas Policy and the National Forest Policy (Sections 2.5.4) may provide an opportunity for the teak and Caribbean pine plantations within the PAs of this southern region to be allowed to revert (or be actively reforested) to natural forest once harvested. Alternatively, exploration of the potential for adjustment of the island's PAN through de-gazettement and restoration may yield possibilities for promoting and maintaining areas of greater, more contiguous forest cover within this region. As discussed in Section 2.5.2, the establishment and maintenance of secondary forest can be used to increase connectivity of forested areas within the SHZ (both inside and outside the PAs), thereby helping to increase its potential to support the survival of these modelled species into the future. Additionally, the co-operation of private land owners in order to facilitate the establishment of such reforestation and connectivity may be gained by the introduction of community incentives such as 'payments for environmental services (PES)' which are discussed further in Section 6.2.1. In a similar manner, encouraging the replacement of row-crop and intensive agriculture with agroforestry such as cocoa, coffee and nutmeg plantations within the privately-owned areas of the north-eastern corner of the island may help to both quell the spread of settlement and create secondary forest.

Further, in conjunction with these strategies, solutions are also required to address: (i) the intense competition for already limited land that is required for settlement, agriculture, industry and other anthropogenic activity and (ii) illegal and widespread squatting for agriculture and settlement. Despite the above mentioned implementation of the National Protected Areas Policy and the National Forest Policy, any development of conservation strategies involving the allocation and management of areas for the future survival of these species will require the co-operation of science (Chapter 6) political will and co-operation from the private stakeholders who may own the lands which border the peripheries of the PAs. There is also a need to address the tenure rights of agricultural and residential squatters before community participatory schemes such as the PES can be effective both within the SHZ and the north-eastern region of the island. However, before any recommendation can be made with respect to the area of land which will be needed to ensure the future survival of these species into the future, further analyses (involving the use climate data derived from multiple GCMs) which are beyond the scope of this thesis are needed. These are highlighted in Chapter 6.

Finally, even if it was possible to expand and merge these southern PAs to facilitate survival of these species, would it be possible to sustain their survival beyond forty years into the future? This would depend on several factors including: (i) the stabilisation of greenhouse gas concentrations and (ii) the prevention of encroachment of the PAN by anthropogenic activity. Assuming that (ii) was possible, any progression of climate change beyond the levels used in these analyses would be likely to result in a further reduction or even disappearance of the climate space of these species. Because of the small, fixed, limited geographic space that is available within the Caribbean SIDS for the establishment and substantial increase of their respective PANs, perhaps an alternative approach would be to incorporate similar SDM analyses that focus on detecting future suitable climate space across the entire Caribbean region rather than on just one island. This would require a great deal of collaboration and coordination of conservation initiatives across many levels of planning – ranging from the selection of species to be targeted for regional conservation to the eventual assisted translocation of target species to PAs within the region that have been deemed suitable for their future survival. In addition, such a ‘regional PAN’ would require a more comprehensive modelling approach involving the construction of model ensembles based on multiple SDM algorithms (Araújo and New 2007) as well as climate data derived from multiple GCMs. Suggestion for such analyses are outlined in Sections 6.2.3 and 6.2.6. While such an endeavour is likely to be complex, the successful collaboration and ‘combining’ of the PANs of individual islands has the potential to provide much needed additional space and therefore opportunity to preserve target species into the future.

5.5 Tables

Bioclim variable	**Area of island projected to experience novel climate conditions within a SRES A2 scenario (%)**	**Location of novel climate conditions within Trinidad for SRES A2 scenario Where: (Black = novel climate conditions) (White = conditions within range of present climate conditions)**
BIO4	3.7	
BIO9m4	7.5	
BIO12	17.8	
BIO13	36	
BIO14	11	

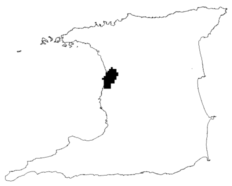
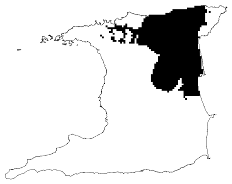
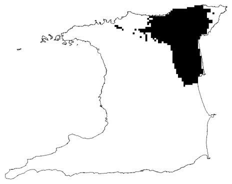
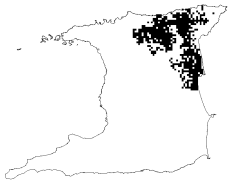
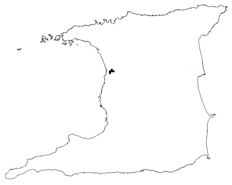
BIO15	1	
BIO16	23.4	
BIO17	15.3	
BIO18	10.9	
BIO19	0.1	

Table 5.2: Area and location of novel climate conditions projected for Trinidad within a SRES A2 scenarios.

Species	**Net loss of species' potential future distributions due to the limitations forest cover during 2007 (%)**
Brosimum alicastrum	27.7
Calophyllum lucidum	0
Carapa guianensis	16.9
Eugenia confusa	11.1
Ilex arimensis	10.6
Mora excelsa	37.3
Sterculia puriens var. *glabrescens*	0
Tabebuia stenocalyx	13.9
Tabernaemontana attenuata	35.2
Tovomita eggersii	37.1
Virola surinamensis	40.3

Table 5.3: Net loss of species' potential future (SRES A2 scenario) distributions due to limitations in forest cover during 2007.

	SRES A2 Temperature - 1 °C	**SRES A2 Temperature**	**SRES A2 Temperature + 1 °C**
SRES A2 Precipitation + 10% Precipitation	Scenario 1	Scenario 2	Scenario 3
SRES A2 Precipitation	Scenario 4	Scenario 5	Scenario 6
SRES A2 Precipitation - 10% Precipitation	Scenario 7	Scenario 8	Scenario 9

Table 5.4: Climate scenarios used for the RCM sensitivity analysis.

	Change in area of potential species distribution (%)			
Species	**Temperature increase**	**Temperature decrease**	**Precipitation increase**	**Precipitation decrease**
Brosimum alicastrim	0	0	↓ (-11.7)	↓ (-2.6)
Calophyllum lucidum	↓ (-93.4)	↑ (157.8)	↓ (-55.8)	↑ (297.7)
Carapa guianensis	↓ (-10.4)	↑ (29.9)	↑ (5.2)	↑ (68.1)
Eugenia confusa	↓ (-26.4)	↑ (31.1)	↑ (170.4)	↑ (147)
Ilex arimensis	↓ (-69.1)	↑ (79.5)	↓ (-4.5)	↑ (35.8)
Mora excelsa	↑ (22.6)	↓ (-55.7)	↓ (-11.1)	↑ (3.9)
Sterculia puriens var. *glabrescens*	↓ (-99.2)	↑ (381)	↓ (-32.6)	↑ (101.3)
Tabebuia stenocalyx	↓ (-50.2)	↑ (121)	↑ (81.6)	↑ (194.2)
Tabernaemontana attenuata	↑ (152.9)	↓ (-56.9)	↓ (-1.3)	↑ (33.5)
Tovomita eggersii	↓ (-27.8)	↑ (43.3)	↑ (51.4)	↑ (168.7)
Virola surinamensis	↓ (28.9)	↓ (-70)	↓ (-24.1)	↑ (42.8)

Table 5.5: Anticipated response of species to deviations in temperature and precipitation relative to the SRES A2 scenario.

Bioclim variable	**Description of Annual Differences (between present and SRES A2 conditions) across the island of Trinidad**
BIO12	(i) Projected to decrease by approximately 5% along the central-western regions of the island (Figure C.9) (ii) As one proceeds in an eastward direction, these drier conditions give way to conditions which range from 5% decrease to stable (no change) within: (a) the central part of the island (b) the NW peninsula (iii) The remainder of the island is projected to experience between 1% and 31% increase in precipitation: (a) the largest increase of precipitation (ranging between 22% and 31%) being limited to the central Northern Range and its periphery (b) increase between 15% and 22% projected for: Areas nearer to the coast (southern, eastern and the eastern half of the north coast) (c) smaller increases from 10% to 15% projected for: the north-eastern tip of the island
BIO1	(i) A somewhat inverse pattern to that of the projected change in BIO12 (Figure C.33) (ii) No decreases in annual temperature projected for any region within the island (iii) Instead, an increase of approximately 1.3 to 1.4 °C is anticipated for the western region of the island including portions of the southern reaches of the NW peninsula (iv) There is a gradual decrease to an anticipated 1.2 °C increase within: (a) the central part of the island (b) the northern parts of the NW peninsula (v) Lowest increase of approximately 1 °C projected for (a) the southern and eastern coasts (b) the entire north-eastern corner of the island

Table 5.6: Anticipated changes (annual differences) in BIO12 and BIO1 from present to SRES A2 conditions.

Bioclim variable	**Description of Seasonal Differences (between present and SRES A2 conditions) across the island of Trinidad**	
	Wet Season	**Dry Season**
BIO12	(i) Very different to dry season (ii) Pattern of projected change was remarkably similar to that of BIO12 (annual) (iii) Main difference: north-western peninsula is projected to have a slightly lower, more uniform difference [compared to that of BIO1 (annual)]	(i) Very different to wet season. (ii) Western and central regions of the island projected to experience the highest increases of precipitation (from 10% to 20%) (iii) Lower changes in precipitation projected (range = 1%↓ to 3%↑) within: (a) southern and eastern peripheries (b) north-eastern corner of island
BIO1	(i) Very similar patterns to: (a) dry season's differences (b) differences projected for BIO1 (annual) (Table 5.6) (ii) Greatest increases in temperature: concentrated along the central western periphery of island (iii) This increase [from (ii)] dropped by approximately 0.1 °C within the central and north-western peninsula.	(i) Very similar patterns to: (a) wet season's differences (b) differences projected for BIO1 (annual) (Table 5.6) (ii) Greatest increases in temperature: again concentrated along the central western periphery of island (iii) This increase [from (ii)] dropped by approximately 0.1 °C within the central and north-western peninsula.

	(iv) Similar to BIO1 (Table 5.6): the southern, eastern and north-eastern regions of the island are projected to experience the lowest increase in temperature (v) The most obvious differences between the dry and wet season: the outer 'cooler' zone along the southern, eastern and north-eastern areas of the island is larger than during the dry season; (inverse applies for the wet season)	(iv) Similar to BIO1 (Table 5.6): the southern, eastern and north-eastern regions of the island are projected to experience the lowest increase in temperature (v) The most obvious differences between the dry and wet season: the 'hotter' zones along the western and central regions of Trinidad as well as the north-western peninsula appeared larger during the dry season than during the wet season; (inverse occurs during wet season).

Table 5.7: Anticipated changes (seasonal differences) in BIO12 and BIO1 from present to SRES A2 conditions.

Bioclim variable	**Description of Differences (between present and SRES A2 conditions) across the island of Trinidad**
BIO13	(i) Similar general pattern to differences expected for BIO12 (Table 5.6) (ii) Highest precipitation increases projected to occur consistently within the central Northern Range and its periphery (iii) This was followed by a consistent mild to moderate increase in precipitation along southern coast of the island (iv) In contrast, the western region of the island, in particular, is projected to experience decreases or very small increases in precipitation (v) These relatively dry conditions are projected to gradually extend to: (a) the central region of the island (b) the NW peninsula
BIO14	Similar pattern to BIO13
BIO15	Similar pattern to BIO13
BIO16	Similar pattern to BIO13
BIO17	(i) Similar general pattern to differences expected for BIO12 (ii) Highest precipitation increases projected to occur consistently within the central Northern Range and its periphery (iii) This was followed by a consistent mild to moderate increase in precipitation along the southern coast of the island (iv) In contrast, the western region of the island in particular is projected to experience decreases or very small increases in precipitation (v) These relatively dry conditions are projected to gradually extend to the central region of the island exclusive of the NW peninsula

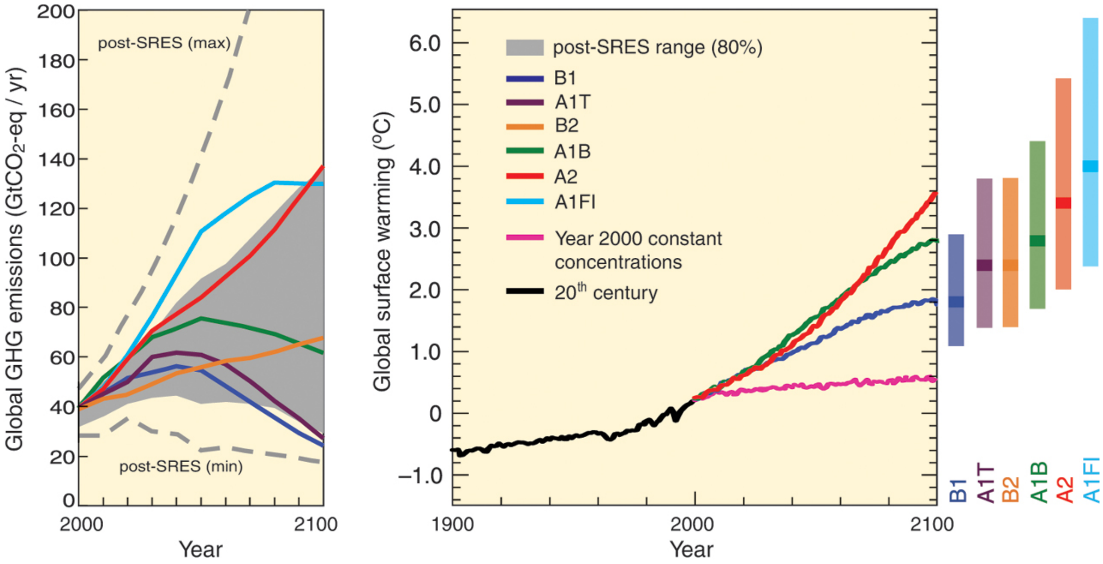
	(vi) NW peninsula is projected to experience increases in precipitation that are more similar to that of the southern coast than the western and central regions of the island (Figure C.24)
BIO18	Similar pattern to BIO13
BIO19	Similar pattern to BIO13
BIO9m4	(i) Projected increase between 1.4 °C and 1.9 °C for: (a) the western and central regions of the island (b) most of the NW peninsula (Figure C.6) (ii) Lower increases of up to 1.2 °C projected along the southern and south-eastern edges of the island (iii) Unlike BIO1 (Table 5.6), the lowest increases of approximately 0.5 °C are projected for: (a) the majority of the eastern parts of the island, extending into the north-eastern tip of the island (b) along the majority of the northern coastal periphery.
BIO4	(i) Very different pattern (Figure C.3) to BIO9m4 above (ii) Greatest changes (increase between 5 °C and 6 °C) projected within: (a) the SW peninsula (b) the southern and eastern edges of the island (iii) The remainder of the island projected to experience changes that range between: an increase in temperature variation by 3 °C and a decrease of up to 1.2 °C

Table 5.8: Anticipated changes in remaining Bioclim variables from present to SRES A2 conditions.

Difference map for Bioclim variable	**Correlation with species collective change map**
Bio1 (dry season)	0.08
Bio1 (wet season)	0.12
Bio1 (annual)	0.18
Bio12 (dry season)	0.63
Bio12 (wet season)	0.67
BIO12 (annual)	0.69
Bio13	0.67
Bio14	0.66
BIO15	0.23
Bio16	0.34
Bio17	0.74
Bio18	0.15
Bio19	0.11

Table 5.9: Correlation between Bioclim difference maps and the Collective Change Map.

5.6 Figures



Scenarios for GHG emissions from 2000 to 2100 (in the absence of additional climate policies) and projections of surface temperatures

Figure 5.1: Left Panel: Global GHG emissions (in GtCO$_2$-eq) in the absence of climate policies: six illustrative SRES marker scenarios (coloured lines) and the 80th percentile range of recent scenarios published since SRES (post-SRES) (gray shaded area). Dashed lines show the full range of post-SRES scenarios. The emissions include CO$_2$, CH$_4$, N$_2$O and F-gases. Right Panel: Solid lines are multi-model global averages of surface warming for scenarios A2, A1B and B1, shown as continuations of the 20th-century simulations. These projections also take into account emissions of short-lived GHGs and aerosols. The pink line is not a scenario, but is for Atmosphere-Ocean General Circulation Model (AOGCM) simulations where atmospheric concentrations are held constant at year 2000 values. The bars at the right of the figure indicate the best estimate (solid line within each bar) and the likely range assessed for the six SRES marker scenarios at 2090–2099. All temperatures are relative to the period 1980–1999. Figure taken from the Climate Change 2007 Synthesis Report (IPCC 2007, Figure SPM.5).

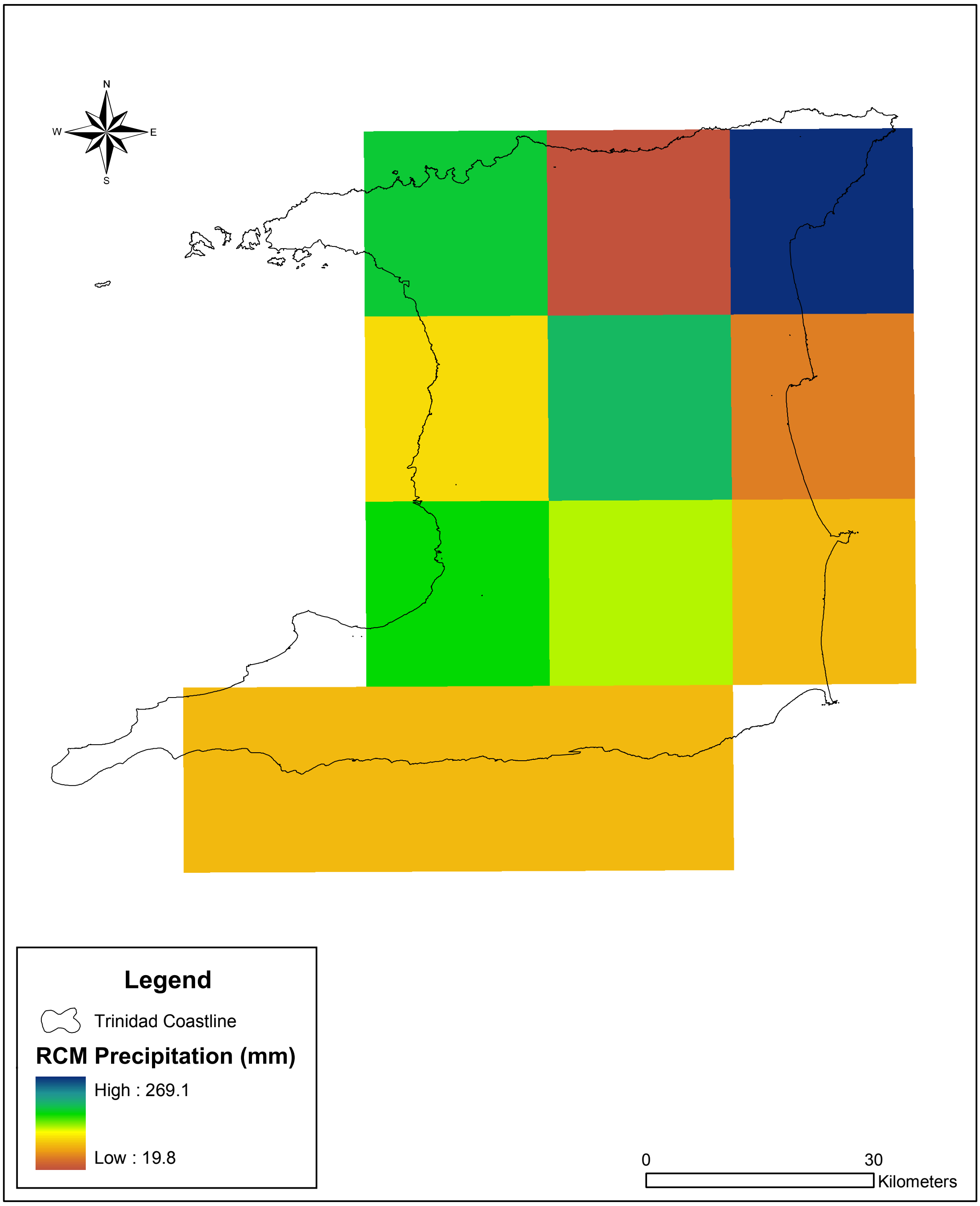


Figure 5.2: Simulated distribution of Precipitation across Trinidad for October 2010 (from the PRECIS RCM at a 25 km^2 resolution).

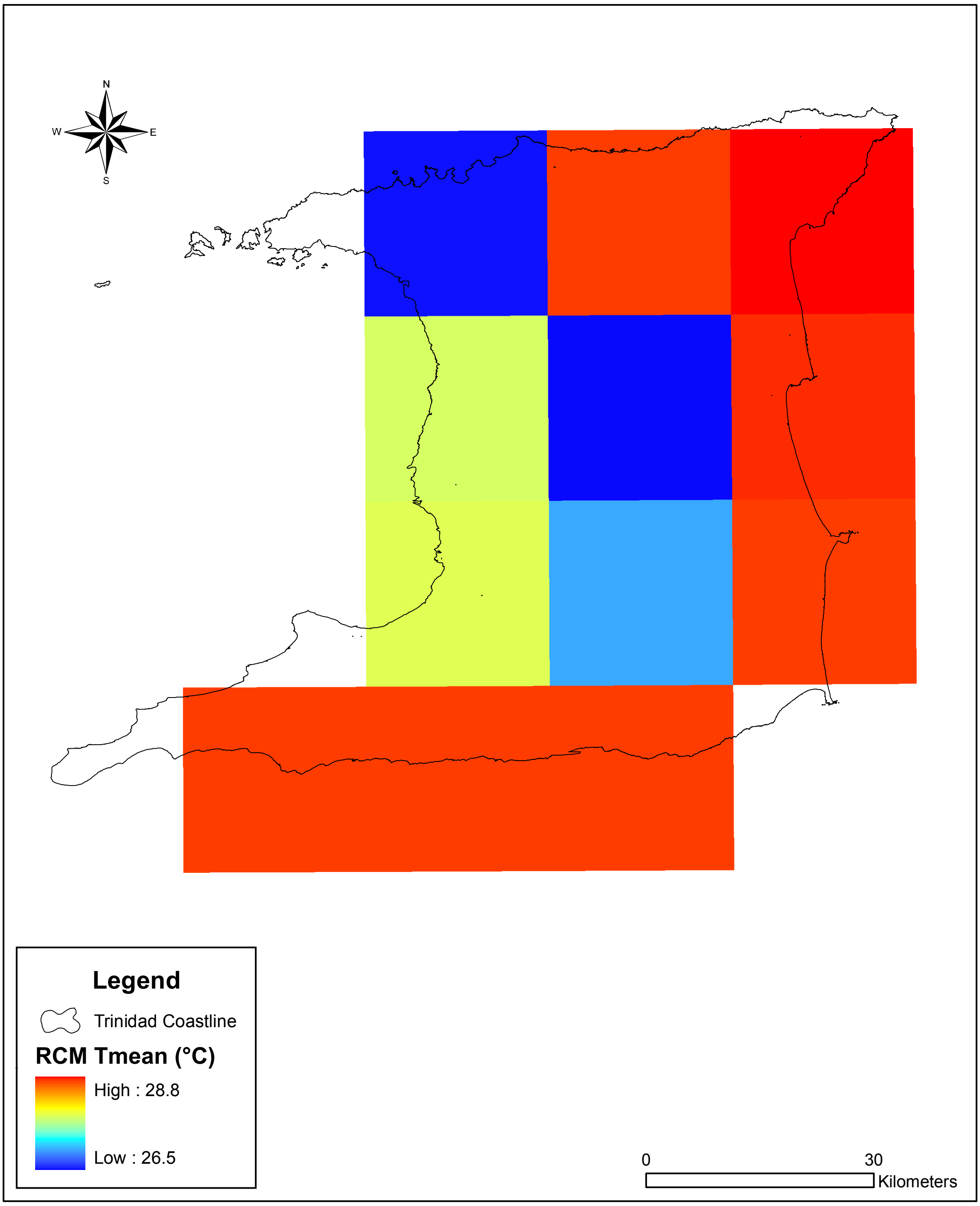


Figure 5.3: Simulated distribution of Tmean across Trinidad for October 2010 (from the PRECIS RCM at a 25 km^2 resolution).

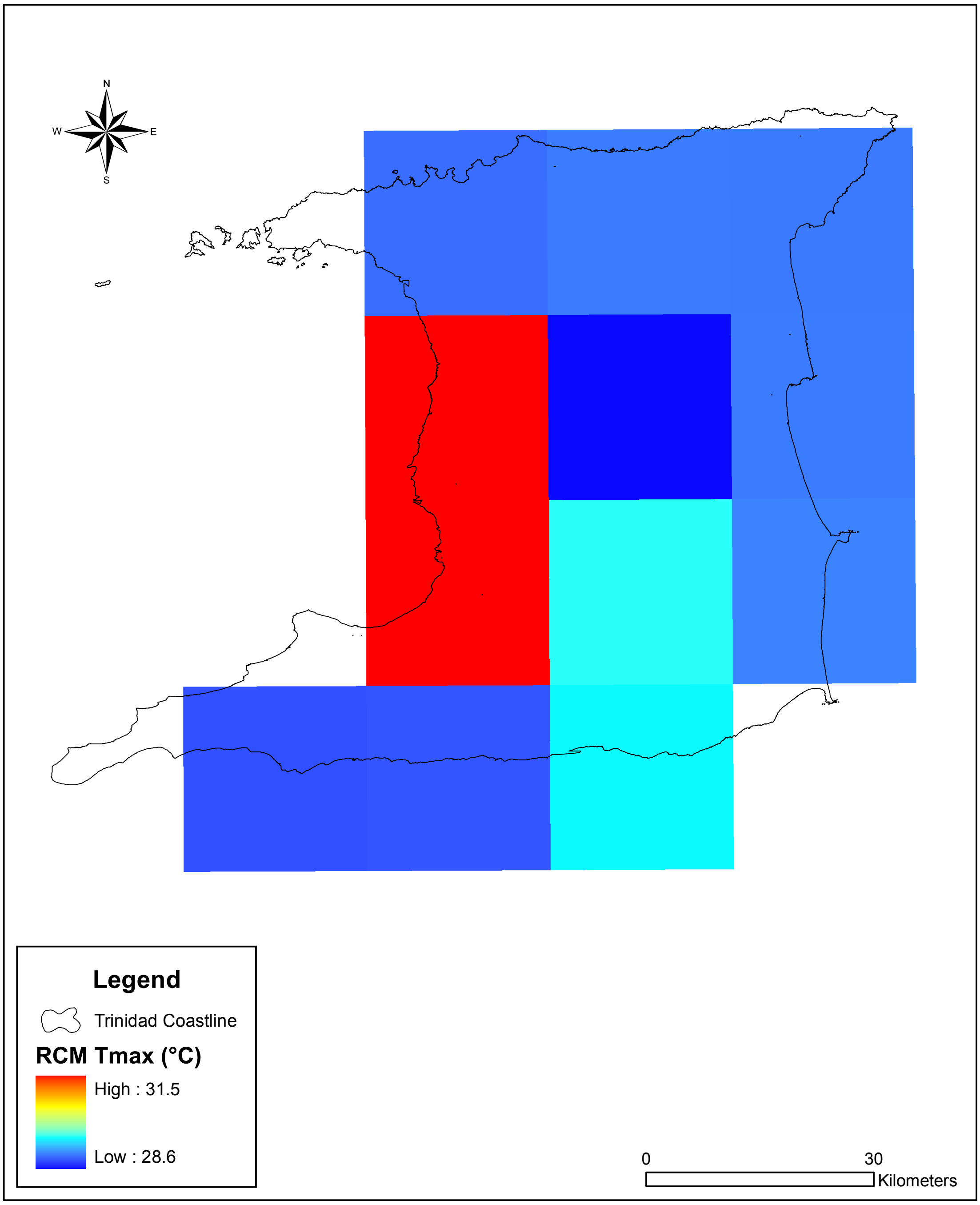


Figure 5.4: Simulated distribution of Tmax across Trinidad for October 2010 (from the PRECIS RCM at a 25 km^2 resolution).

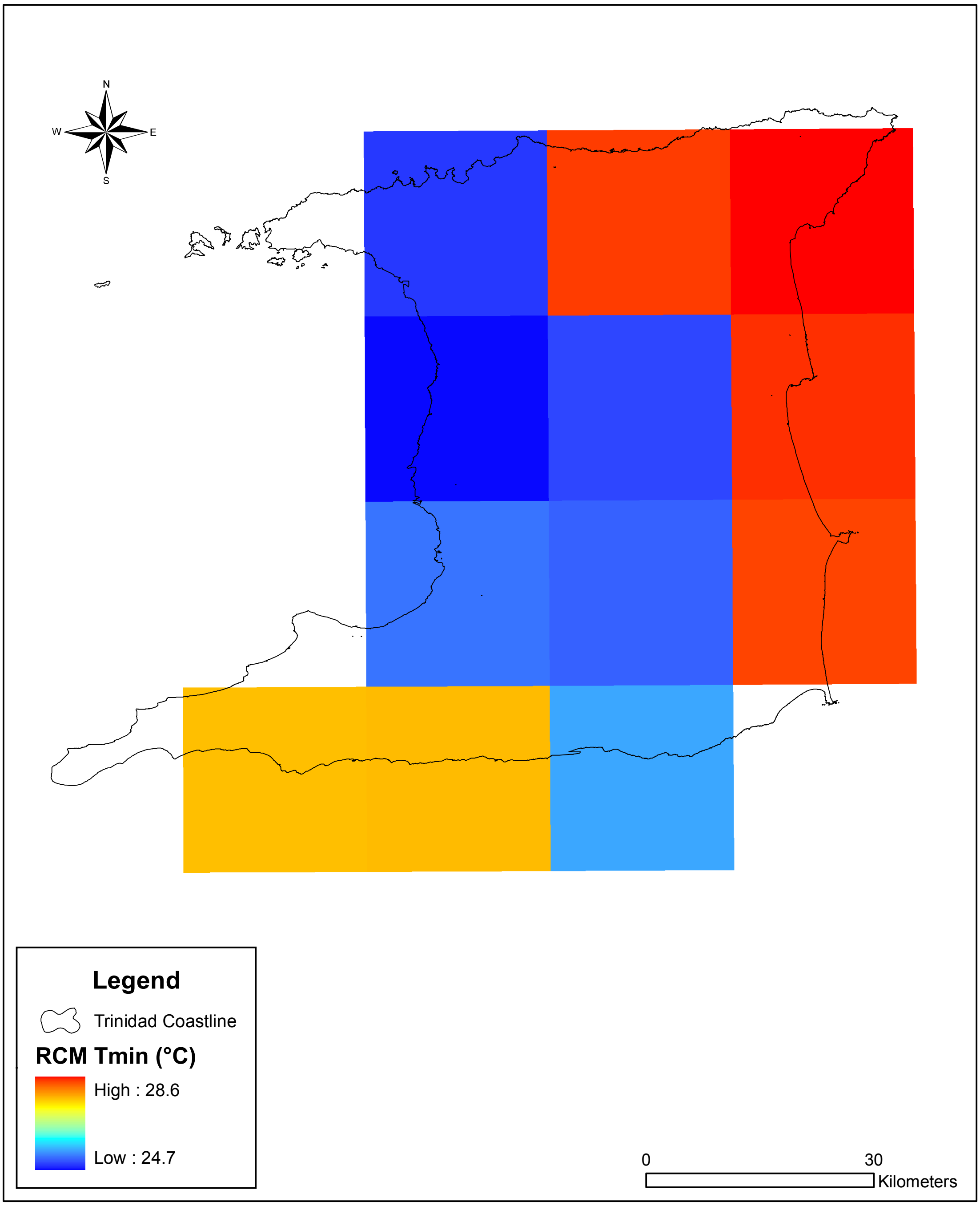


Figure 5.5: Simulated distribution of Tmin across Trinidad for October 2010 (from the PRECIS RCM at a 25 km^2 resolution).

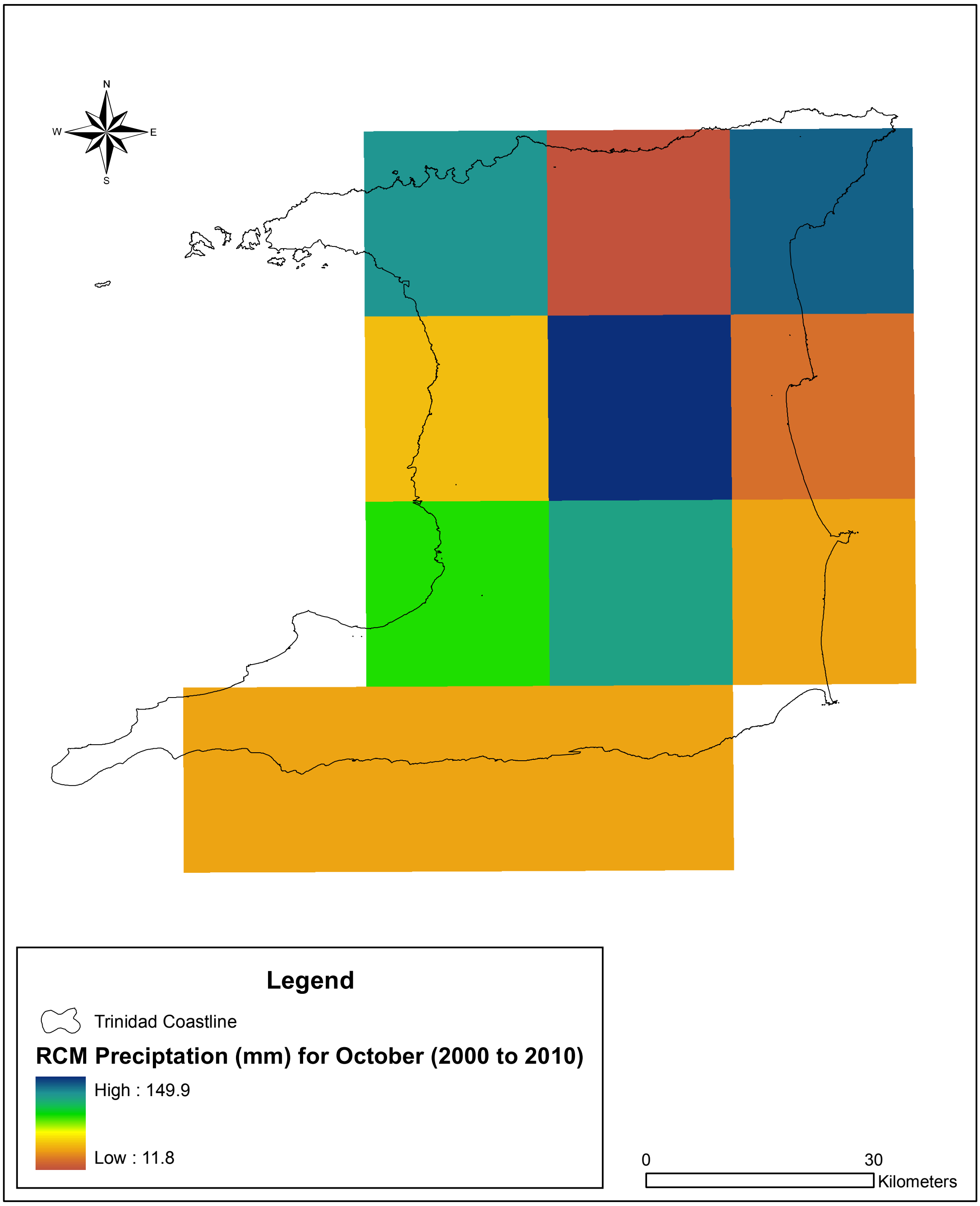


Figure 5.6: Distribution of Precipitation for October during the present period (2000 to 2010) (at a 25 km^2 resolution).

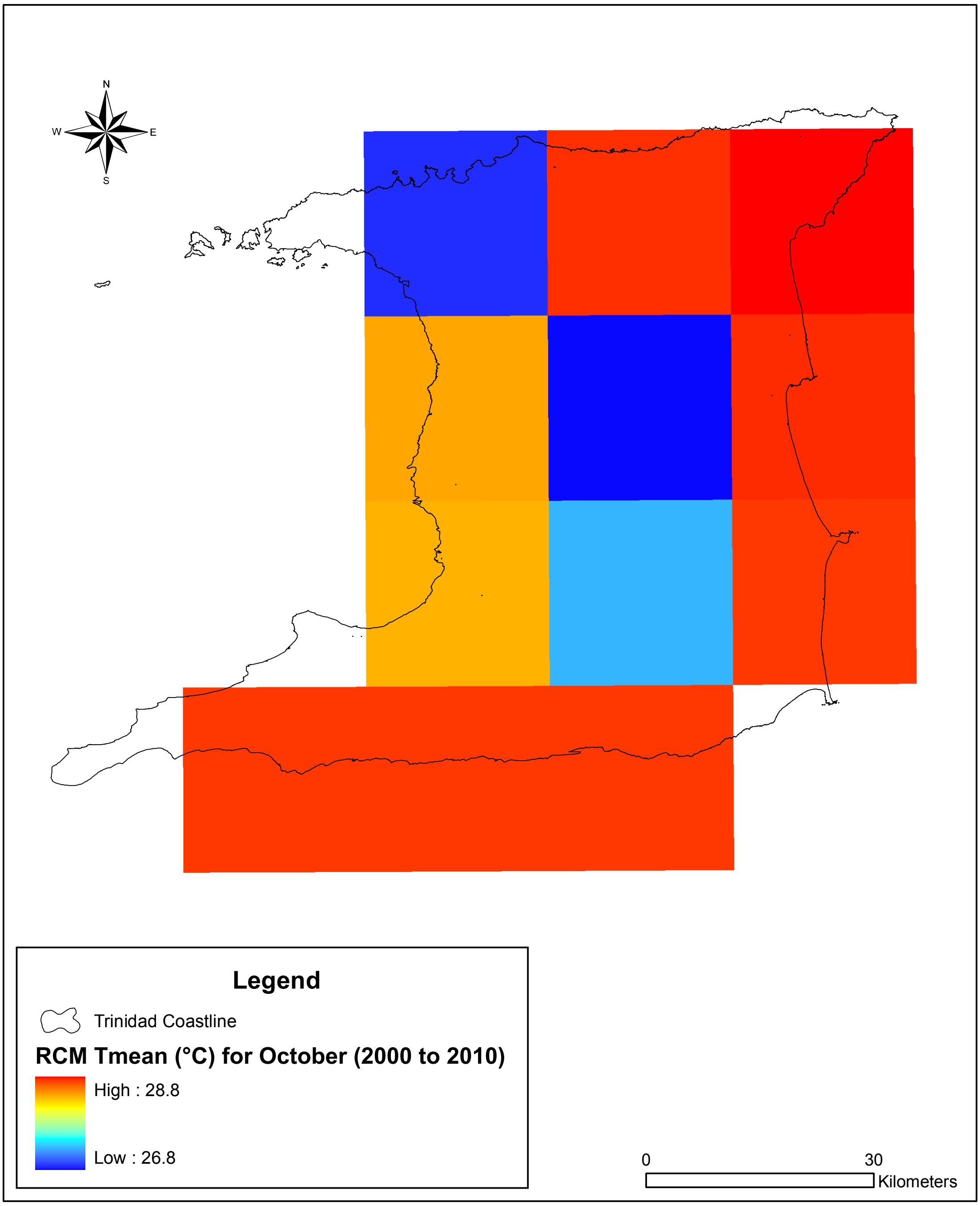


Figure 5.7: Distribution of Tmean for October during the present period (2000 to 2010) (at a 25 km^2 resolution).

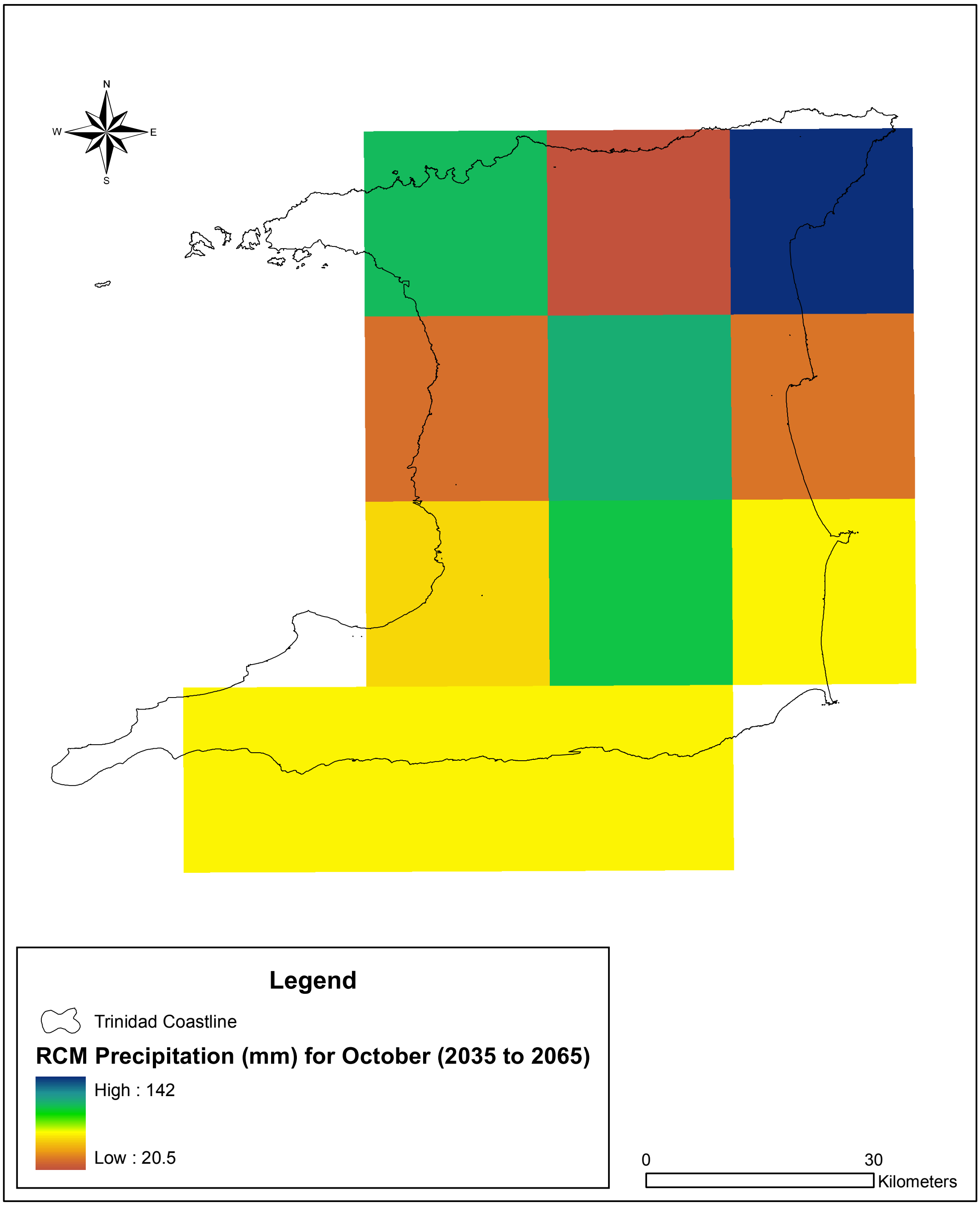


Figure 5.8: Distribution of Precipitation for October during the future period (2035 to 2065) (at a 25 km^2 resolution).

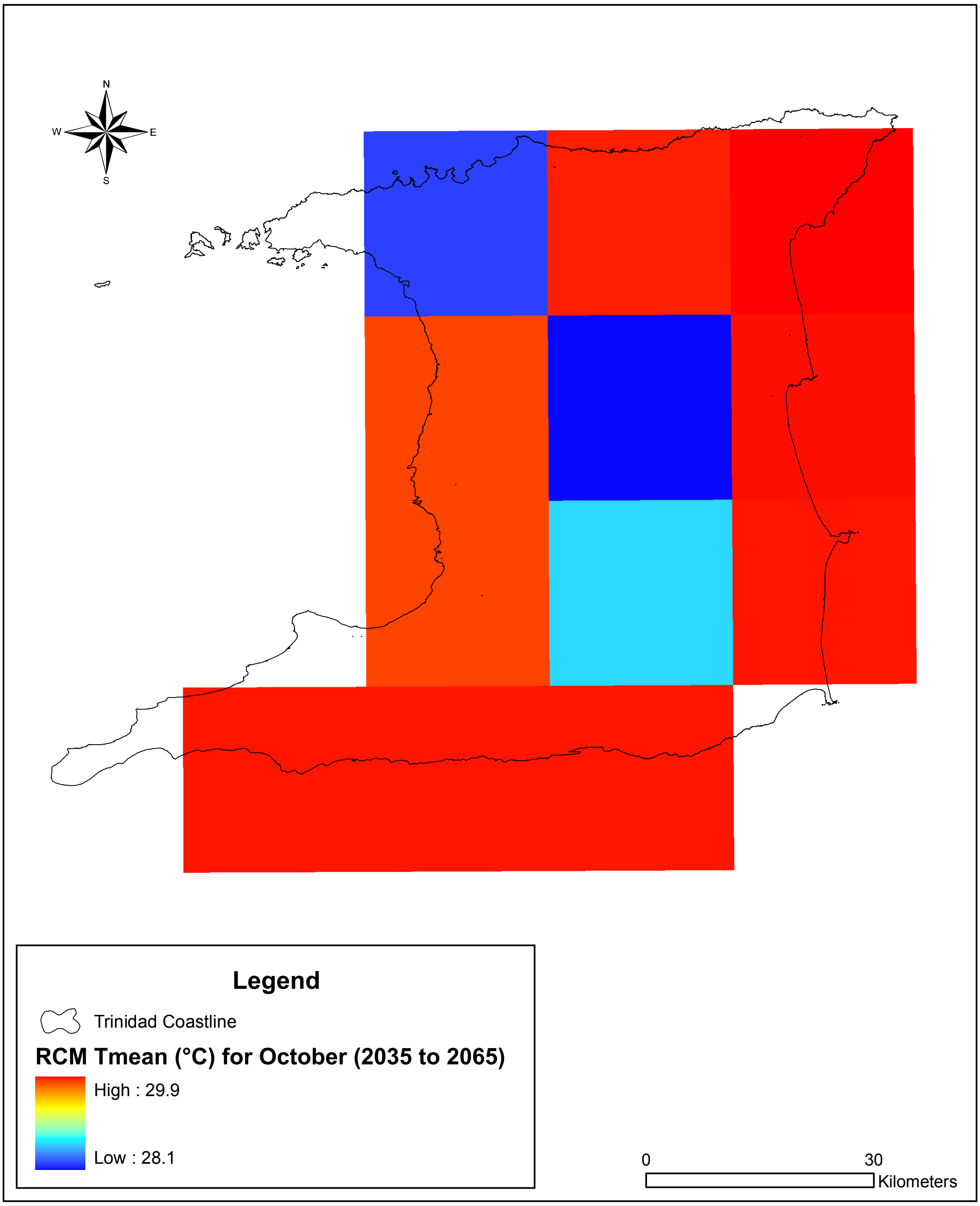


Figure 5.9: Distribution of Tmean for October during the future period (2035 to 2065) (at a 25 km^2 resolution).

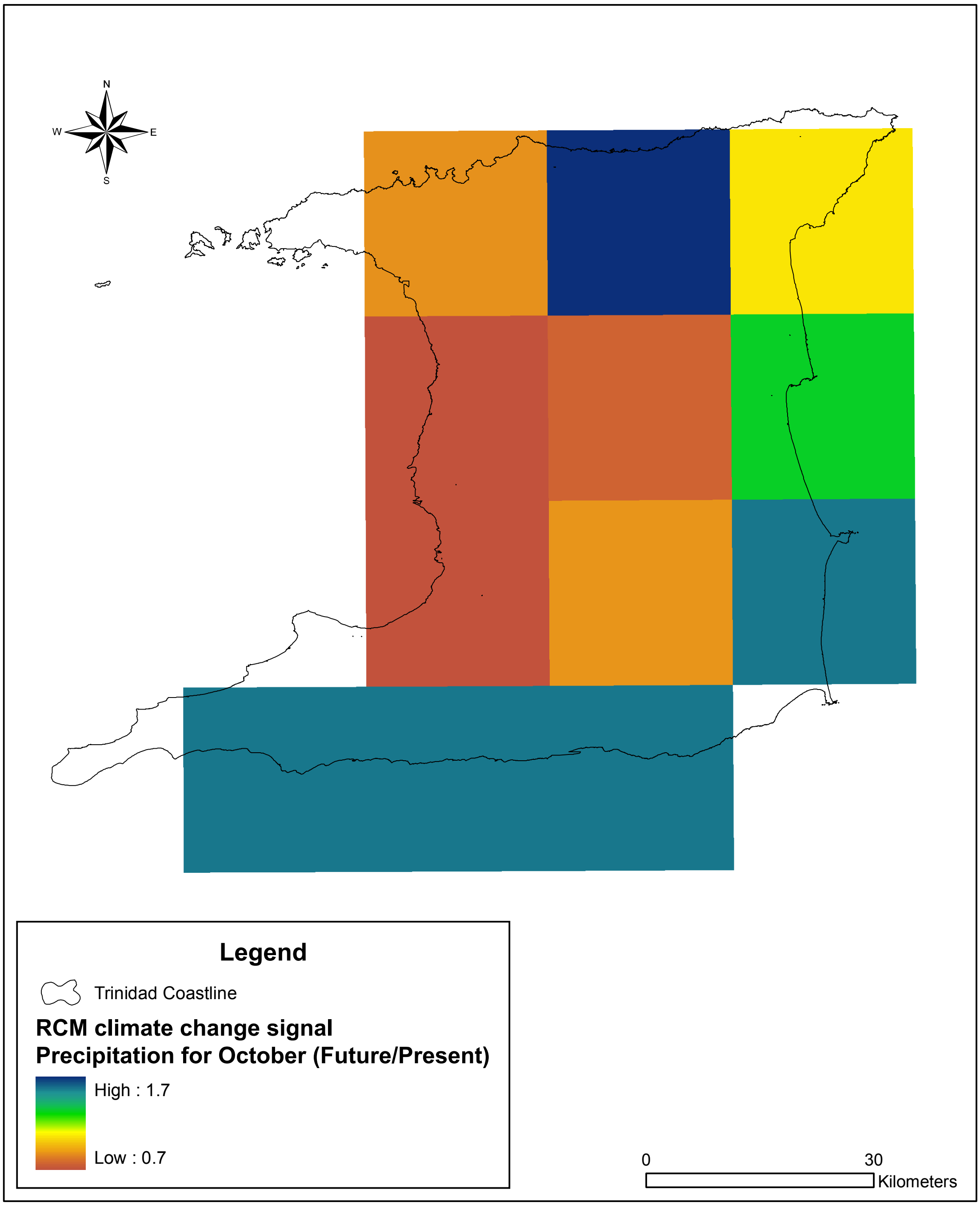


Figure 5.10: Climate signal (future/present) for Precipitation during October (at a 25 km^2 resolution).

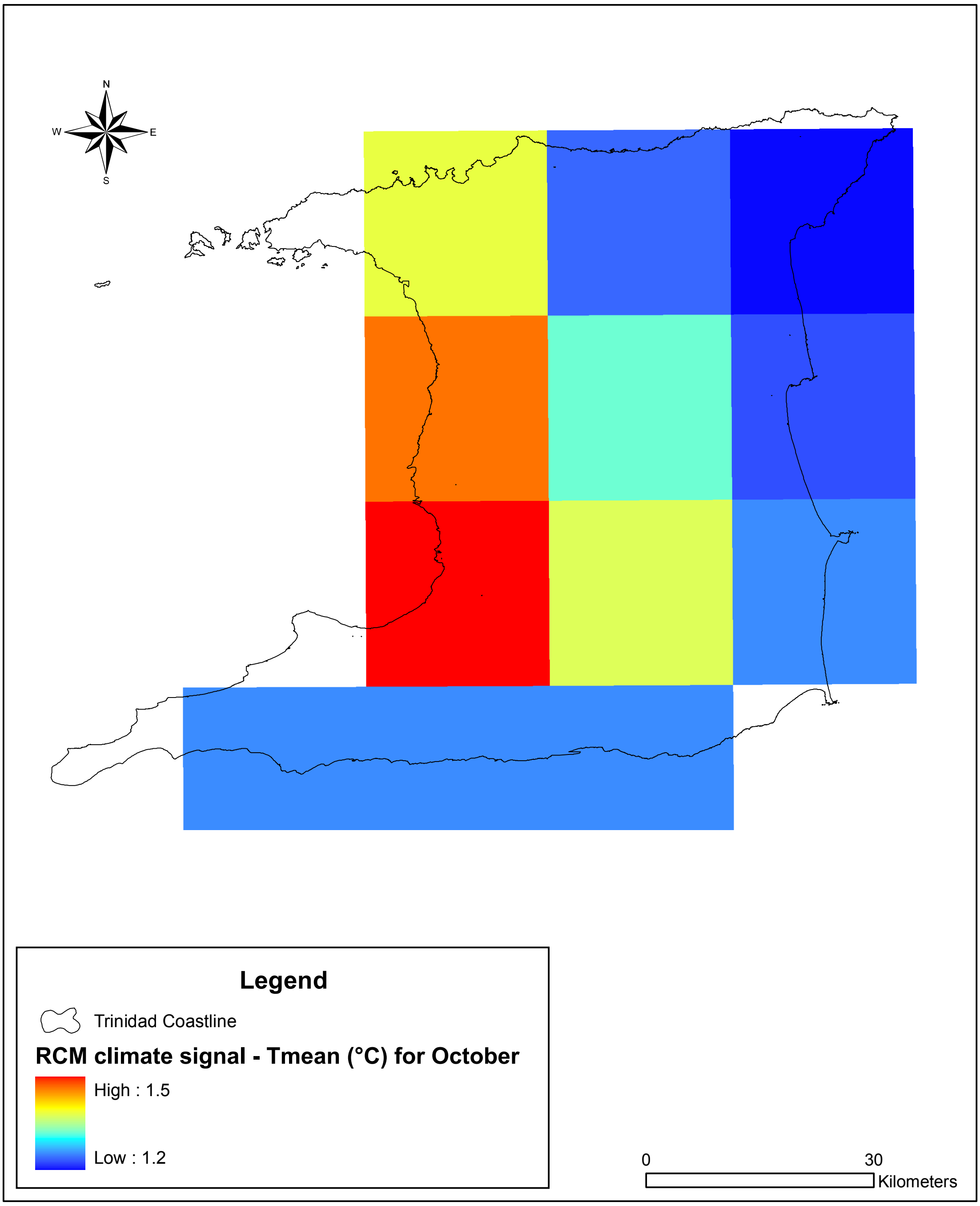


Figure 5.11: Climate signal (future-present) for Tmean during October (at a 25 km^2 resolution).

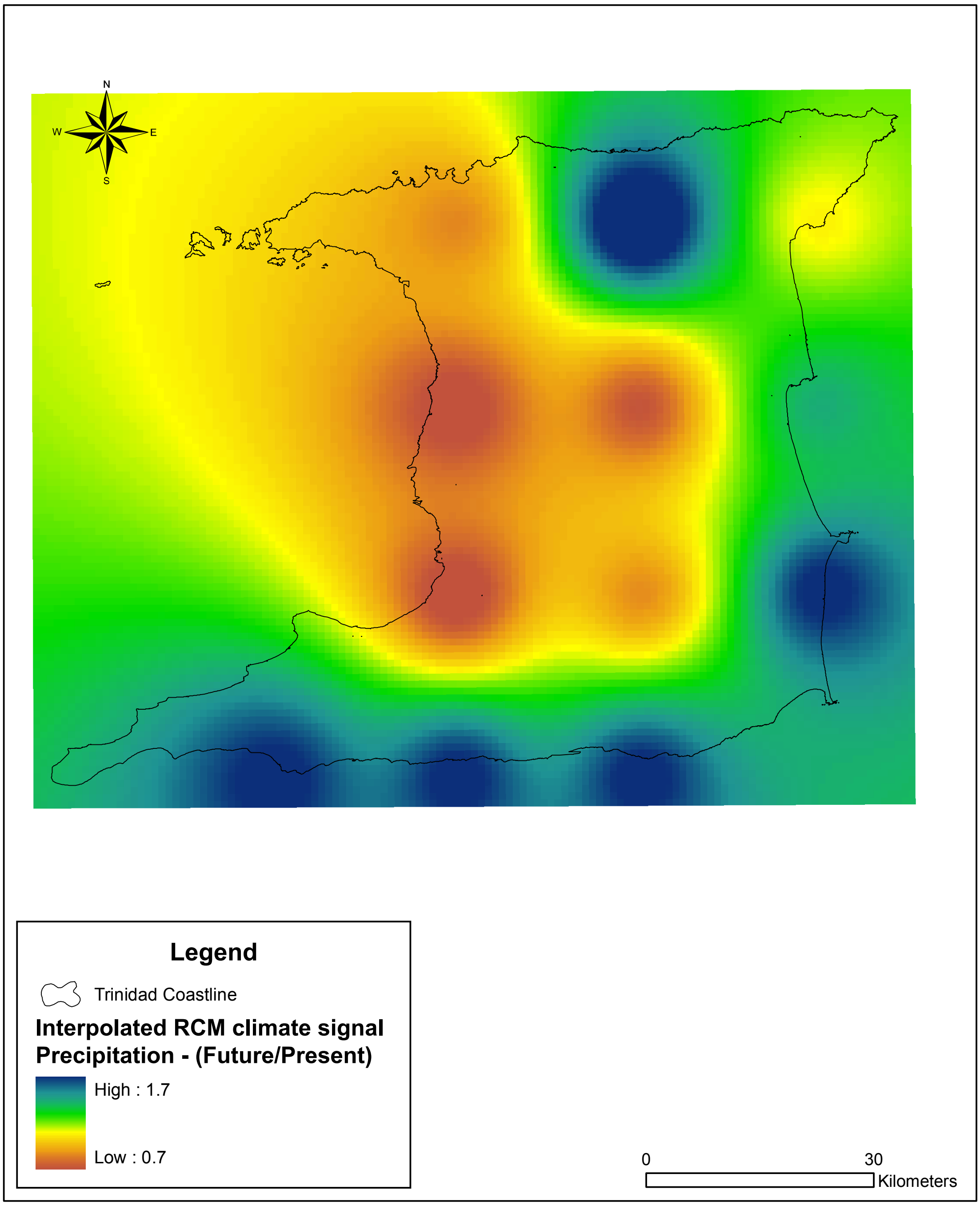


Figure 5.12: Climate signal for precipitation (future/present precipitation) during October interpolated to 1 km^2 resolution (from 25 km^2) using IDW.

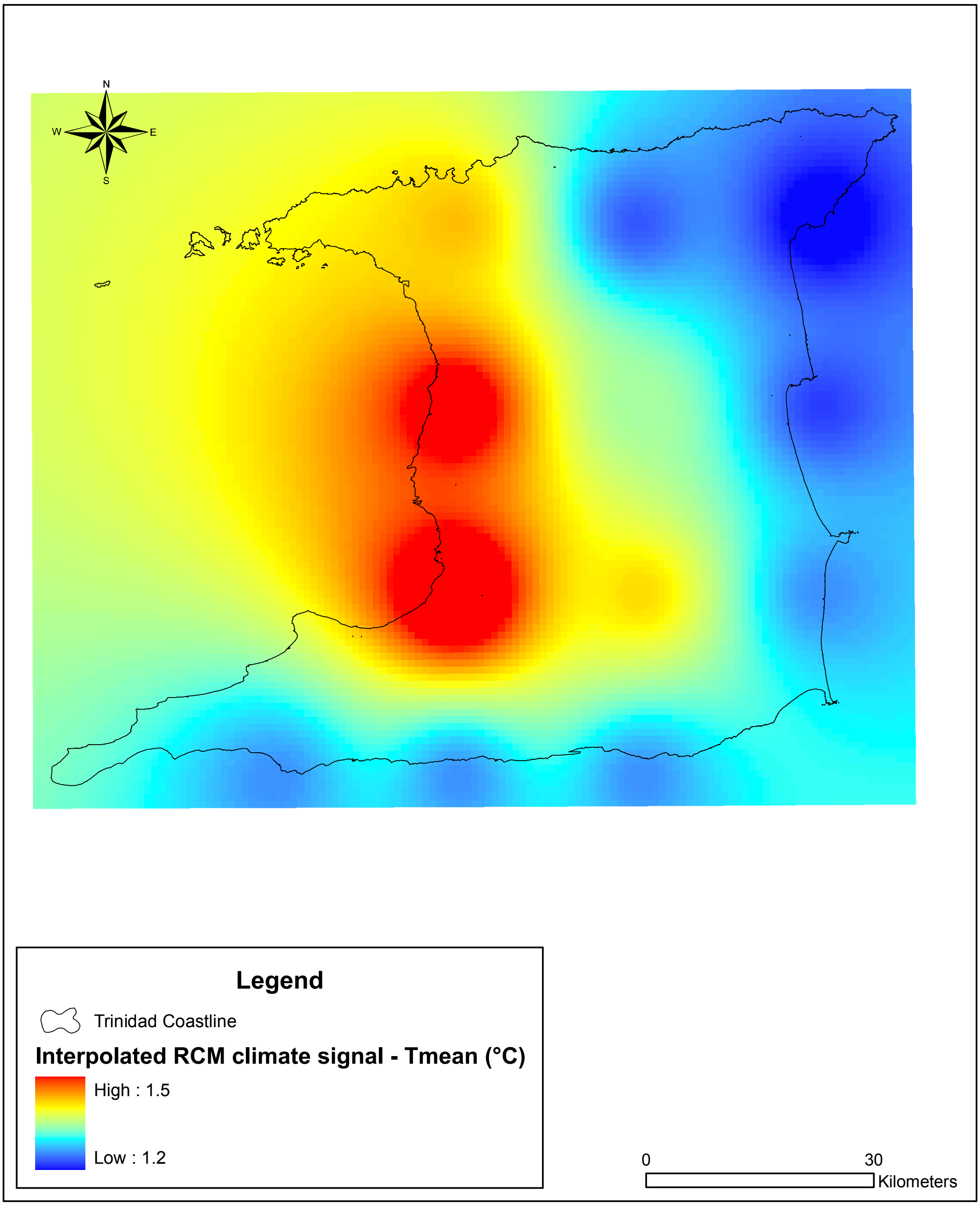


Figure 5.13: Climate signal for Tmean (future-present Tmean) during October interpolated to 1 km^2 resolution (from 25 km^2) using IDW.

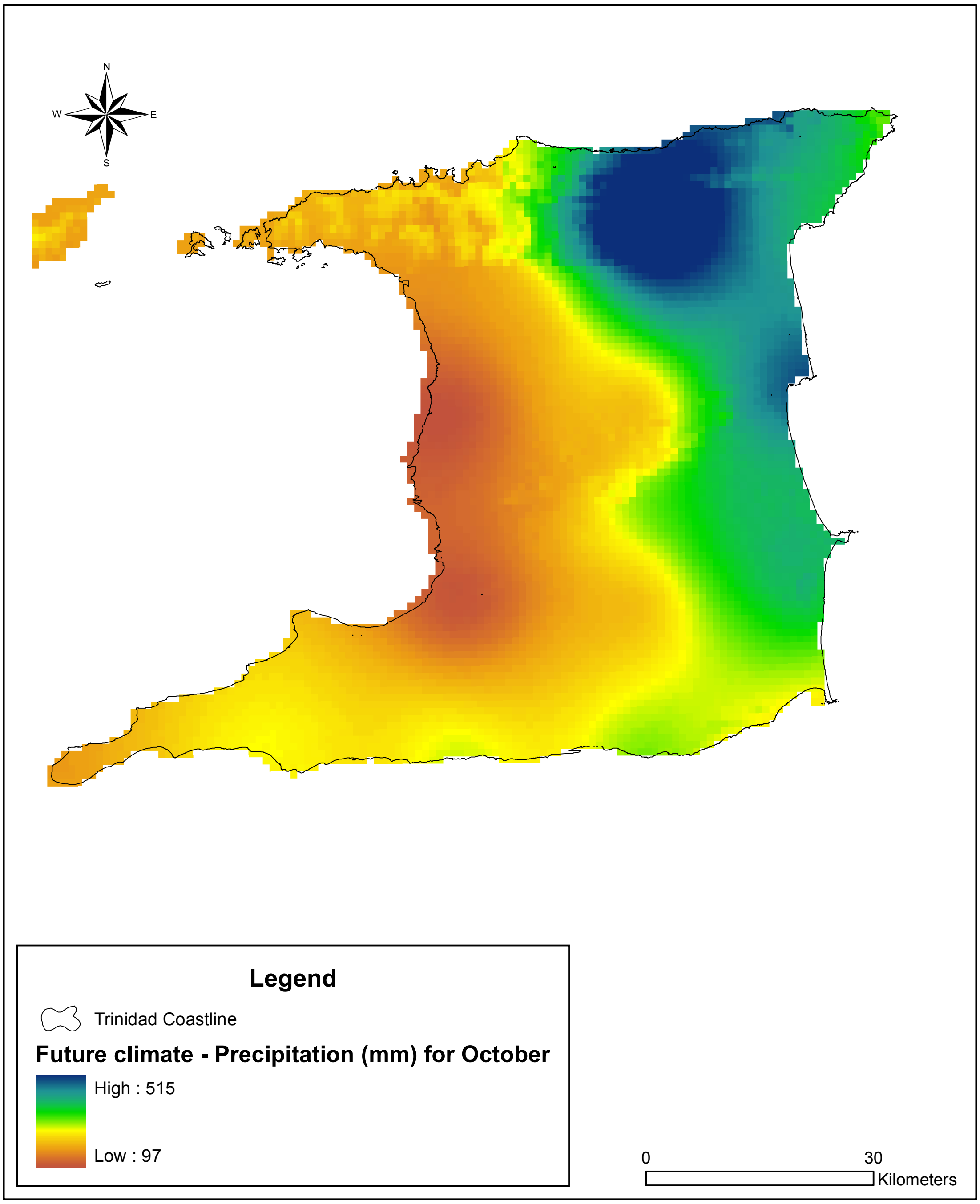


Figure 5.14: Future precipitation for October (climate signal + present climate) at a 1 km^2 resolution.

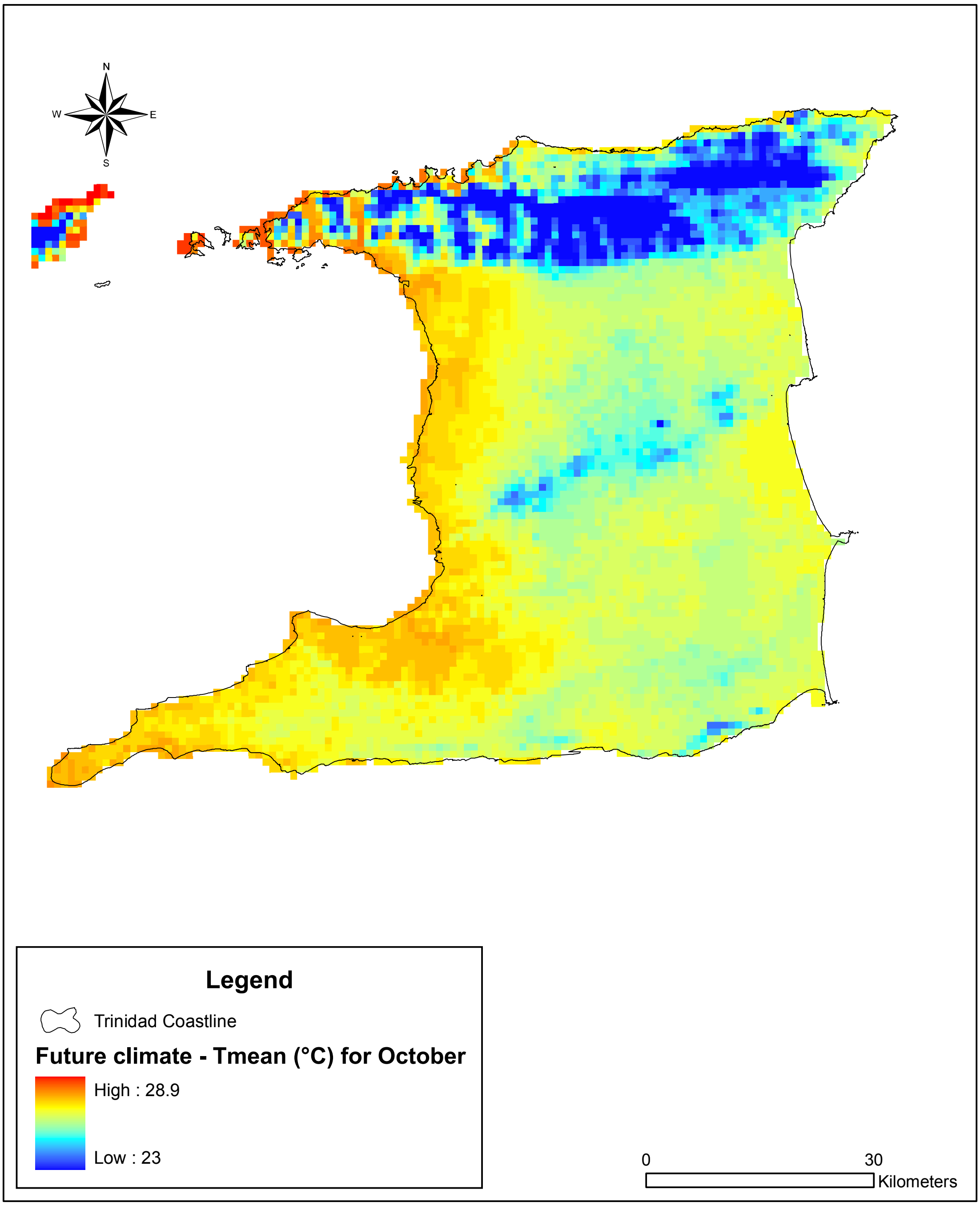


Figure 5.15: Future Tmean for October (climate signal + present climate) at a 1 km^2 resolution.

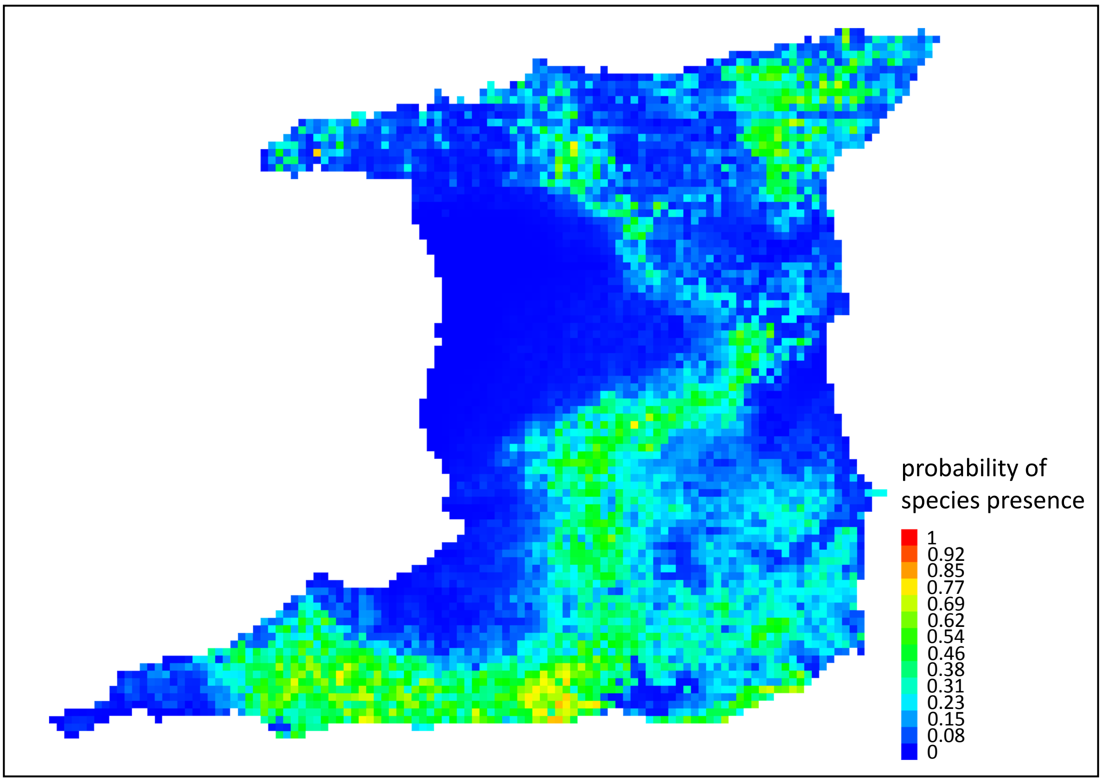


Figure 5.16: Raw MaxEnt logistic output grid for *Brosimum alicastrum* (future climate).

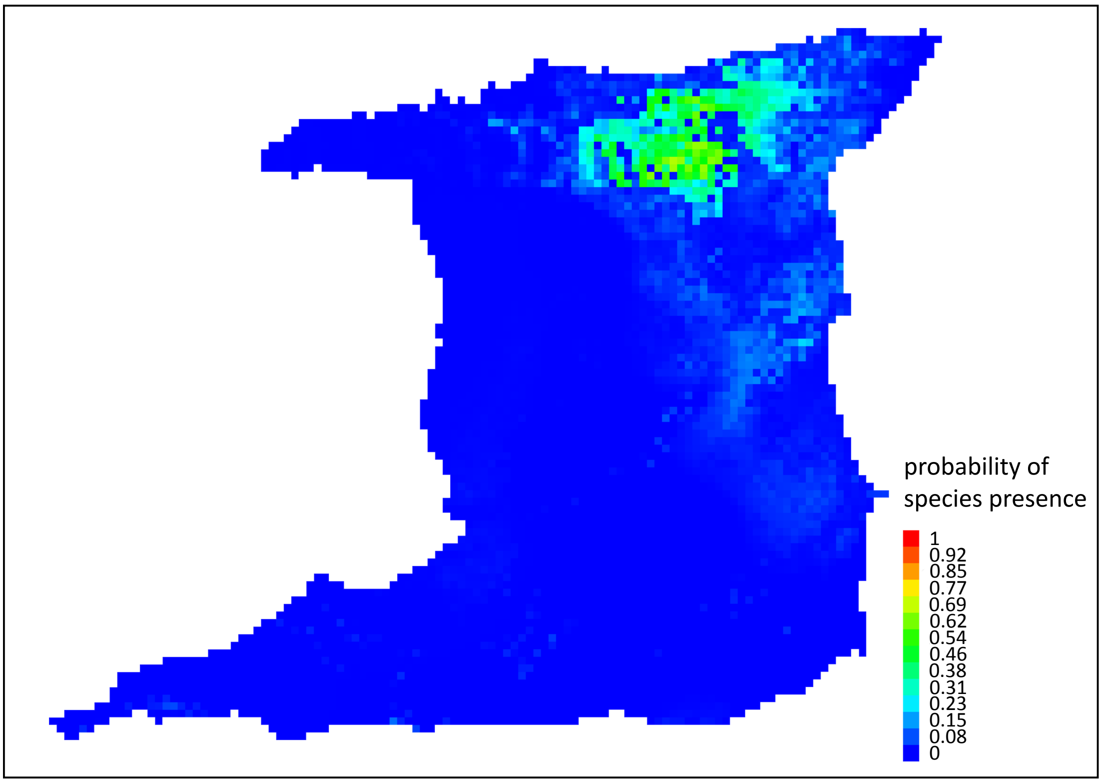


Figure 5.17: Clamping image of *Brosimum alicastrum*.

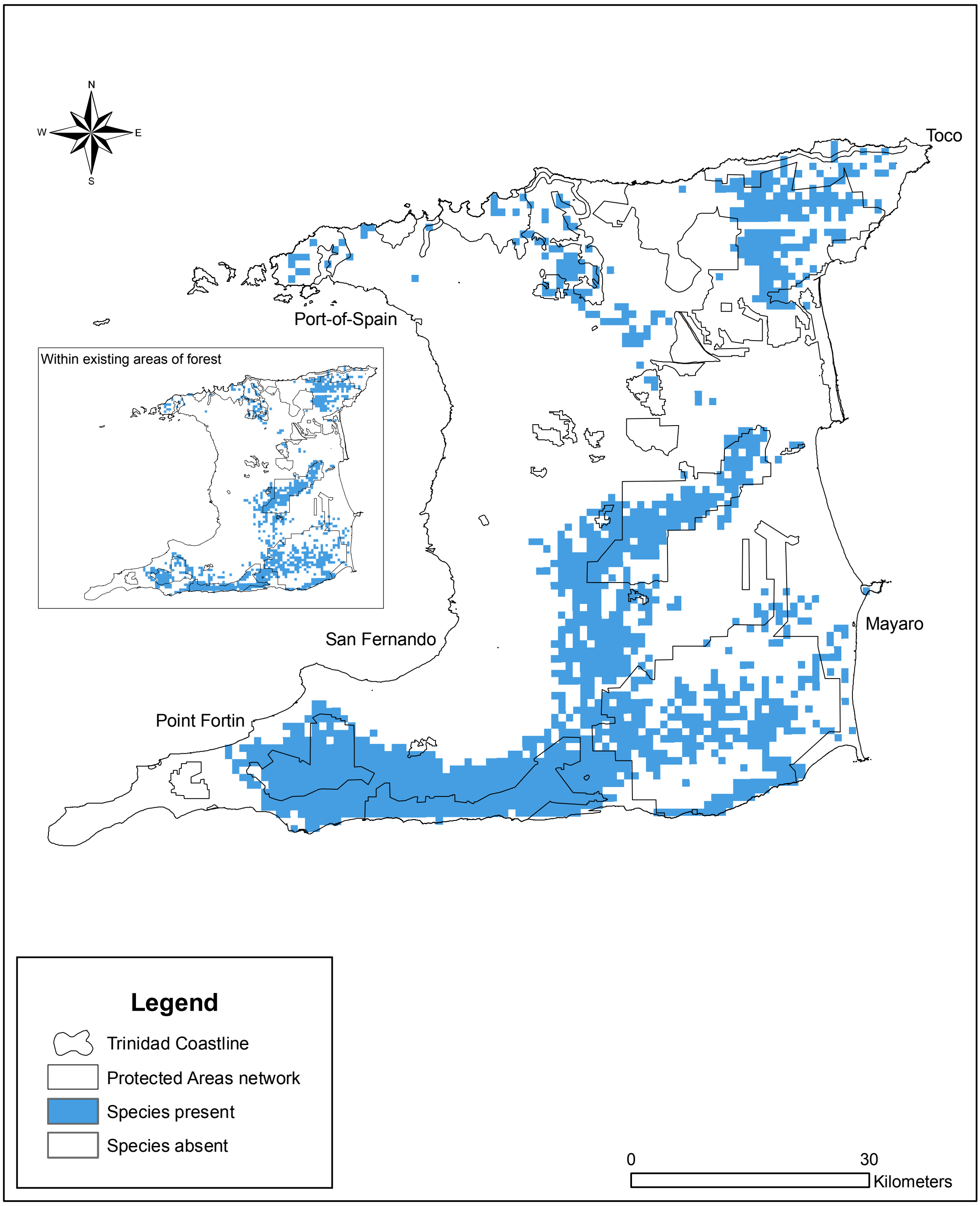


Figure 5.18: Projected future distribution of *Brosimum alicastrum*.

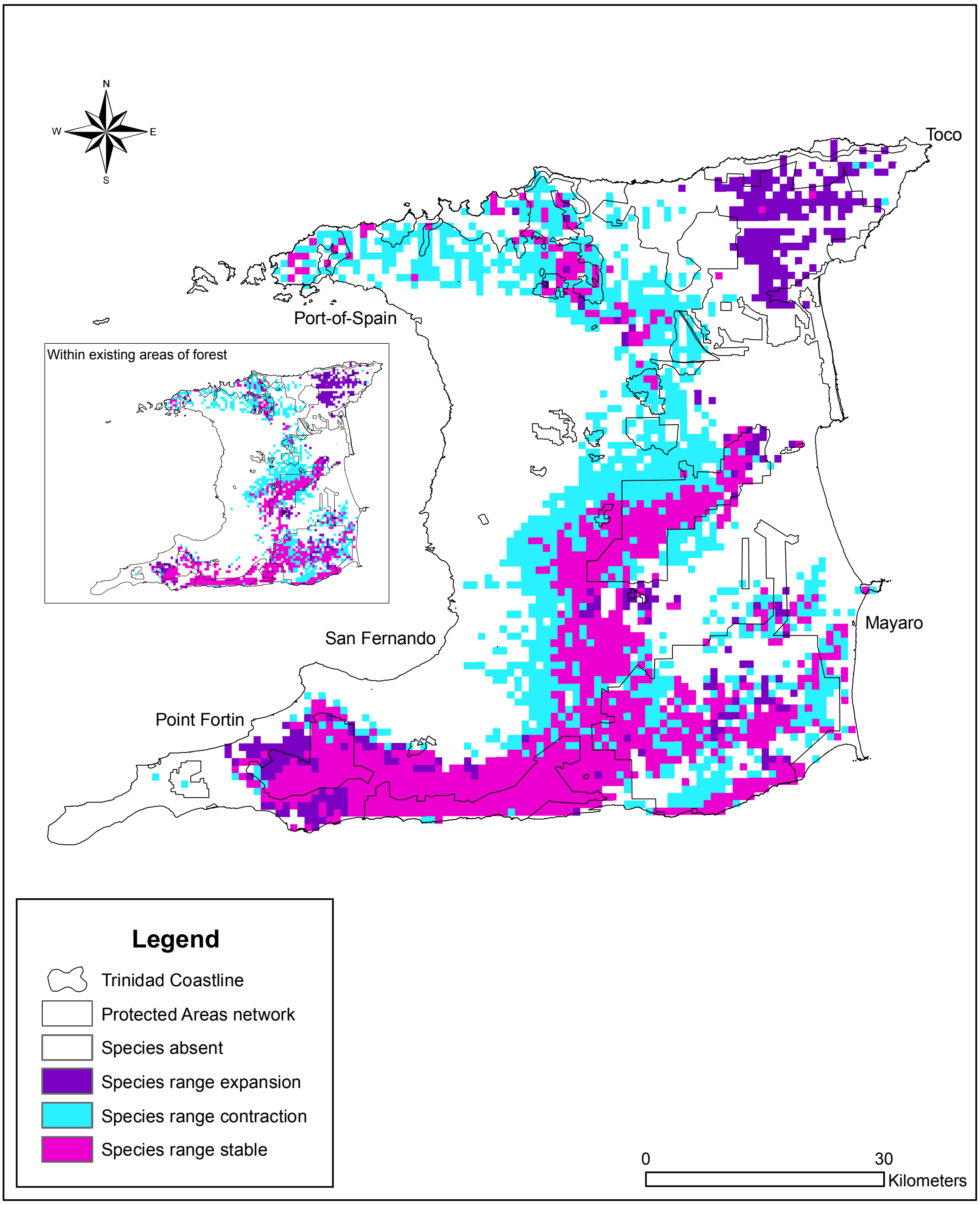


Figure 5.19: Potential species distribution change map of *Brosimum alicastrum*.

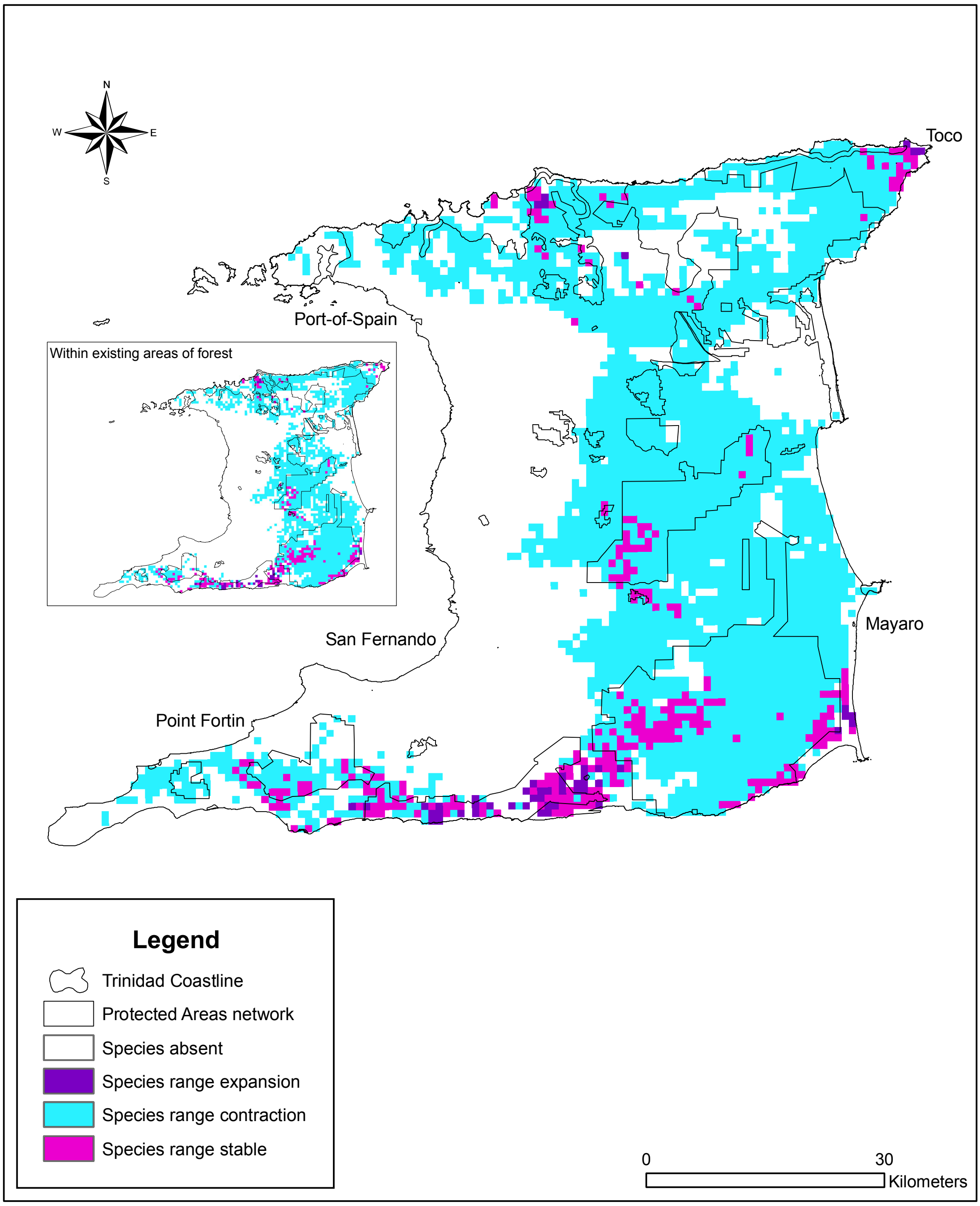


Figure 5.20: Potential species distribution change map of *Carapa guianensis*.

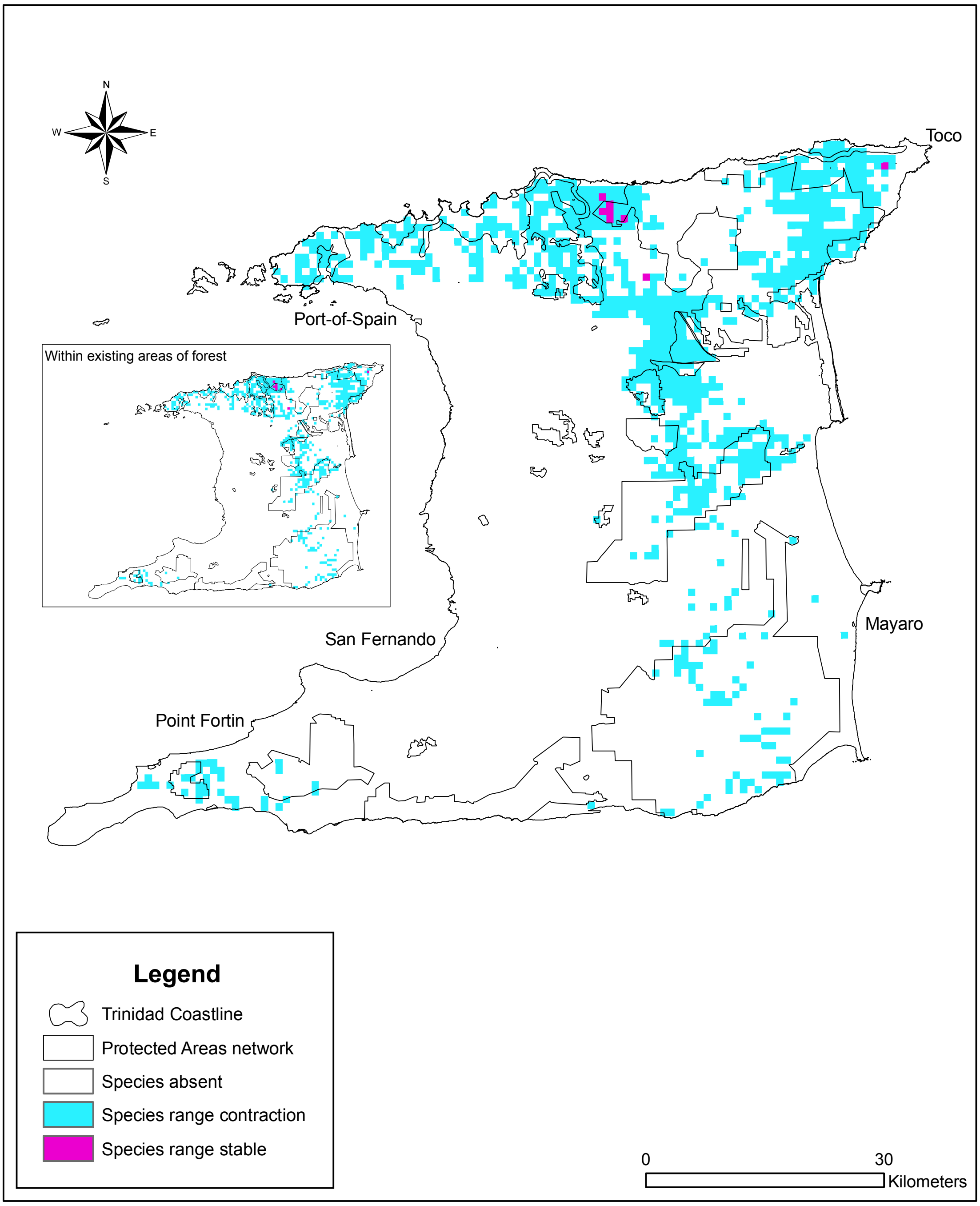


Figure 5.21: Potential species distribution change map of *Calophyllum lucidum*.

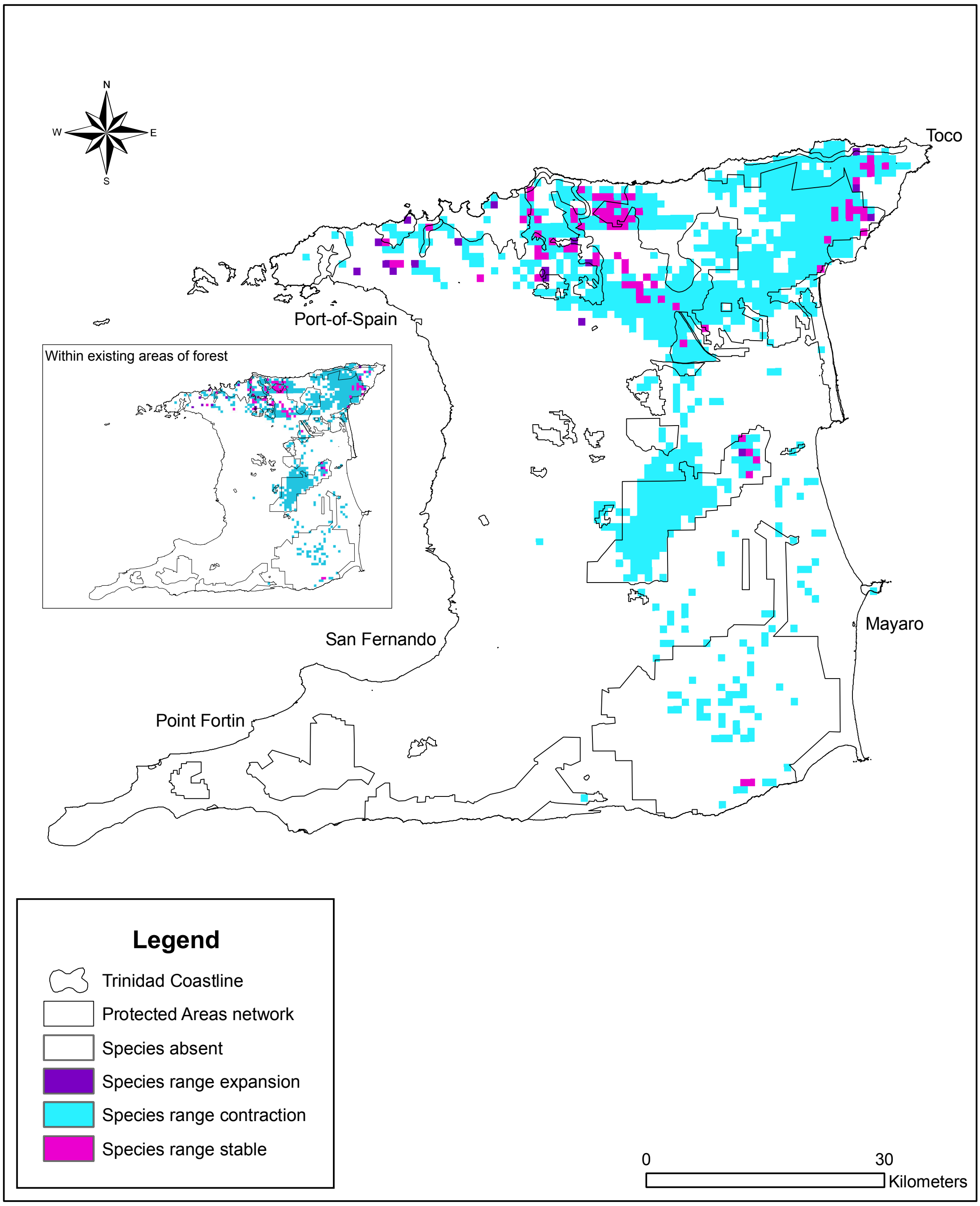


Figure 5.22: Potential species distribution change map of *Eugenia confusa*.

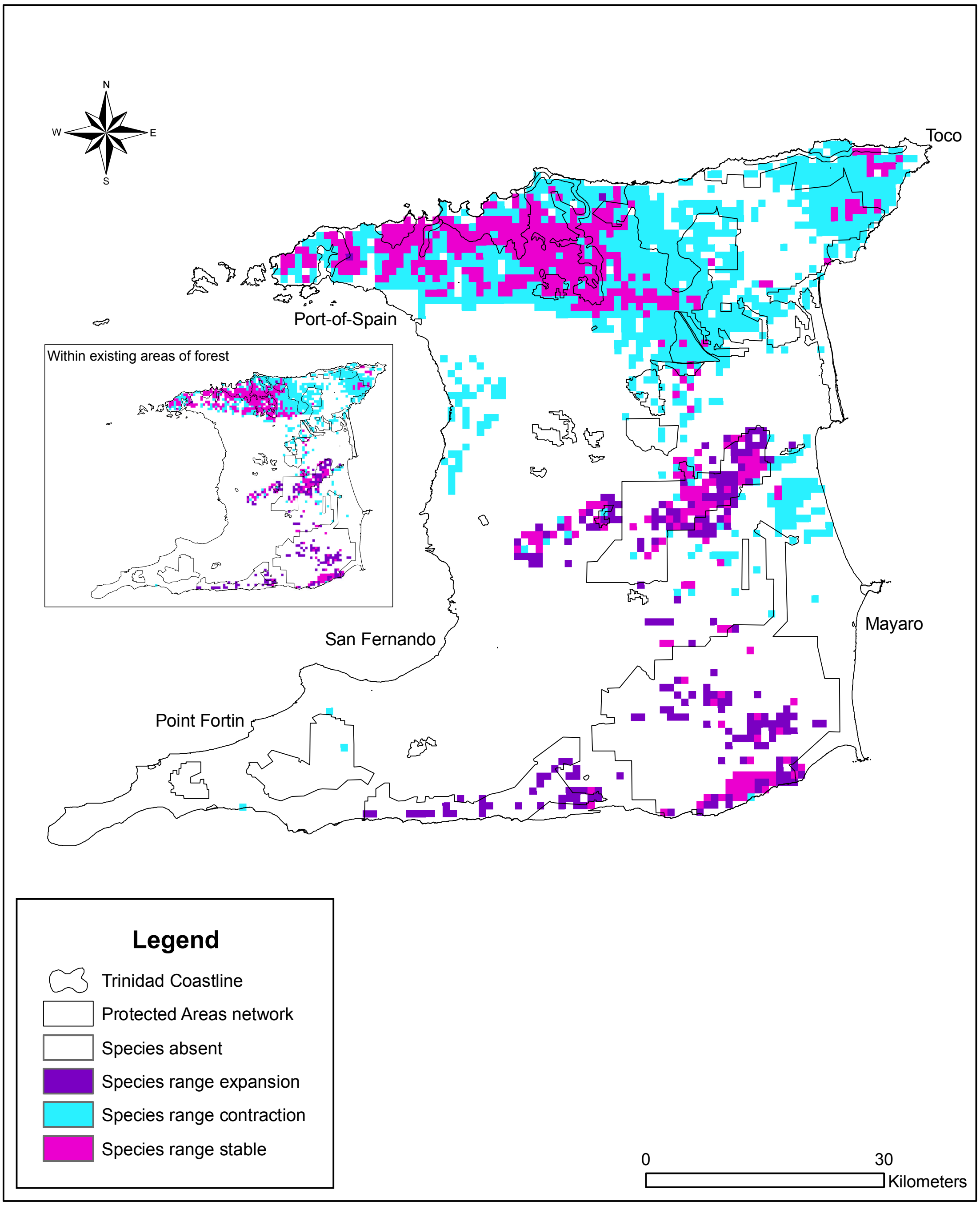


Figure 5.23: Potential species distribution change map of *Ilex arimensis*.

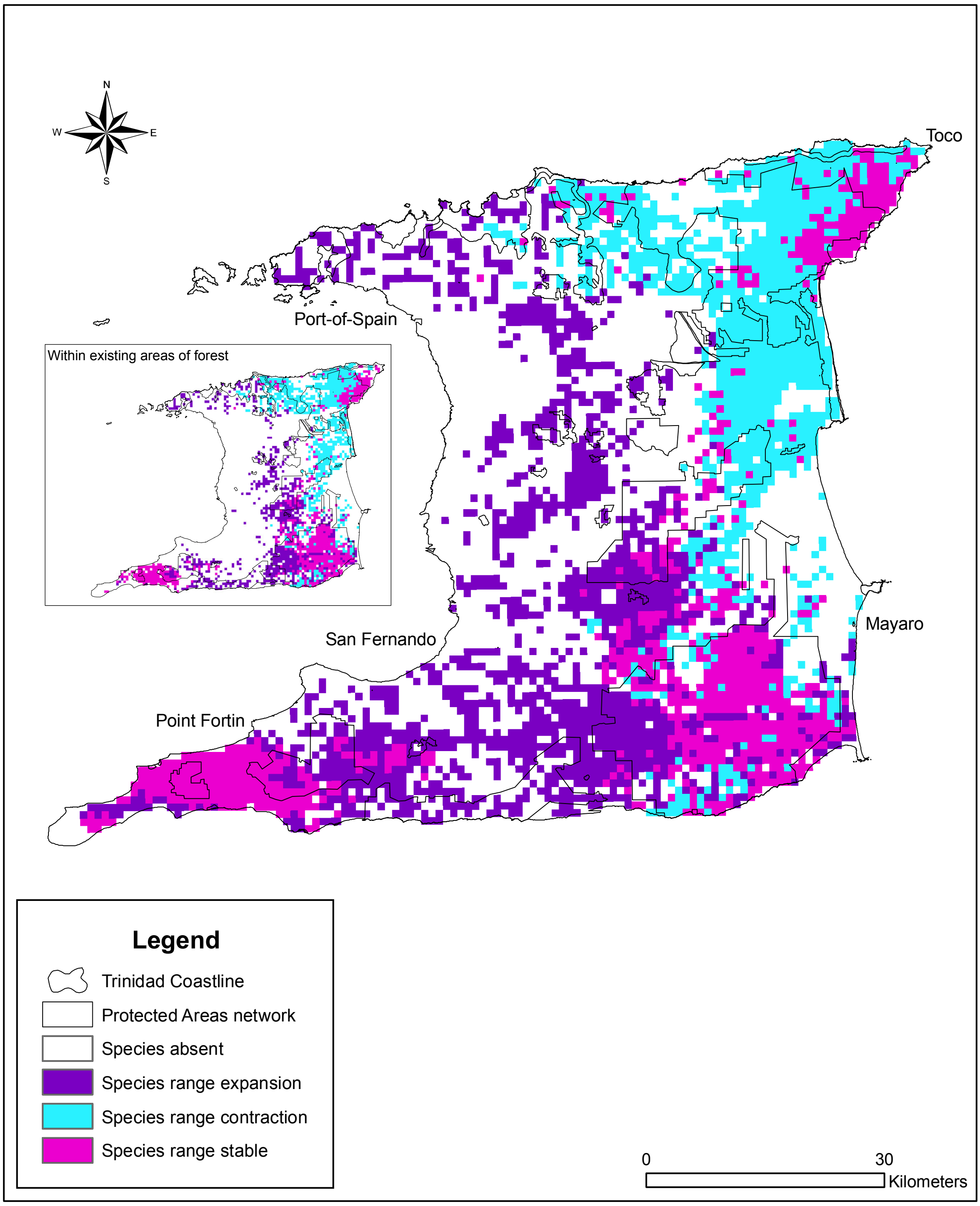


Figure 5.24: Potential species distribution change map of *Mora excelsa*.

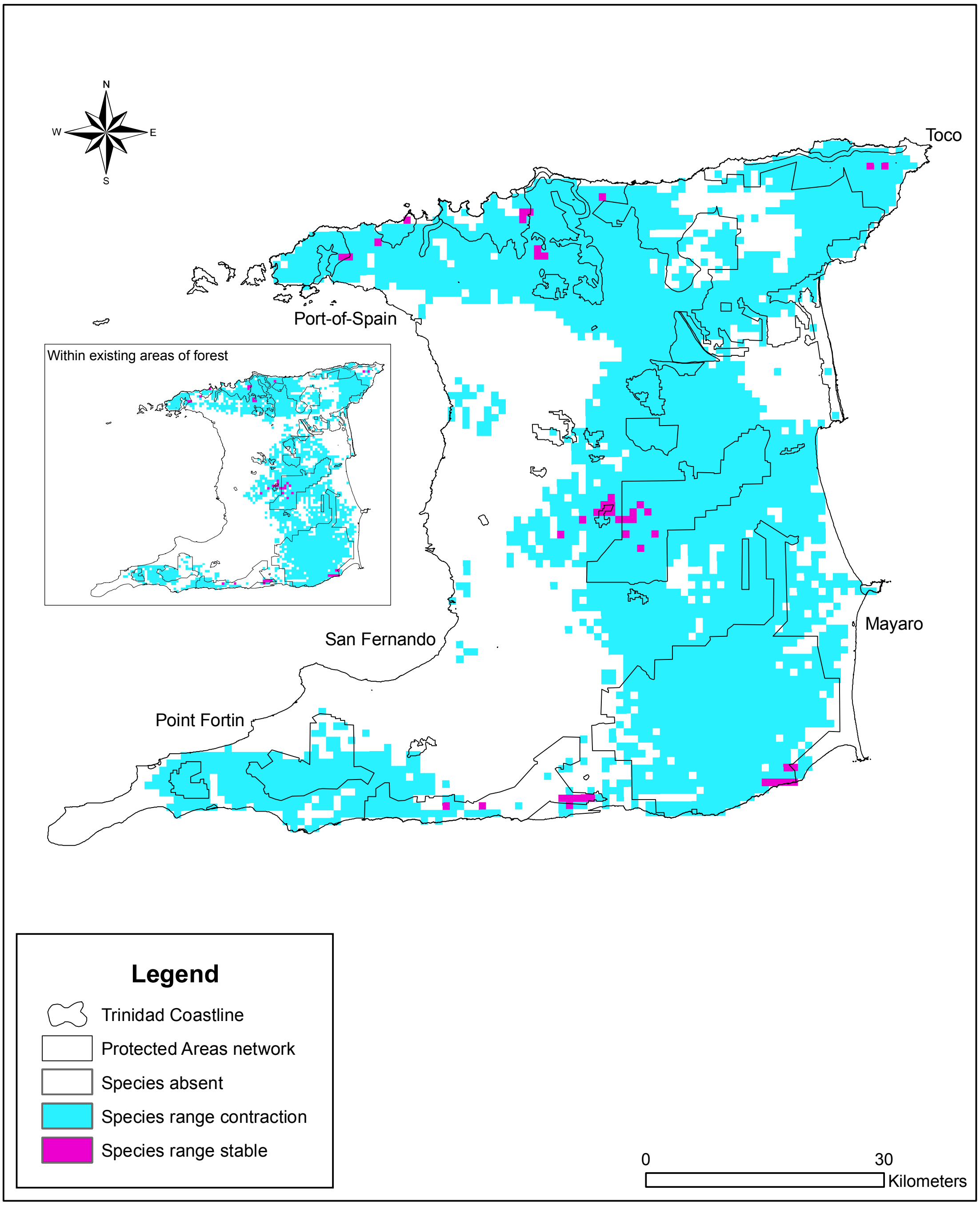


Figure 5.25: Potential species distribution change map of *Sterculia puriens* var. *glabrescens*.

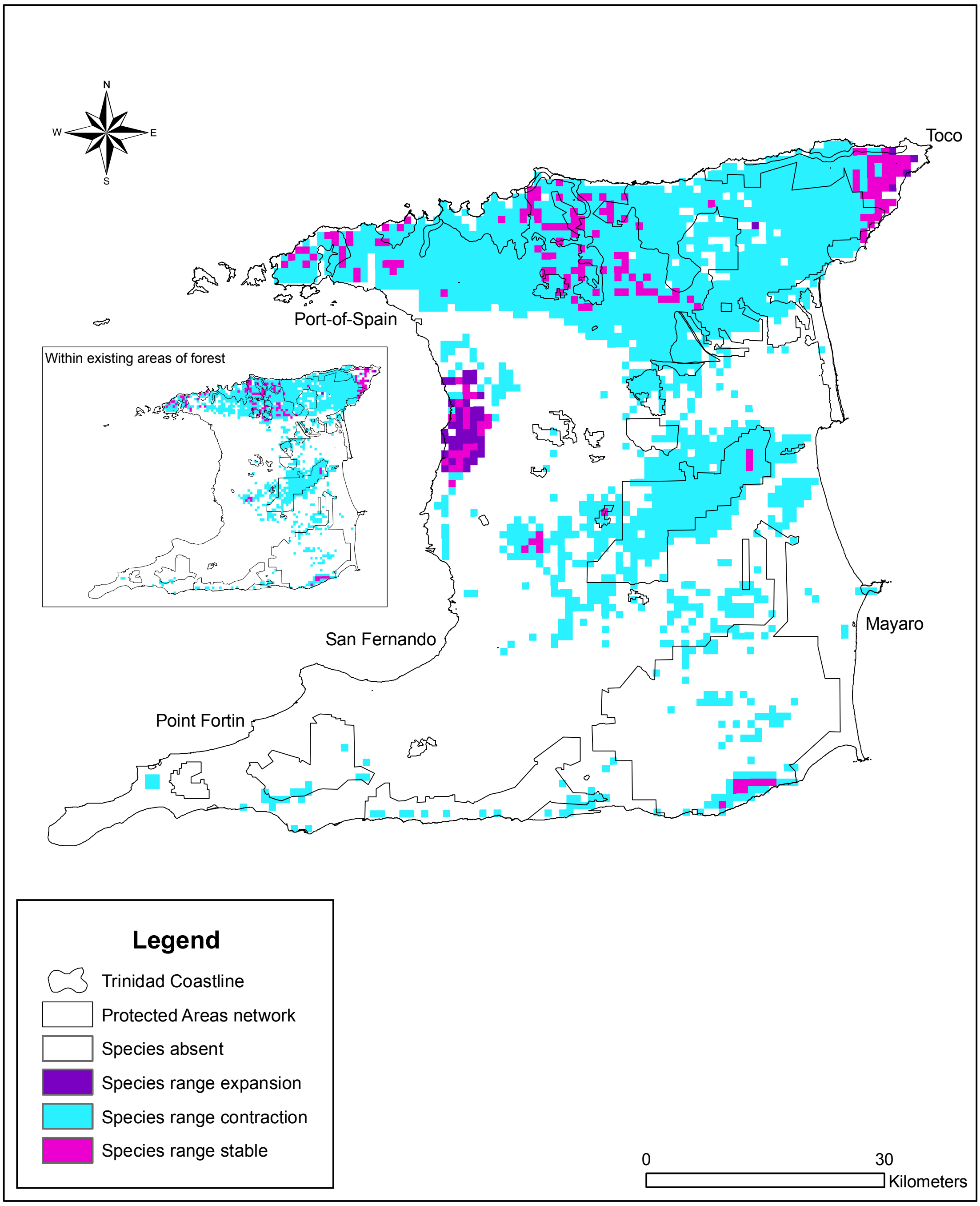


Figure 5.26: Potential species distribution change map of *Tovomita eggersii*.

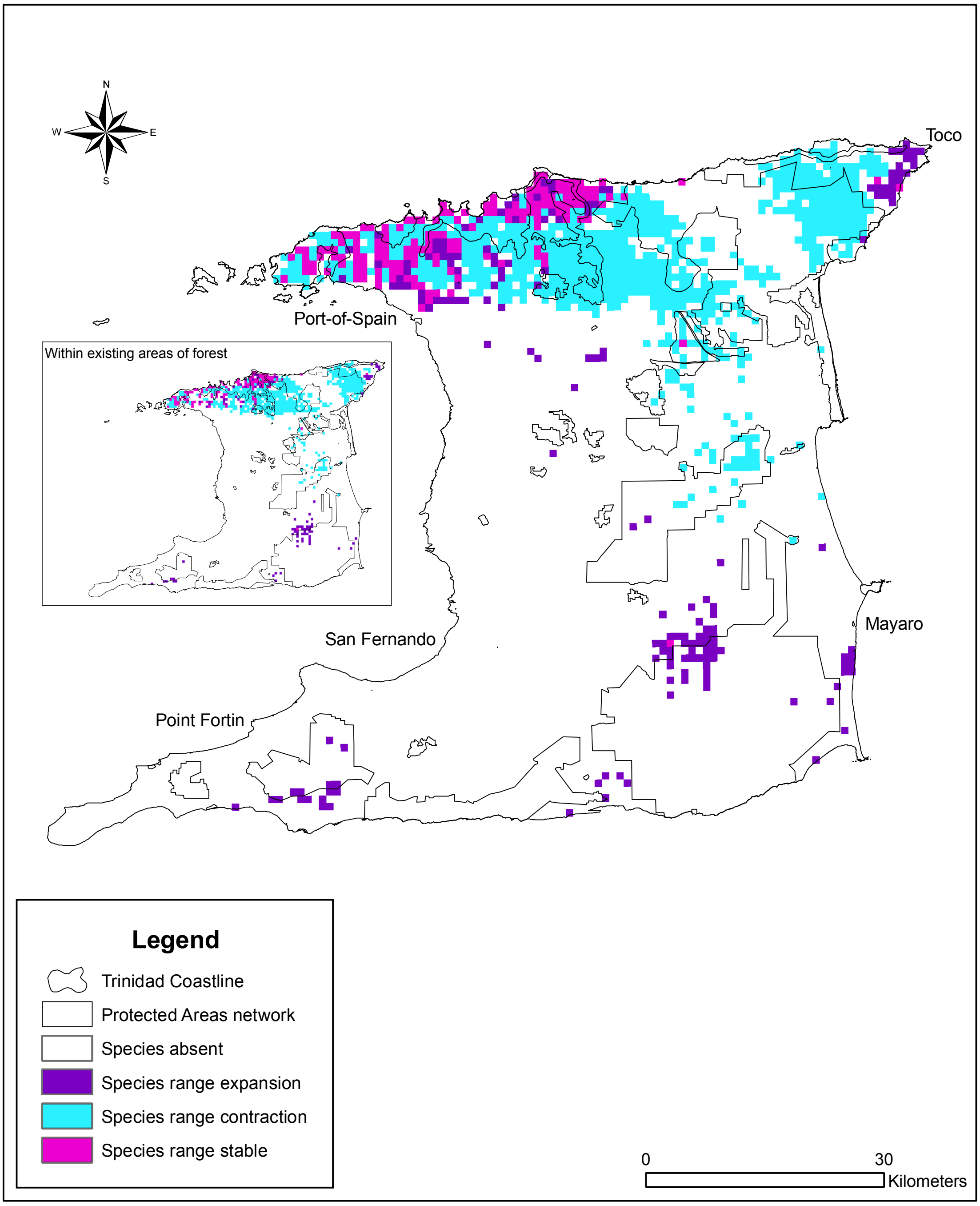


Figure 5.27: Potential species distribution change map of *Tabernaemontana attenuata*.

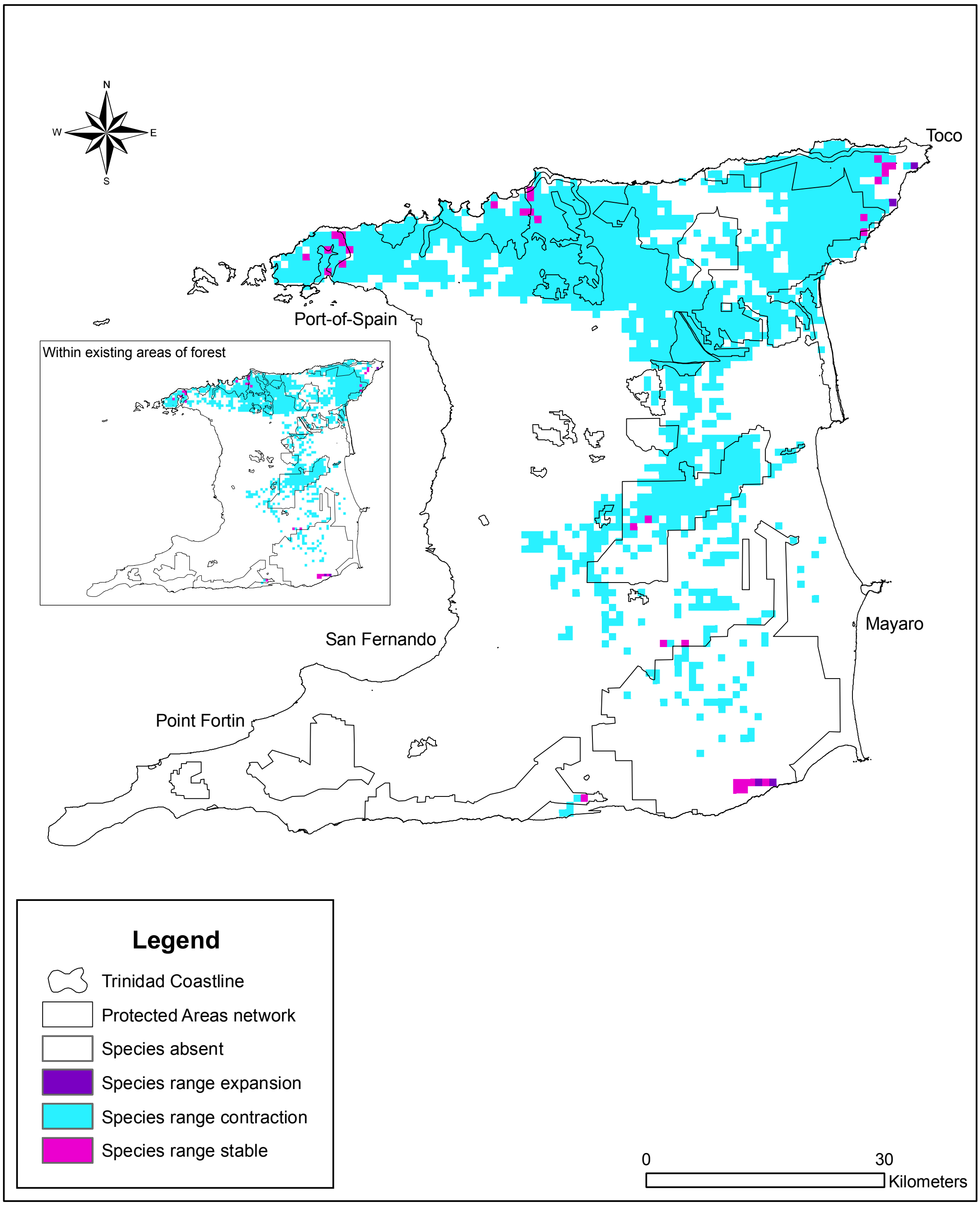


Figure 5.28: Potential species distribution change map of *Tabebuia stenocalyx*.

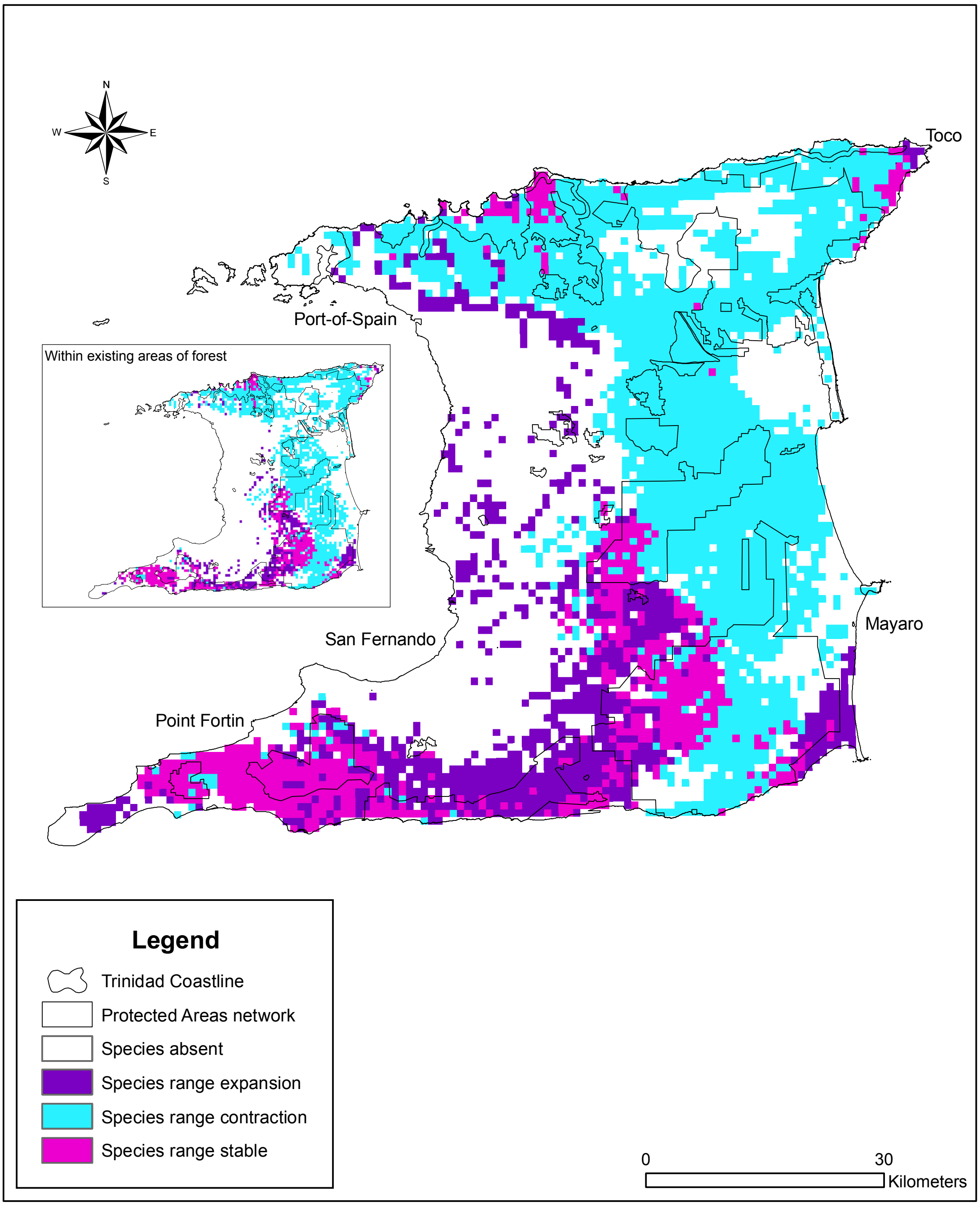


Figure 5.29: Potential species distribution change map of *Virola surinamnesis*.

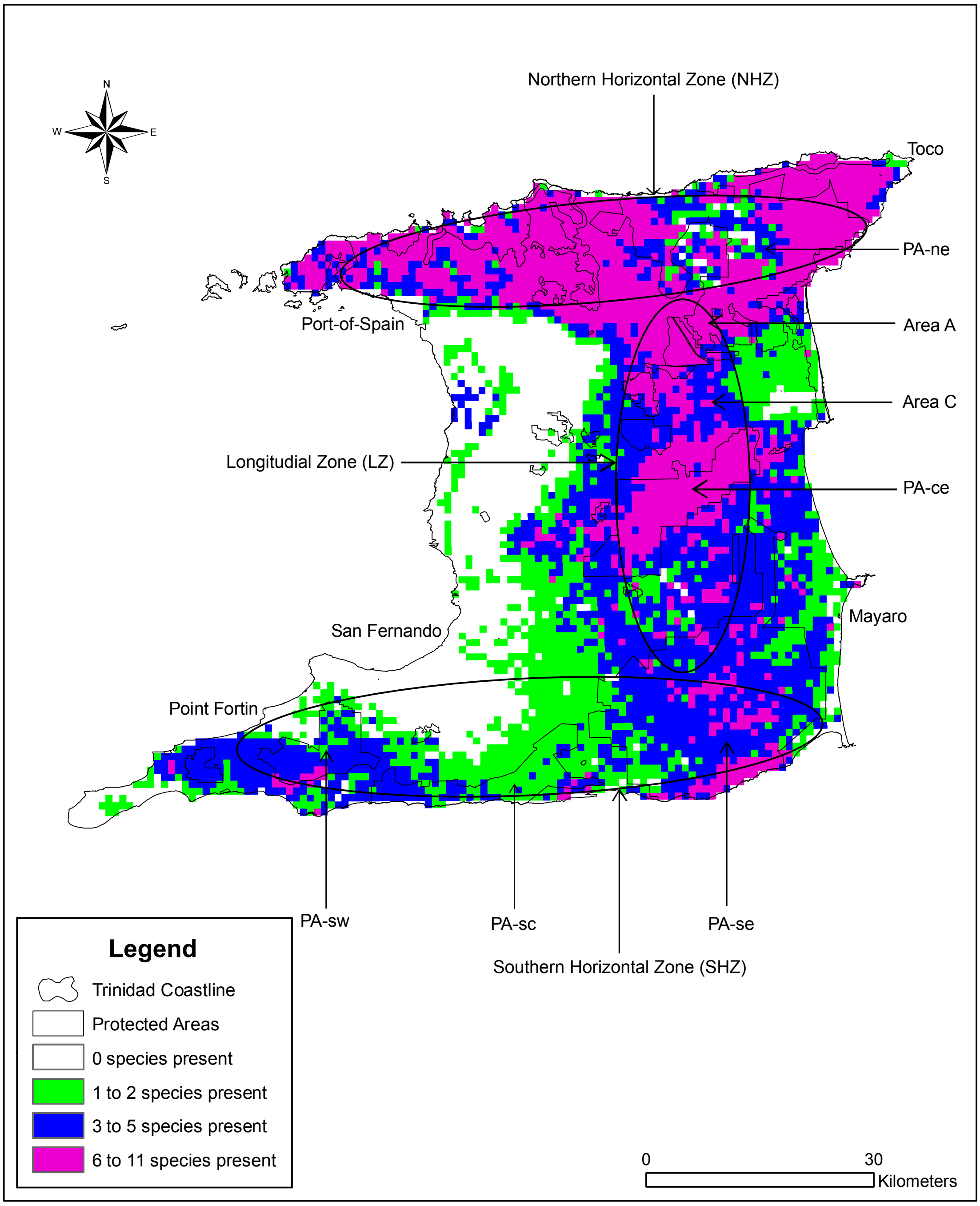


Figure 5.30: Number of the 11 modelled species per pixel for the present climate.

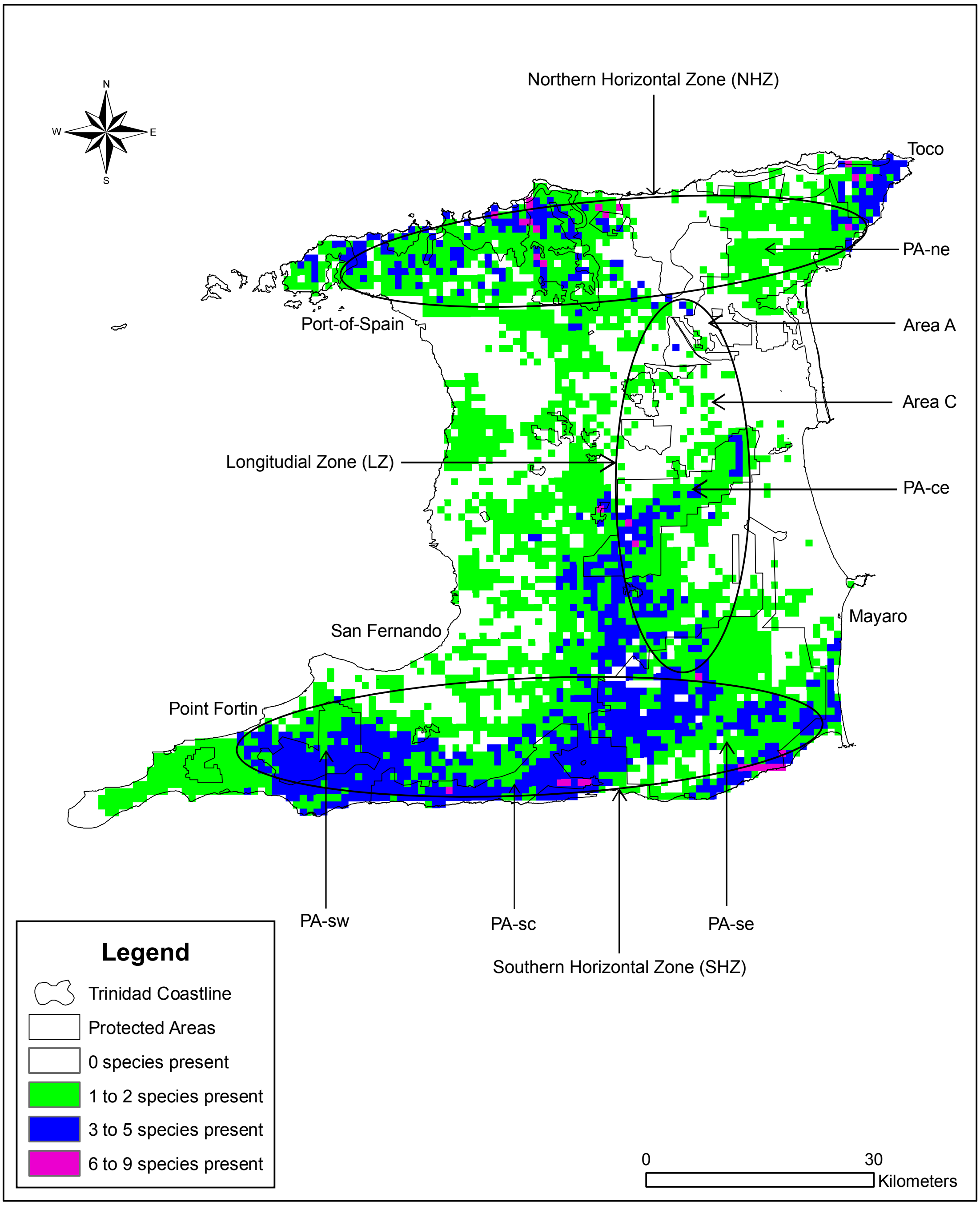


Figure 5.31: Number of the 11 modelled species per pixel for the future (SRES A2) climate.

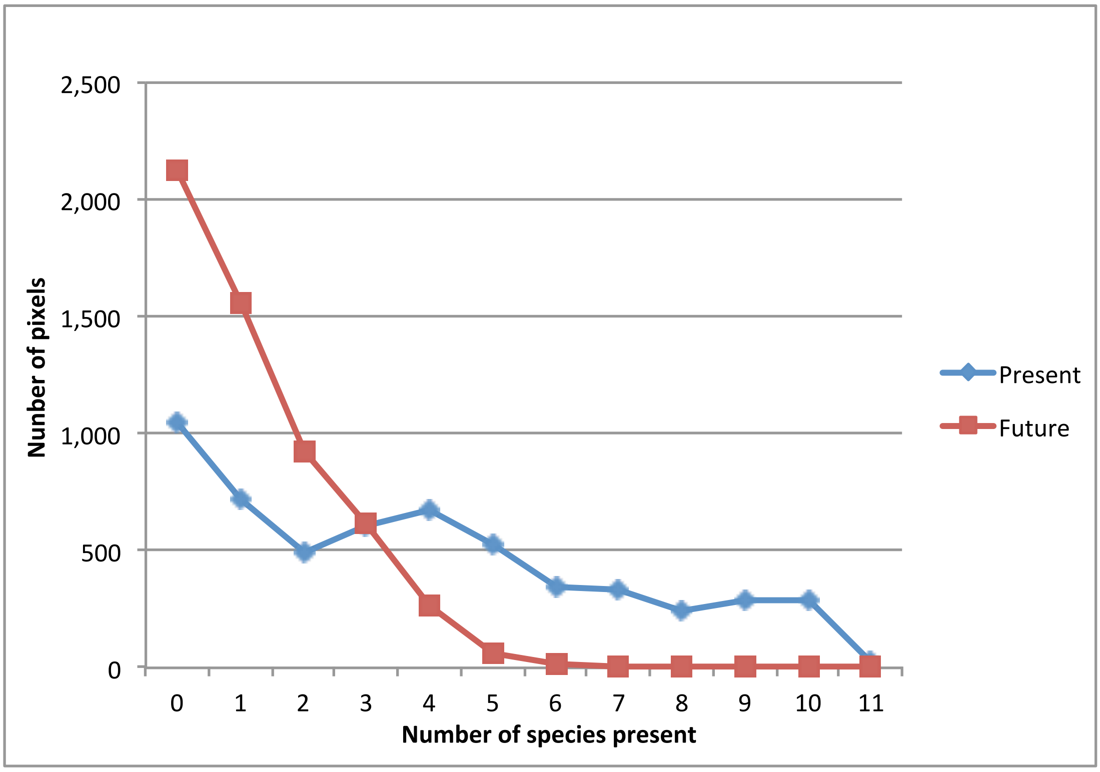


Figure 5.32: Frequency distribution of species during both present and future climates.

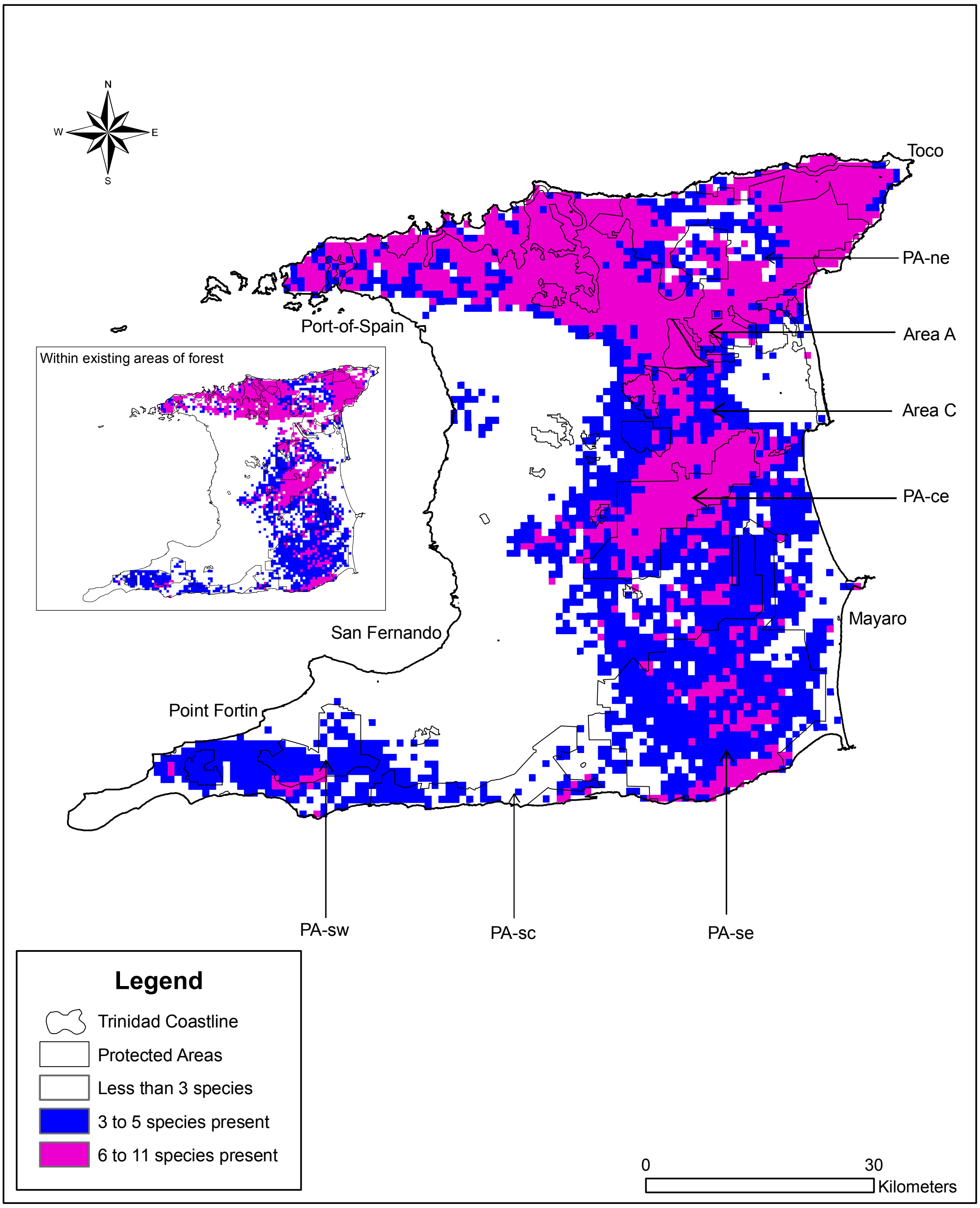


Figure 5.33: Collective species presence/absence map for the present climate.

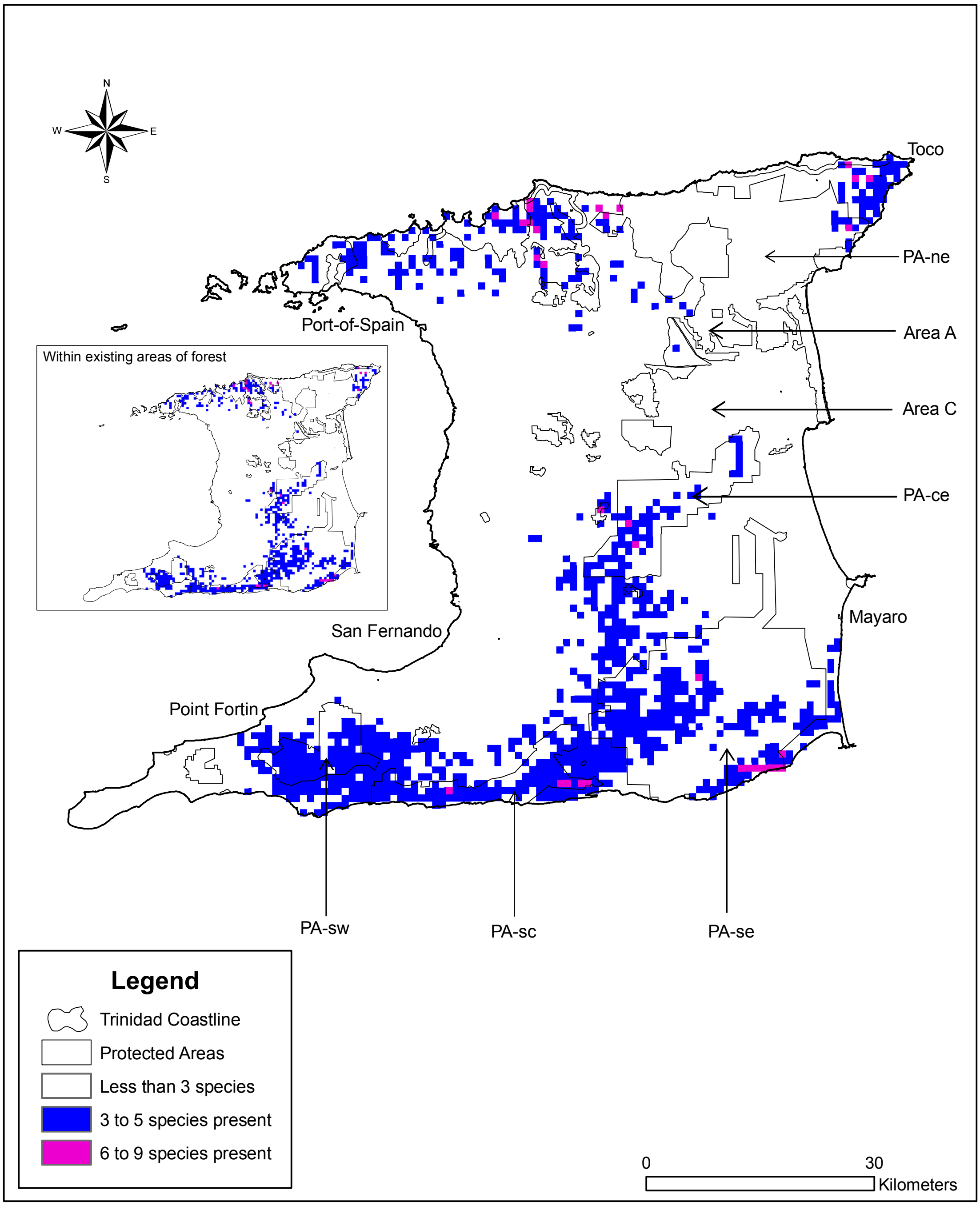


Figure 5.34: Collective species presence/absence map for the future (SRES A2) climate.

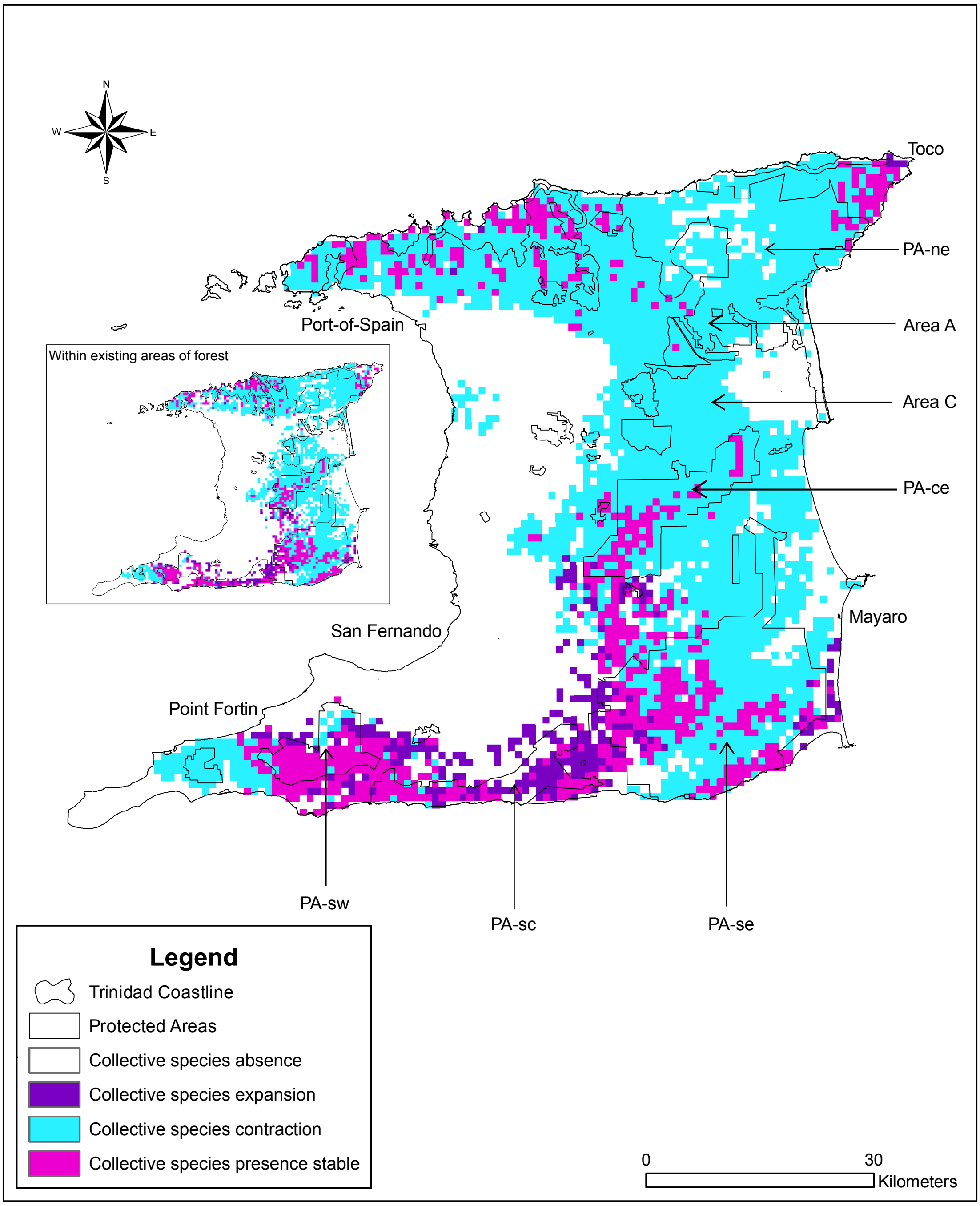


Figure 5.35: Collective species change map (present vs future [SRES A2] climate).

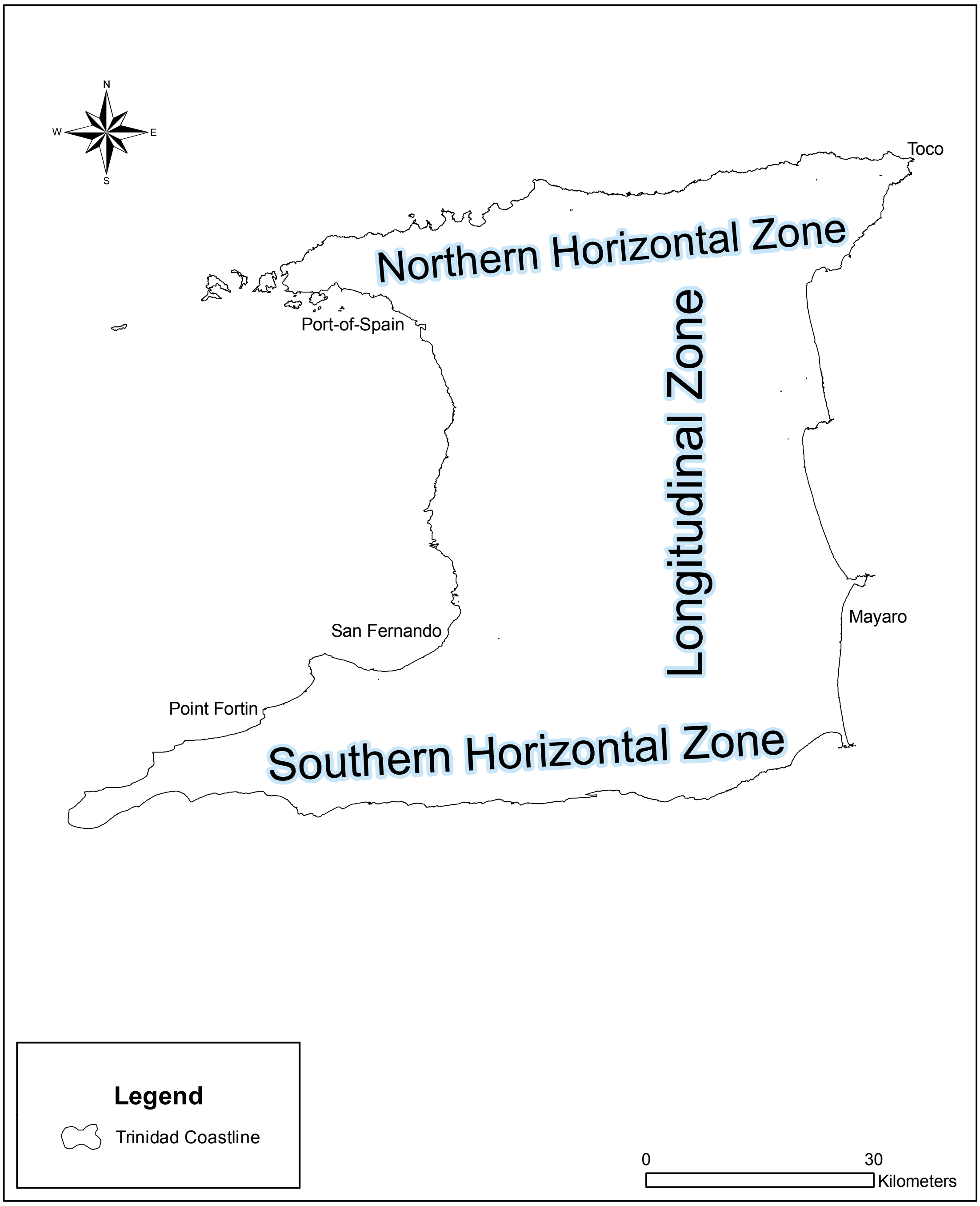


Figure 5.36: Location of zones of high species density.

Chapter 6

Conclusion

"No man is an island, entire of itself; every man is a piece of the continent, a part of the main…"

John Donne 1624 *Meditation XVII*

This chapter synthesises the interconnections among the main conclusions from this thesis and consists of two main parts. The first highlights the main findings of the analyses conducted, while the second outlines the problems encountered, especially from a small island perspective, and where possible, suggests plausible solutions or future work which may help in their resolution.

6.1 Synopsis of main findings

Four main objectives were addressed in this thesis:

6.1.1 Objective: (i) documentation of change in forest cover occurring at varying scales within Trinidad between 1969 and 2007 and (ii) assessment of the effectiveness of the PAN in maintaining forest cover during this period

It was found that Trinidad is currently experiencing an increasing rate of deforestation both inside and outside of its PAN. This has resulted in the reduction of forest cover (internal and external of the PAN) to areas which are presently smaller than what existed in 1969. Additionally, there has been a noticeable eastward migration of the 'band of deforestation' external to the PAN from areas of high anthropogenic development in the western half of the island. This has led to progressive encroachment into the forests outside the PAN to the point where deforestation is now immediately adjacent to many portions of the PAN boundary, with no forested buffer areas to separate development from the PAN.

6.1.2 Objective: assessment of the distribution and ecology of Trinidad's vegetation in order to develop a list of tree species (based on ecological and commercial importance and global/regional rarity) to be used in the SDM analyses

Contrary to the main account of Trinidadian vegetation communities upon which the current management strategies for state-owned forests are based (Beard 1946b), Trinidadian vegetation communities were found to exist as a continuum and not as discrete units. Furthermore, this continuum appeared to be a response to precipitation and, to a lesser extent, elevation. The pervading influence of precipitation means it may be used as an indirect method of indicating the relevance of climate for the distribution of Trinidadian species.

6.1.3 Objective: to develop models of the potential distributions of selected tree species under present climate conditions using the MaxEnt SDM algorithm

Robust models could not be derived for ubiquitous species, while range-restricted species proved to be ideal candidates. Assessment of these models by a small group of 'experts' yielded positive results and the conclusion that cautious interpretation of SMs in conjunction with expert assessment could enable the use of SDM as a valuable conservation tool within small islands. Further, like with the ecological analyses that were conducted (Chapter 3), the MaxEnt algorithm indicated that precipitation and to a lesser extent elevation appeared to be the main drivers of the potential present distribution of these species.

Additionally, because the small size of the Caribbean SIDS leaves little room for error when allocating areas to be used for the conservation of species, it was recommended that SDM should be conducted using spatially unbiased species occurrence data instead of herbarium data alone. Collection RBS sites within a stratified random framework is proposed as the optimum means of procuring such spatially unbiased occurrence data. It was also suggested that if taken further, RBS surveys conducted across the Caribbean could lead to the development of SDM as a conservation tool which could enhance species conservation planning and management at a regional scale.

6.1.4 Objective: (i) to forecast the potential future distributions of the selected eleven tree species and (ii) to combine these future models with corresponding present models to create a 'collective model output' (highlighting areas across Trinidad and its PAN that are expected to lose, maintain and gain the collective presence of this set of species forty years into an SRES A2 scenario

The construction of future models for these analyses revealed that the majority of species were projected to experience a reduction in suitable climate space (assuming perfect dispersal) [e.g., Berry et al. (2007); Hickling et al. (2006); Lenoir et al. (2008); Walther et al. (2002)]. Indeed, within the majority of the SMs generated, a greater than 50% reduction in distribution range was projected, with comparatively miniscule areas of range expansion. Further, the majority of these species are projected to prefer drier, cooler conditions to those expected under the SRES A2 scenario. The three species which did not conform to this trend (*Virola surinamensis*, *Tabernaemontana attenuata* and *Mora excelsa*) preferred hotter, drier conditions instead. However, no details of their known ecology or physiology (relative to the other eight species) were able to account for this difference.

The collective presence of these species did not conform to the trend observed by many other studies which have reported the poleward and upslope migration of species in response to climate change (Hickling et al. 2006; Lenoir et al. 2008). This was attributed to the strong influence of precipitation patterns upon the distribution and ecology (Chapter 3) of these species; with suitable precipitation conditions projected to shift to the south of the island – in a non-poleward direction and away from regions of high elevation to the north. The collective model also revealed a drastic reduction in expected collective presence, with the latter being limited to (i) the southern, (ii) the north-eastern corner and (iii) a scattering across the north-western parts of the island. This effectively implies that the majority of the large PAs within the island's PAN are expected to be ineffective in future conservation efforts which involve these species.

This implication is further exacerbated by the evidence that there is an increasing rate of deforestation both inside and outside of the Trinidadian PAN (Sections 2.4.1 and 2.4.2; Chapter 2). Consequently, forest cover, both inside and outside the PAN (Section 2.4.2.2) is less than during the post-independence era (1969). Furthermore, eastward migration of a 'band of deforestation' from areas of high anthropogenic development in the west towards the PAN boundaries in the east has occurred in the last two decades (Section 2.4.2.1). Progressive encroachment into the forests outside the PAN has meant deforestation is now contiguous with portions of the PAN boundary; with no forested buffer areas to separate development from the PAN (Figures 2.13 and 2.14).

Finally, during the interpretation of these results, it also became clear that model ensembles built with SMs derived from RCM data generated from other scenarios and GCMs were necessary in order to develop useful, more confident suggestions of the placement of future PAs. While it is unlikely individual islands will be able to maintain the survival of these species into the distant future if climate continues to change, a regional approach to conservation may be the only option ensuring the survival of these species into the future.

6.1.5 Findings in relation to other studies of climate change impacts within islands

Like studies based in many other islands across the globe, this study identified an increasing rate of deforestation and hence, of habitat loss within Trinidad. Additionally, similar to findings within larger islands, the majority of species within this study were forecasted to experience a contraction in suitable climate space (Consiglio et al. 2006; Hannah et al. 2008; Schatz et al. 2008). However, altliudinal shifts in suitable climate space were not discerned as seen in studies such as Benning et al. (2002). This is believed to be as a result of these species being better suited to a combination of cooler, drier conditions – which are not projected to occur within areas of higher elevation to the North of the island. Even when the effects of an atmospheric lapse rate is incorporated to produce cooler conditions within such higher elevations, these areas are also projected to experience increased precipitation levels and hence were projected to be unsuitable for the future survival of these species.

6.2 Problems encountered and possible solutions

The process of modelling potential present and future distributions of the 11 tree species within Trinidad has shown that SDM within small islands is possible. However, six unique challenges are associated with the application of SDM at the small island scale. The following section outlines these problems, and where possible, suggests possible solutions or future work which may help in their resolution. Finally, it should be noted that this discussion is limited to the application of SDM to the flora and not to mobile faunal species within these islands.

6.2.1 The stemming of Trinidad's increasing rate of deforestation

Increasing deforestation rates (Section 6.1.1) in conjunction with increasing populations and demand for land imply that in many of the Caribbean SIDS (Section 2.1), there is an urgent need to control, reduce and ultimately stop deforestation from occurring both inside and outside of the PAN.

Recommendation

There are several strategies which may help to maintain forest cover outside the PAN and hence contribute to both the maintenance of forest cover and biodiversity as well as to the buffering of the PAN. Firstly, forest restoration within areas that have been degraded and abandoned by agriculture or settlement can be sustainably restored using mixtures of native species – especially those which, apart from having a high timber value (future income to stakeholder), can also provide resources for wildlife (Lamb et al. 2005; Montagnini 2001). Additionally, efforts should be made to sustain agricultural land use types such as cocoa and coffee plantations which have over the years been replaced by monoculture systems. These plantations provide natural harbours to both wild and agricultural biodiversity (Moguel and Toledo 1999; Rice and Greenberg 2000). Such systems can also be designed to incorporate integrated fire management strategies (e.g., fire breaks) which can be invaluable mechanisms in reducing the threat of annual forest fires across the country (Section 2.5.4) (Myers 2006). Further, there are many small holdings of agricultural land which, for the most part are used for intensive row-crop monocultures. The implementation of policies which target these smallholders with the intention of disseminating agro-ecological knowledge and encouraging diverse farming landscapes will be an effective way of promoting a matrix of semi-natural areas across these islands (Castillo and Toledo 2000).

Such initiatives could be supported by economic instruments such as PES – which pays landowners to protect remaining forest within their holdings and to integrate trees into their farming systems. There are several successful examples of such schemes in Central American territories such as Costa Rica (Pagiola et al. 2005). Additionally, the establishment of private forest reserves by local NGOs have also shown potential in helping to maintain forest cover outside the PAN.

For example, the Asa Wright Nature Centre in Trinidad has over the years, been actively involved in purchasing land within the Arima watershed. As a result of this action, forest cover has been maintained over large areas of the watershed which were being competed for by limestone quarrying and intensive agricultural activity. Finally the active involvement of local communities in the management of these forests and other natural areas has been shown to be equally, or in some cases, even more effective in maintaining forest cover than efforts which are based solely on exclusion (Ellis and Porter-Bolland 2008; Porter-Bolland et al. 2012). However, for such incentives to be successfully maintained, there is an urgent need for updated and enforced legislation (Section 2.2 which restricts deforestation, regulates logging and promotes the maintenance of secondary forest (Wallace et al. 2005).

6.2.2 Lists of target species for conservation within the Caribbean SIDS required

Based on the pervading message from the SDM literature, shifts together with a reduction in the distribution range of many species are expected to occur as the climate continues to change (Berry et al. 2005; Hickling et al. 2006; Lenoir et al. 2008; Pereira et al. 2010; Thuiller et al. 2011). While such changes are likely within large continental land masses, the small, fixed geographical spaces of small islands may result in eventual species extinction on individual islands within the Caribbean SIDS. Hence assessment and prioritisation of species, considered valuable enough for investment into their conservation within a future changing climate, is urgently needed.

It is therefore noteworthy that the distributions of only three members within the set of eleven species used for these analyses are known to be confined to

Trinidad and/or its immediate environs (Guyana and Venezuela); while just five and three species have known distributions which also extend to the Lesser and Greater Antilles respectively (Tables 6.1, 3.4 and 3.5). Instead, the overall distributions of the majority (nine) of these species also occur, to varying extents, within further reaches of the South American continent. Additionally, four members of this set of species are also known to have distributions which extend to Central America and/or the southern parts of the North American continent. Hence the majority of members within this particular set of species are not irreplaceable. This is unsurprising given the continental nature of Trinidad together with the criteria used for choosing the set of species used for these analyses.

However, the extensive distribution of these species outside of Trinidad does not imply that SDM does not have the potential to be a useful conservation tool within the Caribbean SIDS. For example, while the species used in these analyses may not require urgent conservation from a global perspective, their conservation may be of importance at the island or regional scale (e.g., planning for timber production and harvesting). Additionally, as mentioned in Section 1.1.3, these islands are well known for their high levels of biodiversity and endemicity – which occupy increasingly threatened habitats. Hence, the use of SDM for informing the conservation of endemics and other globally rare or threatened species within the islands of this region remains perfectly justified.

Further, as seen within the set of species used for this study (Table 6.1), there are species which may occur on more than one island, hence the application of SDM for conservation purposes within the Caribbean may be more informative when conducted within a regional instead of an island scale. Indeed, authors such as Kark et al. (2009) have pointed out that cross-border collaboration can be an effective and less costly way of increasing the efficiency of conservation planning efforts. Such results can then be compared to extra-Caribbean SIDS distributions in order to assess the urgency for overall conservation. However, as mentioned within Section 6.2.7, before the application of SDM at a regional scale for conservation purposes, some immediate steps need to be taken. Firstly, there is a need for the agreement and involvement among the stakeholders of the region such as Caribbean Community (CARICOM) and Venezuela. Further, in order to determine which species should be prioritised for conservation, research is first necessary to determine species distributions within the islands of the Caribbean from which a regional (and individual island) list can be developed.

However, within Caribbean SIDS there are no set guidelines and accompanying regional list of species that have been highlighted as being important for conservation into the future. The method used to select species for the SDM analyses in this thesis is but one example of a means for generating such a species list. Indeed, because of the unique characteristics of the flora of each island within the Caribbean, the set of criteria used to determine the final species choice for future conservation may ultimately be very different among individual islands. This choice depends upon the perspective adopted by both policy and conservation planners, in conjunction with the characteristics of each island's flora which may be of greatest value or concern.

For example, Trinidad, because of the continental nature of its flora, is not home to many endemic species (approximately 2% of its flora); and until the recent passing of the National Forest Policy and the National Parks Policy by Cabinet in 2011, very little local legislation supported by scientific publication for the preservation of these few endemics existed (GOTT 2009a; 2009b). In view of this, the list of species that were used for these analyses was instead developed by combining the criteria which did not include endemicity as a specific criteria (ecological importance, commercial importance and global/regional rarity) – but instead included it indirectly under the global/regional rarity criterion. These criteria were perceived to encompass broad ranging factors that are expected to be important during both the present-day and in the future – especially for tree species. However, they may not all be as relevant to non-tree (including animal) species; for example, the commercial importance criterion may not be of as much practical value as a criterion based on the level of threat from hunting/poaching or other uncontrolled forms of the harvesting of wild populations. In a similar manner, this method and criteria may be very different to the method that is likely to be developed within an island such as Jamaica, where the high levels of endemism would be expected to feature as a major criterion.

Further, even if such lists of target species did exist for these islands, spatially unbiased occurrence data is also needed to use SDM as a tool for developing conservation strategies that incorporate future climate change. While species distribution data does exist within herbarium collections (both local and international) for many of these islands, the extent of these collections varies from island to island depending on the purpose of the collecting institutions or individuals (Baksh-Comeau, pers. comm. 2010). Furthermore, apart from not indicating species abundance or rarity within an island, herbarium data are spatially biased and do not accurately represent the distribution of a given species across these islands (Schulman et al. 2007) (see Section 6.2.5 below).

Recommendation

It is first necessary to determine what species exist within each individual island before deciding which species should be conserved. Island wide RBS surveys, which sample all existing vegetation within a randomly stratified framework of sites, will provide both spatially unbiased location data for SDM analyses, as well as a much needed baseline (or updating thereof) of the existing flora and associated abundances within a given island. The small size of the majority of these islands confers a unique advantage as it allows for realistic and detailed stratified random sampling across a given island; whereas a similar survey at a continental scale would not be possible because of the sheer size of the area that would need to be sampled (Feeley and Silman 2011).

However, such an endeavour is not a 'quick-fix' solution and is expected to require a great deal of resources in terms of finance, personnel and taxonomic skills. But as seen with the financing of the RBS survey in Trinidad, there are several sources of international funding such as the World Bank and the Inter-American Development Bank (IADB) that are now being made available to help SIDS in their attempt to adapt to future climate change. In addition, enlistment of local institutions such as local universities and Forestry Departments within governments can aid in the allocation of resources and personnel who will also benefit from capacity building of this science within the island. Finally, RBS surveys that are conducted within islands which do not have a herbarium will more than likely require collaboration with already existing herbaria on other islands within the Caribbean. This creates an environment of regional co-operation and sharing of expertise which will be necessary if SDM is to be used successfully as a tool to aid adaptive conservation within this region. Once such a survey has been completed, conservation managers and planners will have the information required to generate a list of species which should be targeted for future protection – based on the unique features of the island's flora.

These suggestions of (i) conducting of RBS surveys across these islands in order to (ii) generate a list of species for conservation within the region fall within the first and second steps of the Systematic Conservation Planning (SCP) framework that has been prescribed by authors such as Margules and Pressey (2000) as an effective means of allocating limited resources for biodiversity conservation.

Consisting of six inter-linked stages, the SCP framework for a given study region includes: (i) compilation of data on the biodiversity of study region; (ii) identification of conservation goals for the study region; (iii) reviewing of existing conservation areas; (iv) selection of additional conservation areas; (v) implementation of conservation actions and (vi) maintenance of the required values of conservation areas. In an ideal world, this SCP framework represents a flexible and accountable means of addressing competing land uses and allowing for critical review of decisions (McDonald 2009).

However, in reality, this framework has proven difficult to achieve, with success being limited to implementation of only parts of – but not the entire framework. Within the Caribbean, the same situation is expected – as the economic, political and social requirements of these densely populated islands continue to take precedence over the allocation of conservation areas. Additionally, as mentioned in Chapter 1, the limited resources of these islands impedes delivery of several components within the stages of SCP – such as the measuring of the extent to which quantitative targets of PAs have been achieved, or the identification of under represented targets/features within existing reserves. Additionally, required maintenance of conservation areas has thus far, had a poor performance rating, with many PAs failing to prevent illegal encroachment and poaching due to a lack of enforcement (Chapter 2). Also, there is a characteristic lack of management actions such as zoning around PAs which are required in SCP to aid in their maintenance or monitoring. Furthermore, even if the application of SCP was successful in preventing the ad-hoc placement of conservation areas, this would not be able to prevent the ad-hoc placement of competing and irreversible forms of development such as housing and industry – which continue to occur as human population levels continue to rise within these already densely populated islands.

Finally, a further advantage of conducting of RBS surveys is that abundance data can also be collected which can be used to analyse the ecological dynamics of the vegetation communities within an island (as seen in Chapter 3). Such analyses are invaluable aids to SDM analyses as they can be used to assess environmental parameters that are important drivers of the ecology of vegetation communities within an island. This provides an independent, non-modelling based perspective which can be compared to the results derived from the SDM analyses. As was the case with this study, such information is also critical for aiding the interpretation of SDM analyses at the small island scale as there is currently no literature that defines whether there are fractal alternatives to a continental 'macro-scale' which is believed to be the scale at which climate drives changes in species distributions.

6.2.3 Non-range restricted species produce poor models

One of the limitations that can be expected with the use of SDM is that ubiquitous species will be expected to produce less robust models than range restricted species. This limitation will not affect the use of SDM for many range restricted endemic and other rare species, however it will restrict the use of SDM for widely occurring species that may be important for commercial or economic reasons, for example, ubiquitous timber species.

Recommendation

One effective means of increasing the confidence of the area within which a given species is expected to exist in the future is by the creation of model ensembles (Araújo and New 2007). Because, the variance of output among alternative SDM techniques can range from small to large – especially when used to project species distributions within novel conditions such as climate change, some authors have suggested the use of several models (ensembles) in order to explore the range among projections. The construction of model ensembles is flexible and can involve the use of several model algorithms, predictor variables, initial conditions and so forth to yield more robust forecasts (Araújo and New 2007).

Model ensembles designed to increase the confidence of output for ubiquitous species can involve the overlaying of SMs produced by several SDM algorithms (and climate scenarios) instead of just one, which is then followed by the highlighting of the areas within which the individual SMs that comprise the ensemble overlap. Within these highlighted zones, areas with a greater degree of SM overlap represent a higher level of confidence that a given species will be likely to exist. Such a model ensemble would provide a measure of central tendency and a range of confidence values at which the distribution of a given species can be defined; this provides greater confidence, flexibility and increases the ability of conservation planners to develop conservative estimations compared to using SMs generated from only one SDM algorithm. Such flexibility will be especially useful in light of the limited amount of land that is available for conservation purposes within many SIDS.

Such model ensembles are being carried out by an increasing number of conservation applications. Examples include broad scale conservation studies which examine the impact of climate change upon the distributions of various species. For example, Thuiller et al. (2005) used model ensembles to project the distributions of 1,350 European plant species into the late 21st century – under seven climate change scenarios. Marini et al. (2009, 2010) used model ensembles to assess and improve upon present conservation actions for almost 40 bird species by (i) estimating the overlap between existing reserve locations and the present (and future) predicted distributions as well as (ii) determining areas that were climatically suitable for reintroduction programmes of these species. Additionally model ensembles have been applied to the assessment of invasive species such as studies of weed risk assessment (Crossman and Bass 2008). Also, Carvalho et al. (2011) used model ensembles to assess how uncertainties associated with species distributions can affect resource allocation decisions within conservation programmes.

Finally, it should be noted that these analyses did not incorporate such ensembles because the aim of this work was exploratory – seeking to determine the utility of SDM for conservation planning under climate change within the Caribbean. Hence, these analyses sought to assess whether SDM could be applied to the Caribbean small island setting; and how these results could be used in combination with PA networks to plan adaptation responses. Further, it was also not the aim of this study to create policy suggestions – which would certainly require the use of multiple SDM algorithms and climate scenarios to capture uncertainty in a more robust manner.

6.2.4 Does the macro-scale exist within an island setting?

Within the nested hierarchy of factors believed to influence a species' distribution across a range of spatial scales, climate is believed to impact particularly at a macro-scale, while biotic interactions are believed to be the main driver at the local scale (Pearson and Dawson 2003; Wiens and Bachelet 2010; Wiens et al. 2009). However, there is no indication in the literature as to how this applies to a small island setting. Are small islands too small for climate to be a factor that influences species distribution within them? And hence are biotic interactions the main drivers of species distributions at this scale? Or do fractal alternatives for the continental macro-scale exist within an island setting? Additionally, could climate have an effect on the distribution of species at much finer scales within the mountains of these islands due to the Massenerhebung

Effect? Because of the virtual absence of almost any SDM modelling within a small island setting, there are no answers to these questions. However, the results of this study have indicated that, at the scale of a small island the size of Trinidad, climate (precipitation) may in fact be a driver of the distribution ranges of the tree species that were selected for this study.

Recommendation

When applied to a small island setting, the construction of robust SMs of present potential species distributions which incorporate climate parameters in conjunction with expert opinion can be used as an indirect means to infer whether climate variables influence species distributions. This can be further supported by concurrence with patterns derived from independent ecological analyses (non-modelling based) that incorporate climate parameters. For example, the construction of strong SMs which were based upon climate parameters in conjunction with positive expert assessment was found to concur with the findings of Chapter 3. These indicated that precipitation was a major driving force that influenced the vegetation communities within the island. This combination of results was used as an indirect means to support the relevance of forecasting future species distribution models based upon changes in climate at the scale of a small island the size of Trinidad.

6.2.5 Spatial bias of species observation data

The current state of advancement within SDM algorithms does not adequately account for the spatially biased species occurrence data derived from herbarium collections. Such spatial bias can lead to the inflation of test AUC scores and can be very misleading during the interpretation of model results. This problem may be further exacerbated within a small island setting in which the small limited space leaves little room for error.

Biased background techniques have been suggested to reduce the effects of spatially biased data within SMs generated by MaxEnt (Phillips et al. 2009). The literature indicates that this technique produces lower AUC test scores but does not define an acceptable range of values which would indicate whether an SM can be considered to be robust (Elith et al. 2011). Additionally, this technique was developed with the intention of generating SMs within fixed geographic areas and under fixed climatic conditions; and its benefits do not necessarily transfer when the models are projected to future climate conditions (Phillips et al. 2009). Finally, apart from no indications of performance with respect to small versus large scale study areas, this method is not a solution for the problem of spatially biased data but simply a means of reducing the effect of such bias.

Recommendation

This problem of spatial bias can be prevented by the sampling of species within a stratified random sampling design across a given island (Section 6.2.2). The results of such a sampling endeavour will provide detailed, spatially unbiased occurrence data that will produce less misleading and hence more robust models. Additionally, the collection of spatially unbiased occurrence datasets from a number of small islands has the potential to be used for the calibration of performance of SDM algorithms such as MaxEnt at a small island scale, which is an area of uncertainty within the SDM literature that is yet to be addressed.

6.2.6 RCM data urgently needed

There is an acute paucity of available RCM data for the Caribbean region. In order for SDM to be effectively applied as a conservation tool within the Caribbean, it is necessary to construct and compare SMs that have been based on a variety of likely future climate scenarios which have been generated from several GCMs. Hence sole reliance on the RCM data generated from the HadAM3H GCM is inadequate.

This problem is exacerbated by recent findings which indicate that while the IPCC's SRES scenarios were relevant in the previous decade, they are becoming less and less representative of current conditions (Canadell et al. 2007; Raupach et al. 2007; Sokolov et al. 2009). This has come about as a result of many reasons including the underestimation of global population increases and too much optimism being allocated to the potential of sustainable development (Moss et al. 2010). Hence a new suite of up-to-date scenarios are required.

Recommendation

A new generation of future climate scenarios is currently being developed from RCPs that have recently been agreed upon by the IPCC; these are expected to be released with the IPCC's upcoming Fifth Assessment Report (AR5) that is scheduled between 2013 and 2014 (Moss et al. 2010). These scenarios represent projections that are expected to characterise a broad range of potential future climate conditions that have been based upon updated and new information on climate processes, greenhouse gas emissions, demographic estimations, economic data, emerging data from new technologies and observation data of changes in land cover, land use and other environmental factors (Moss et al. 2010). They are also designed to better facilitate the needs of impact and adaptation studies which require data at higher spatial and temporal resolutions, as well as better representation of extreme events.

This new system consists of scenarios built around four RCPs which represent updated estimations of radiative forcing levels. These four RCPs are currently being used in the Climate Intercomparison Project 5 (CMIP5) to produce model ensemble projections (and associated scenarios) for future climate change which will be assessed within the AR5. If these CMIP5 ensemble-based projections and scenarios are applied to model ensembles of SMs generated from multiple SDM algorithms within the Caribbean SIDS; the confidence levels of the resulting SMs produced will be greatly enhanced.

6.2.7 Need for adaptive studies which incorporate climate change into terrestrial conservation planning

It should be noted that details of the results described in this study were based on a group of 11 tree species, and hence, may not represent in detail, the response of all species within Trinidad. Indeed, a group consisting of different species to the ones used in this study may have yielded different responses to a future SRES A2 scenario. However, it should also be noted that general trends such as species range contractions and the shifting of suitable climate space reported by this study also conforms to the findings of many other studies within the literature. Therefore it is likely that the application of these methods to a different group of species may yield projections which, while different in specific details, may indicate similar overall trends.

A thorough literature search yielded no adaptive studies within the Caribbean SIDS that focus on incorporating climate change into the planning and placement of terrestrial PAs. As shown in these analyses (and from other studies at the continental scale), plant species may be expected to decrease the sizes of their distribution ranges as their climate space across a given island continues to be altered with the changing climate. Hence, PANs within these islands may not be able to sustain the survival of many species into the future as climate continues to change.

Apart from extending PAN networks to facilitate these changes, a range of other adaptation strategies have been suggested from studies based in other threatened island systems such as the Galapagos islands and the United Kingdom – to conserve both the range and ecological variability of species and their associated habitats. These include but are not limited to the conservation of other high quality (but non-protected) habitats, minimising habitat fragmentation by the maintenance of existing and the creation of new ecological networks, the creation of buffer zones around high quality habitat, prevention of the spread of invasive species and the creation of more resilient landscapes (e.g., agroforestry) (Sachs and Ladd 2011; Smithers et al. 2008).

Many of these require, to varying extents, the extension and/or maintenance of natural habitat beyond the boundaries of the PAN. However, while actual extensions of PAN networks or non-protected natural habitat may be feasible within continental settings, the former may not be very practical within most small islands because of space limitations; while the latter can only be implemented with co-operation from private and political stakeholders – which has yet to be developed within many of the Caribbean SIDS. Furthermore, even if these suggestions were all implemented, their benefits are likely to be limited based on the degree of shifting and/or contraction of suitable species climate space that occurs across a given island.

Recommendation

Taking into consideration that species may exist within more than one island, there is a possibility that while a given species may be expected to disappear completely on islands A and B, it may remain stable or increase its range on islands C and D, respectively. Hence, there is a need for inter-island collaboration and co-operation in order to develop a medium to long-term regional perspective to the conservation of target species instead of simply focusing on individual islands. This enhances the chances of ensuring the survival of these species within the region.

Consideration should be given to whether suitable climate space for a species which is expected to disappear from all islands that it presently inhabits can be found within other islands in the future. If yes, then the future survival of disappearing species may be sustained by Assisted Translocation (AT) to PAs within other islands. The literature on the AT of species is dominated by a debate which focuses heavily on the risks involved with this strategy. However, the AT of plant species is not a novel activity, as humans have been introducing plants to new regions throughout our history. Indeed, modern agricultural and horticultural industries have and continue to translocate species on a wide-scale basis (Veken et al. 2008). Additionally, in attempts to revegetate marginal or highly impacted regions, or to preserve dwindling populations, both restoration ecologists and conservation biologists have been translocating species for decades (Bowles and McBride 1996).

It should however be noted that AT is not a quick procedure, but requires planning, ongoing monitoring and adaptive management. There are also potential impacts upon the recipient communities that are associated with AT that need to be taken into consideration, for example, the associated risk of the translocated species becoming invasive by competitive exclusion of existing species (Levine et al. 2003). However, according to Williamson and Fitter (1996) less than 1% of all species (plants and animals) become invasive when imported to a new region. Furthermore, Mueller and Hellmann (2008) report that the risk associated with vascular plants becoming invasive is relatively low compared to other taxa such as freshwater invertebrates. There is also a risk of pathogens being transported along with the translocated species (Hodder and Bullock 1997) – the prior removal of which may increase the likelihood of the species becoming invasive (Callaway and Maron 2006). Hybridisation is also a risk, although it is possible to assess how readily a plant is likely to hybridise based on an extensive existing literature. For example, hybridisation is known to be an infrequent mechanism used by invasives to disrupt a given site – and is therefore believed to represent a small element of risk from AT (Gurevitch and Padilla 2004).

Additionally, a large number of practical factors need to be considered when undertaking AT such as the genetic structure of the individuals being translocated, the selection of suitable recipient sites as well as the occurrence of essential biotic interactions (e.g., mutualism) within these sites. Additionally it is likely that repeated introductions may be required in order to ensure survival of the translocated species within the recipient site (Mueller and Hellmann 2008). It has also been highly recommended that there be long-term monitoring of both the recipient sites and nearby control sites. This is in order to detect negative impacts of the AT as well as to aid in understanding the details of what is required for greater success in AT – by allowing for the assessment and isolation from impacts of concomitant but unrelated factors. Such requirements make AT an expensive venture, which is usually applied as a ‘last resort’ that is adopted only when other conservation strategies have, or are likely to fail.

Indeed, within the islands of this region AT may be a last resort technique which may be necessary to ensure the survival of many species as their climate space within these small geographic spaces shift or contract. Also, because the forests within many of these islands have been, and continue to be, highly impacted and fragmented from both natural events (e.g., frequent hurricanes), and anthropogenic activity (Bloem et al. 2005; Emanuel 2005; Imbert and Portecop 2008; Lugo et al. 1981); this suggestion of re-locating plant species to new host islands having suitable climate space in the future may be taken a step further.

The highly disturbed vegetation within many of these islands' PAs may provide a good opportunity for an 'experiment' in developing a new paradigm for creating high value ecosystems or 'Novel Community Arks'. Using SDM as a tool to inform the architecture (placement of valued species) of these 'Novel Community Arks', selected PAs would be deliberately populated with valued plant species from the region instead of trying to maintain existing vegetation communities which are neither pristine nor highly valued. Such communities would be engineered to maintain existing ecosystem functions but would be potentially more resilient to projected future climate conditions.

A great deal of apprehension to this suggestion of *circa situ* conservation is expected from concerns of potentially disastrous ecological imbalance and the introduction species which may unexpectedly become invasive within new environments (Hunter 2007; Willis et al. 2010). However, within the Caribbean context, it can be argued that alien species have been, and continue to be introduced to these islands ever since European colonisation. It can further be argued that if these 'experiments' are not successful, then the vegetation within these PAs would ultimately remain disturbed – as they would have been before the setting up of these 'experiments'. Furthermore, this suggestion offers a choice to an otherwise stalemate situation in which the expansion of PANs is neither adequate nor an option. It provides an opportunity to protect ecosystems and improve the resilience of forests which will continue to be impacted by (i) anthropogenic activity, (ii) natural disasters, (iii) fragmentation and (iv) climate change.

Based on SDM conducted on a regional basis, initial 'experiments' of 'Novel Community Arks' within several islands (preferably with low endemism) can be monitored for impacts on the ecological balance within these PAs. The first introductions would consist of tree species as they are major ecosystem pillars and are also generally easier to identify and remove in the case of unforeseen negative feedback effects. These experiments would however, not be a short-term solution as the translocation of these species would have to be carried out over several generations in order to ensure the survival of suitable genotypes within the new environments as well as the development of associations with pollinators, soil mycorrhizae and other organisms necessary for survival. This long establishment time (introduction of several generations) in conjunction with the long growth period required by trees therefore implies that these 'Novel Community Arks' be implemented as soon as possible.

However, while in theory this may offer a plausible solution, apart from adaptive management, much consideration and collaboration between regional conservation agencies responsible for such an option will be needed. This is because apart from being potentially expensive, investigations will be required to ensure that the introduction of new species within a potential host island will not adversely impact upon the ecological balance within this island. Additionally, such an endeavour will require the revisiting of agreements within international conventions such as the Convention on Biological Diversity (CBD) and others which address the individual rights of countries to unique aspects of their biodiversity.

6.3 Concluding remarks

Regional collaboration for PAN establishment will require co-ordination

This study, along with the many others conducted in continental settings, indicate that species biodiversity is likely to be greatly altered as climate continues to change. Presently, there is an extensive literature on using SDM to project potential future species distributions in response to climate change, and the range shifts are likely to result in novel communities. Additionally, as described above, despite the translocation of species being utilised as a strategy to aid the conservation of species facing extinction over the last several decades, there is still an on-going debate focused on the risks involved. While conventional conservation strategies may be sufficient for many species – especially within continental regions, well-conceived, planned and managed translocations of species to neighbouring islands (and continental regions) may be the only means of ensuring the continued survival of valued species within the Caribbean region. Additionally, in contrast to the pervading sentiment that (oceanic) islands generally experience 'ecologically stable' conditions which ultimately give rise to high levels of endemism (Cronk 1997); the small islands of the Caribbean continue to be subjected to both natural and anthropogenic disturbance, and do not have the luxury of space to facilitate shifts in species range. Hence, less conservative strategies may be required in an attempt to secure the survival of valuable plant species within this region. SDM shows potential to be a very useful tool in aiding such adaptation strategies.

As climates change, Caribbean SIDS will eventually run out of the climate space that is required to sustain many of its valuable species. Yet to date, no practical strategy for addressing this situation has been suggested or implemented. A plausible contribution to controlling and, to some extent, managing species loss is the adoption of a regional perspective to biodiversity planning, placement of PAs (where possible), and the establishment of 'Novel Community Arks'; instead of focusing exclusively upon conserving species which presently occur within individual islands Even a regional approach is not expected to conserve all target species but it may increase our ability to manage the rate of species loss. Additionally, a regional approach to biodiversity planning would provide an opportunity for regional collaboration which could produce other benefits, such as capacity building and the construction and maintenance of a much needed regional database of the conservation status for plant species within the Caribbean. Moreover, such a collective approach to biodiversity planning will certainly increase the chances of both individual islands and the region as a whole to adapt in the face of an already changing climate.

6.4 Tables

Species	**Distribution outside of Trinidad**	**Global Range**	**Star**
Brosimum alicastrum	Greater Antilles (Cuba, Jamaica, Puerto Rico), Lesser Antilles (St. Vincent, the Grenadines – Carriacou), United States (Florida), Mexico (Campeche, Chiapas, Quintana Roo, Tabasco, Veracruz, Yucatan), Central America (Belize to Costa Rica, [Panama]), Colombia, Venezuela, the Guianas, Brazil, Ecuador, Peru, Bolivia, Hawaii.	5	GN
Calophyllum lucidum	Guyana, [French Guiana].	3	GD
Carapa guianensis	Greater Antilles (Cuba, Hispaniola), Lesser Antilles (Guadeloupe, Marie Galante, Dominica, Martinique, St. Lucia, St. Vincent, Grenada), Central America (Belize to Honduras, Nicaragua to Panama), Colombia, Venezuela, the Guianas, Brazil, Ecuador, Peru.	5	GN
Eugenia confusa	Bahamas, Greater Antilles (Cuba, Hispaniola, Jamaica , Puerto Rico), Virgin Islands (St. John), Lesser Antilles (Antigua to St. Lucia), United States (Florida).	3	GD
Ilex arimensis	Endemic to Trinidad and Tobago.	1	BK

Mora excelsa	Venezuela, Guyana, Surinam, Brazil.	4	BU
Sterculia puriens var. *glabrescens*	Lesser Antilles (St. Vincent), Venezuela, western Guyana, Ecuador	4	???
Tabebuia stenocalyx	Venezuela, Guyana, French Guiana, Brazil.	5	GN
Tabernaemontana attenuata	Venezuela, Surinam, French Guiana.	3	GD
Tovomita eggersii	Venezuela, Guyana.	3	GD
Virola surinamensis	Lesser Antilles (Martinique), Central America (Costa Rica, Panama), Colombia, Venezuela, the Guianas, Brazil, Ecuador, Peru, Bolivia.	5	GN

Table 6.1: Star ranking and distribution of species outside of Trinidad.

Appendices

Appendix A

Presence-absence analyses

A.1 Method

For this appendix, the analyses carried out are the same as those described within the Methods of Chapter 3 (Section 3.2.2.1 to 3.2.4.7) – apart from the following exceptions:

1. Section 3.2.3.1: the abundance data matrix was presence/absence transformed instead of square root transformed.
2. Section 3.2.4.2: restrictions within the structure of the dendrogram derived from the cluster analysis of this presence/absence transformed data required that clusters were defined at a 10% instead of a 9.17% similarity level.
3. Section 3.2.4.3: restrictions in dendrogram structure again required that the sub-division of selected large clusters be done at an 18% similarity level instead of the 13.26% similarity level used in Chapter 3.

A.2 Results

A.2.1 SIMPROF and Cluster results

The results of the SIMPROF test based on the set of 165 RBS samples collected from sites scattered across Trinidad's forests, show that the real similarity profile (red line) fell a long way outside the 95% limits of the null curve – for virtually its entire length (Figure 3.2). This confirms that that there is statistical evidence for the sub-structures within the data defined by the cluster analysis (Figure A.1) to be justifiably interpreted.

When mapped in geographical space, the RBS components of the eleven clusters defined at a 10% similarity level within Figure A.1 did not appear to be organised in a haphazard manner. These clusters were, for the most part, located within clearly defined 'zones' within the island (Figure A.2). These zones were very similar in terms of (i) location and (ii) RBS site components to the clusters defined and mapped in Chapter 3 (Figures 3.3 and 3.4).

However, clusters g and k (similar to clusters 8 and 5 respectively of Figure 3.4) were located in north-south zones which spanned the entire length of the island. Additionally cluster b (similar to cluster 2 of Figure 3.4) was observed to contain RBS points scattered across the Northern Range. Unlike the results of the analyses in Chapter 3 (Figures 3.5 and 3.6), these clusters, when sub-divided at an 18% similarity level (Figure A.3), did not separate into sub-sections which were located in distinct geographical regions from each other (Figure A.4).

Cluster g remained unchanged (sub-cluster g2) apart from three RBS points (sub-cluster g1) located along the south-western coastline (Figure A.4). Cluster k separated into sub-cluster k1 which consisted of RBS sites located within the south-western peninsula, central Trinidad as well as along the entire span of the

Northern Range (east to west). Sub-cluster k2 was not as widespread – with RBS sites located within both central Trinidad as well as the central region of the Northern Range. Division of cluster B yielded sub-cluster which were also not located in very different regions. Sub-cluster b1 consisted of RBS sites which were mainly scattered from the north-eastern to the central regions of the Northern Range. Sub-cluster b2 was less 'cohesive' with RBS sites scattered to the south of the Northern Range (within central Trinidad) as well as within the north-eastern and north-western ends of the Northern Range (Figure A.4).

A.2.2 NMDS ordinations

Like with the NMDS ordinations illustrated in Figure 3.7 of Chapter 3, the stress level of Figure A.5 was moderately high at 0.16 – indicating some difficulty in displaying the relationships among these 165 RBS samples within two and three dimensions. Nevertheless according to (Clarke and Gorley 2006) these stress levels still gave a potentially useful general two and three-dimensional pictures, however, not much emphasis could be placed on details within the plot. From this prescribed general perspective, both plots indicated that the sub-clusters were closely inter-related to each other. With the exception of sub-cluster C1, no distinct pattern or grouping of RBS sites was discerned.

A.2.2.1 Ordination plots of Groups 1, 2 and 3

Despite the 165 RBS plots being split into three groups based on well-defined subsets of clusters that were shown by SIMPROF to be statistically significant at a similarity level of 0.5%, the stress levels of the two-dimensional NMDS plots were still relatively high. Stress levels of 0.16, 0.18 and 2.0 for the two-dimensional NMDS ordinations of Groups 1, 2 and 3 (Figures A.6, A.7 and A.8) implied yet again, that while useful at the 'big-picture' scale, not much emphasis could be placed on the details within these plots. This scenario is similar to the ordination of Groups 1 and 2 (Figures 3.9 and 3.10) in Chapter 3, where stress levels within the same range required that interpretation be limited to a 'big-picture' scale.

From Figure A.6 it was seen that sub-clusters that appeared cohesive and closely related in terms of the distance between each other. Sub-cluster C1 appeared more distinct from the other sub-clusters – with its RBS sites located close to each other and collectively further away from the all other sub-cluster components. Additionally sub-cluster A1, appeared different to the other sub-clusters as its component RBS sites were spaced further apart (and hence less similar) from each other and from the components of the other sub-clusters. Sub-clusters C1 and A1 represent the same grouping of RBS points referred to as sub-clusters 3A and 6A within the analyses of Chapter 3 (Figure 3.6).

The arrangement of the sub-clusters within Figure A.8 again indicated that they were very similar to each other as there was no major division from one group to another within the plot. Sub-clusters I1, K1 and K2 appeared cohesive as individual groups, with some interspersion of the RBS sites comprising their peripheries. This gave the impression that these sub-clusters, while representing different 'associations' of vegetation, were very closely related to each other. Sub-clusters H1 and J1, while closely situated to sub-clusters I1, K1 and K2, were not as cohesive, with their respective RBS components scattered further distances away from each other. This increased distance among the RBS sites of H1 and J1 corresponded to the scattered distribution of these RBS sites within geographic space (Figure A.4).

A.2.2.2 Summary NMDS

The stress level of 0.15 for the two-dimensional summary NMDS ordination plot (Figure 3.11) again required that not much emphasis be placed on the details of these ordinations. As with the analyses in Chapter 3, these sub-clusters appeared to be arranged in a gradual ‘continuum’ with no sharp division among them except for sub-cluster C1. In this continuum sub-clusters located within the north-eastern part of the island were located at one extreme of the two or three-dimensional NMDS space, which then gradually progressed to the other end of the continuum which contained the sub-clusters that were situated in the south-western parts of Trinidad.

A.2.2.3 Superimposed Precipitation bubble plots

In a similar manner to results in Chapter 3, a distinct gradient was observed when the two-dimensional scatter plots of Groups 1, 2, 3 and the summary NMDS were superimposed with annual precipitation data for Trinidad (Figures A.9, A.10, A.11 and A.12). There was also visual concordance between the order of sub-clusters arrangement within the NMDS plots and amount of annual precipitation received, however, this was not as well defined or smooth as within Figure 3.18 of Chapter 3. Within the summary NMDS (Figure A.12) annual precipitation levels were highest at sub-clusters located to the upper and lower right-hand corners of the summary plot (corresponding to the north-easterly part of the island) and gradually decreased towards the left regions of the graph (in a south-westerly direction across the island) (Figure A.13).

A.2.2.4 Superimposed Altitude plots

A similar, but less distinct gradient was observed when the two-dimensional NMDS scatter plots were superimposed with the altitude above sea level data for the island (Figures A.14, A.15, A.16 and A.17). Visual concordance (although less acute than with annual precipitation) was again observed between the sub-clusters and altitude at sea level. As with annual precipitation, the sub-clusters situated to the right of Figure A.17 were also found to occur within relatively high altitudes; while those located at the left of the plot occurred in areas of low altitude (Figure A.18). Sub-clusters within the Northern Range were clearly defined within this NMDS, with C1 occurring at the highest altitude. This was followed by sub-clusters D1, B2, B1 and K2 in decreasing order of altitude. There was however no representation of RBS sites located within the relatively high altitudes of the north-western part of the Northern Range. This is because, as mentioned above, the RBS components of cluster G, when sub-divided into sub-clusters G1 and G2 did not separate into separate sites that were located exclusively within the north-western peninsula or the south-western peninsula. Instead sub-cluster G2 contained RBS sites located within both the north-western and south-western peninsulas, making it less likely that a site from the north-western peninsula would be selected for the summary NMDS.

A.2.2.5 Superimposed Soil Drainage plots

As with the SDC ordinations in Chapter 3, when the two-dimensional NMDS scatter plots were superimposed with SDC data for the island (Figures A.19, A.20, A.21 and A.22) no distinct pattern or gradient was observed. This is also supported by Figure A.23 within which no relationship between sub-cluster location and SDC could be discerned within geographical space.

In summary, the NMDS bubble plots (Groups 1, 2, 3 as well as the summary plots) of annual precipitation and to a lesser extent altitude above sea level, indicate potential gradients with symbols proportional in size to one or both of these parameters showing visual concordance with the different sub-clusters. The gradient across the annual precipitation summary diagram suggests that annual precipitation is the best overall explanatory variable. In addition altitude above sea level appears to be a secondary explanatory variable for sub-clusters C1, D1, B2, B1 and K2.

As with the Chapter 3 analyses, these results suggest that the vegetation within Trinidad is not composed of unique vegetation types, but is instead, a continuum within which the combination of species change in response to gradual changes in precipitation (and also altitude) across the island.

A.3 Figures

Figure A.1: Cluster dendrogram at a 10% similarity level.

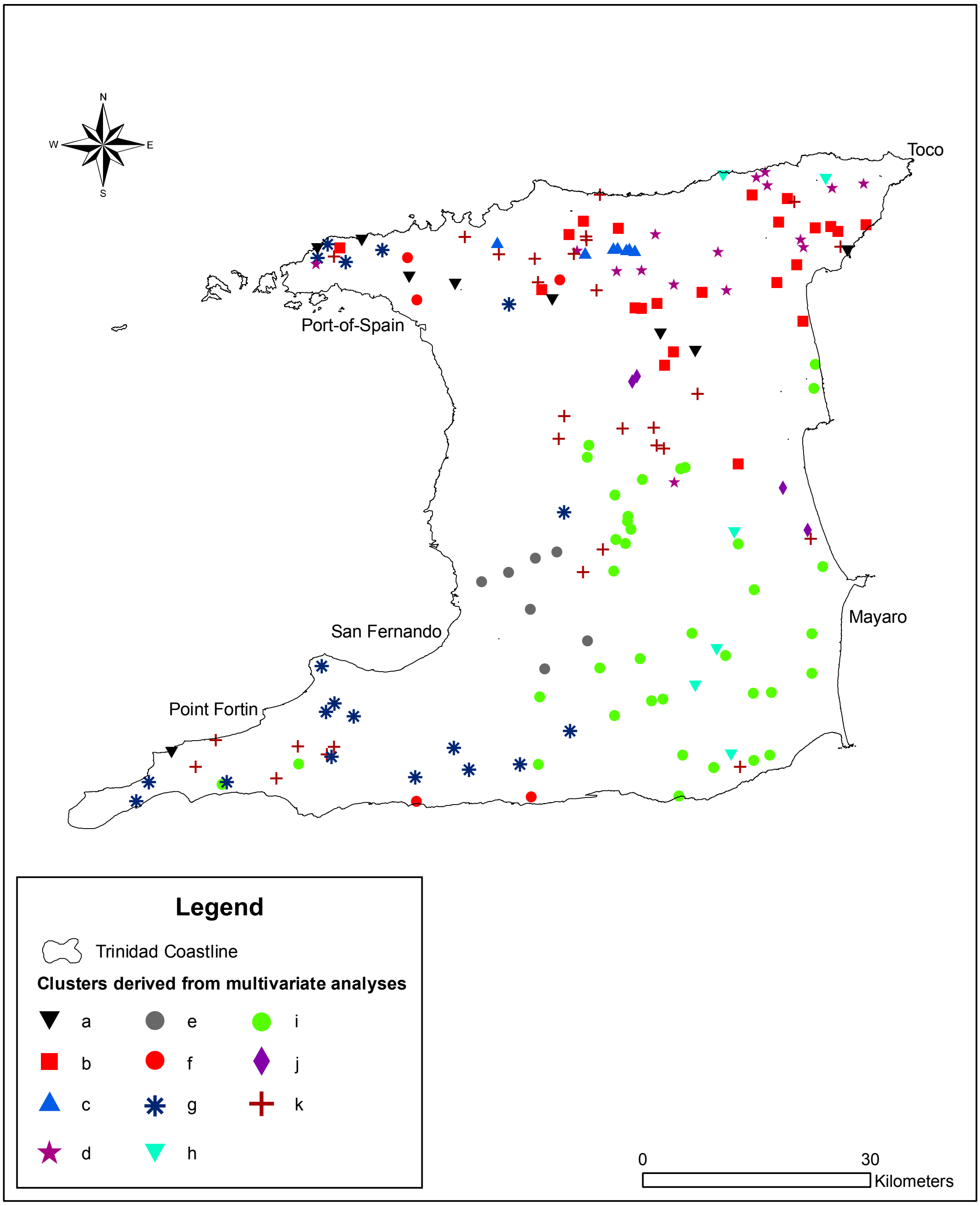


Figure A.2: Clusters derived from presence/absence transformation of abundance data.

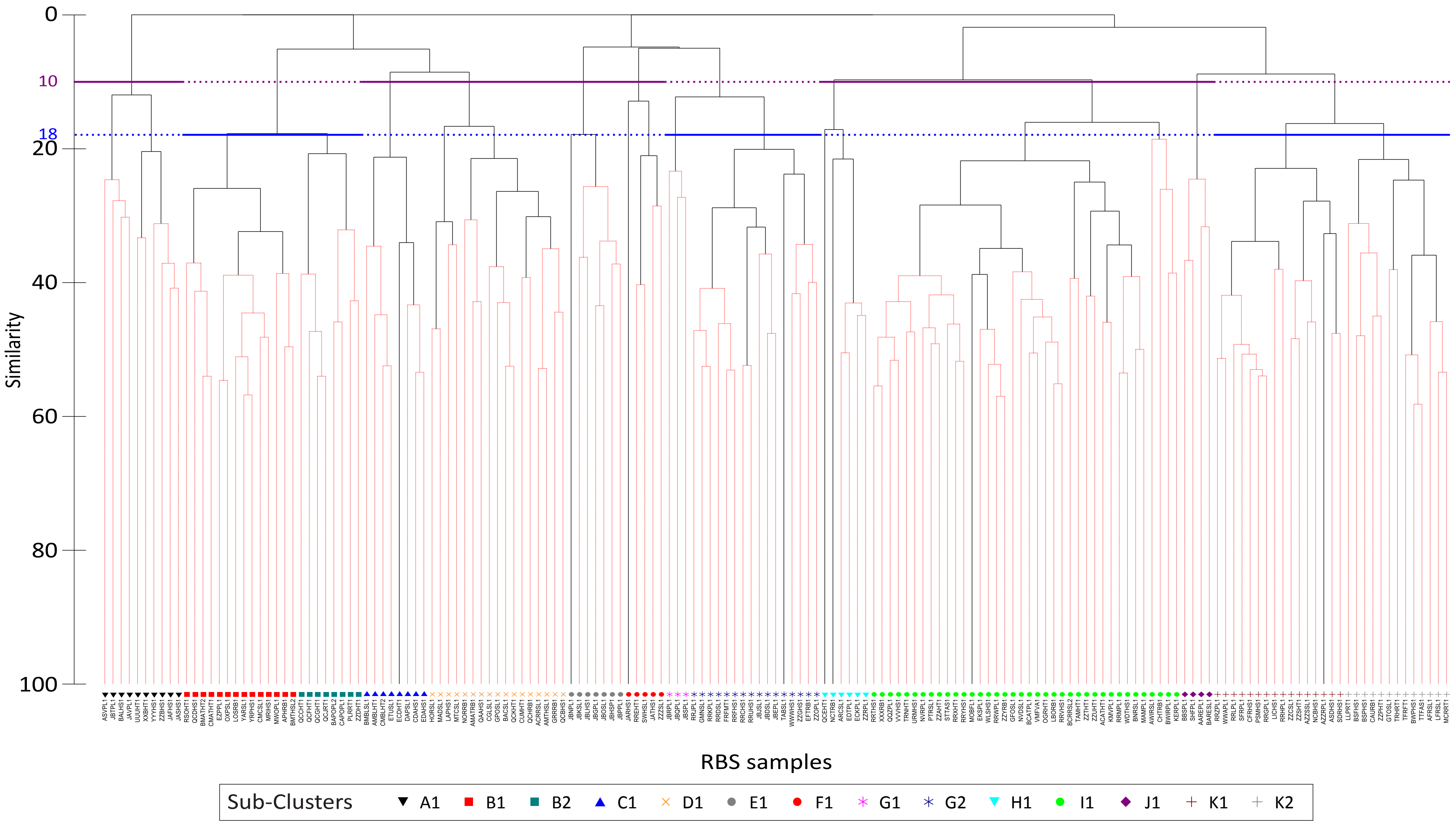


Figure A.3: Cluster dendrogram showing sub-cluster arrangement.

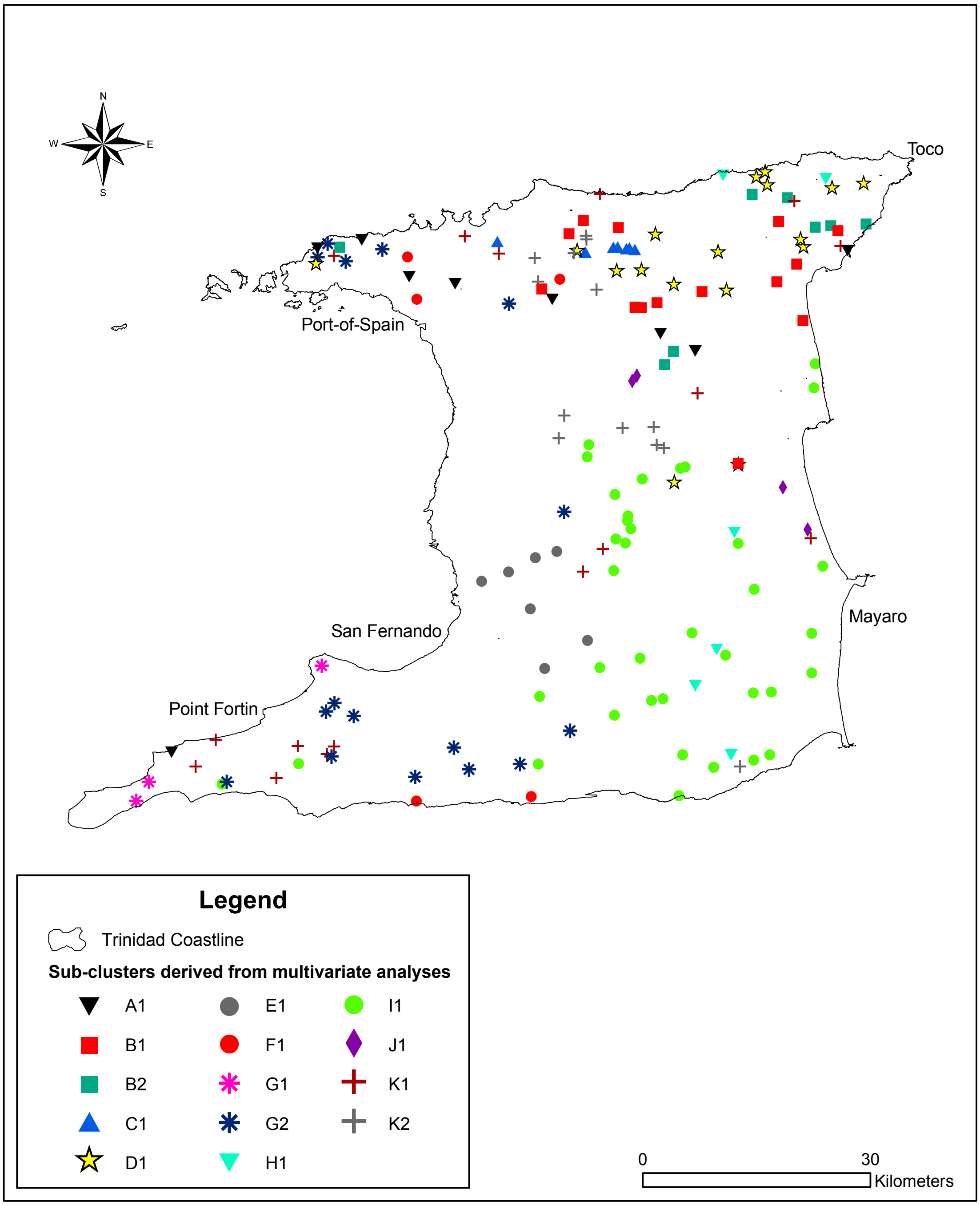


Figure A.4: Sub-clusters derived from presence/absence transformation of abundance data.

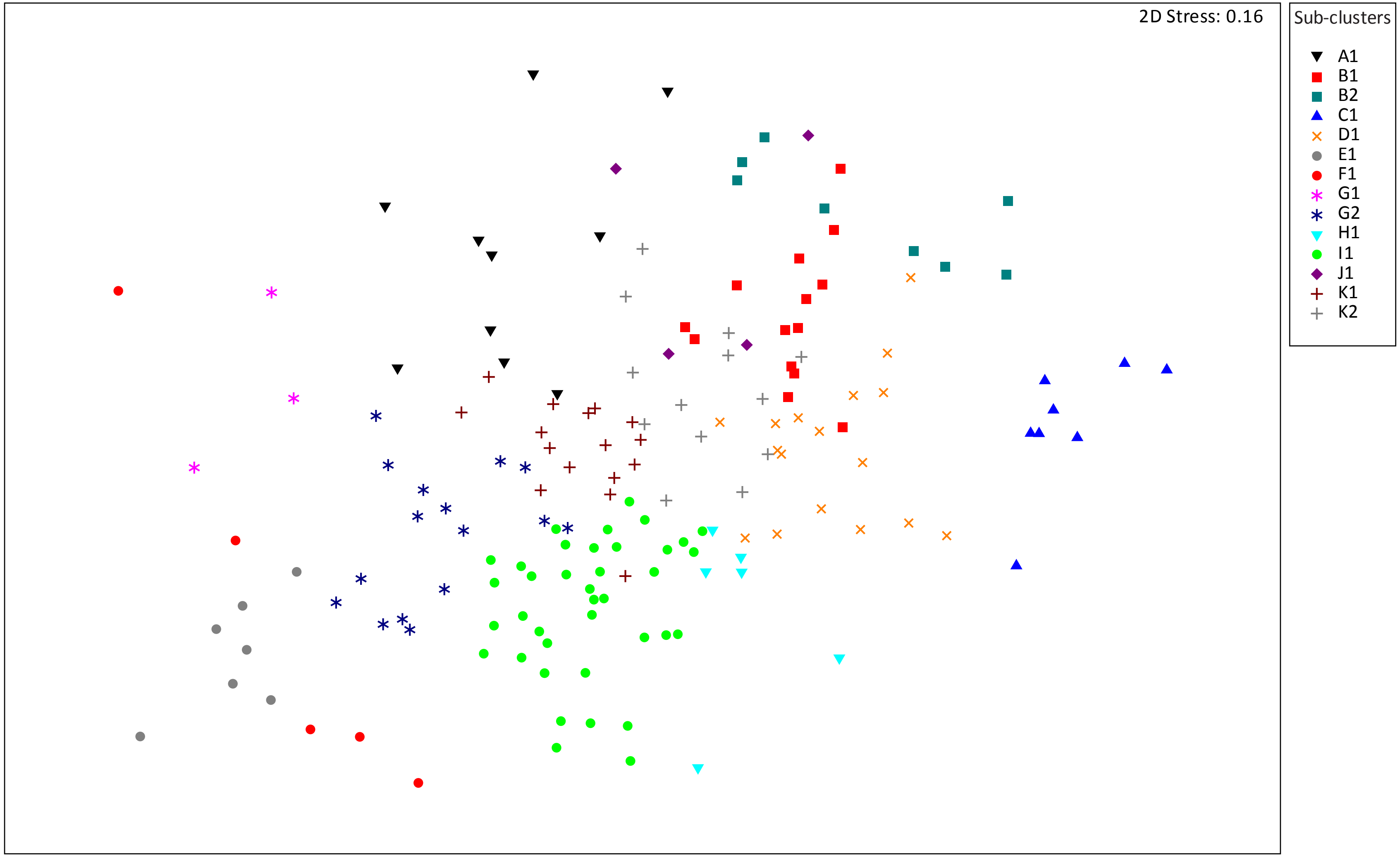


Figure A.5: 2D NMDS of sub-clusters.

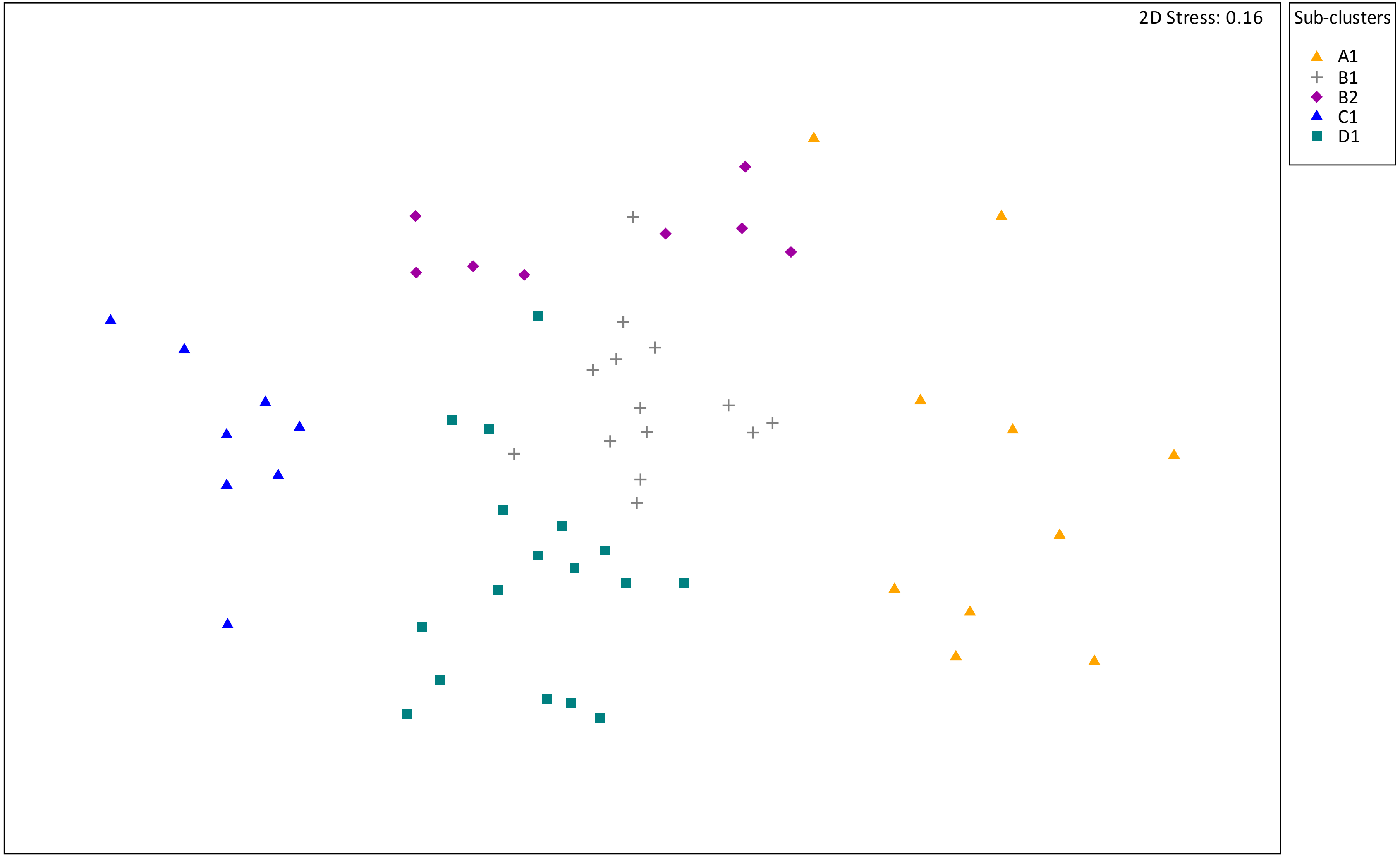


Figure A.6: 2D NMDS of sub-clusters: Group 1.

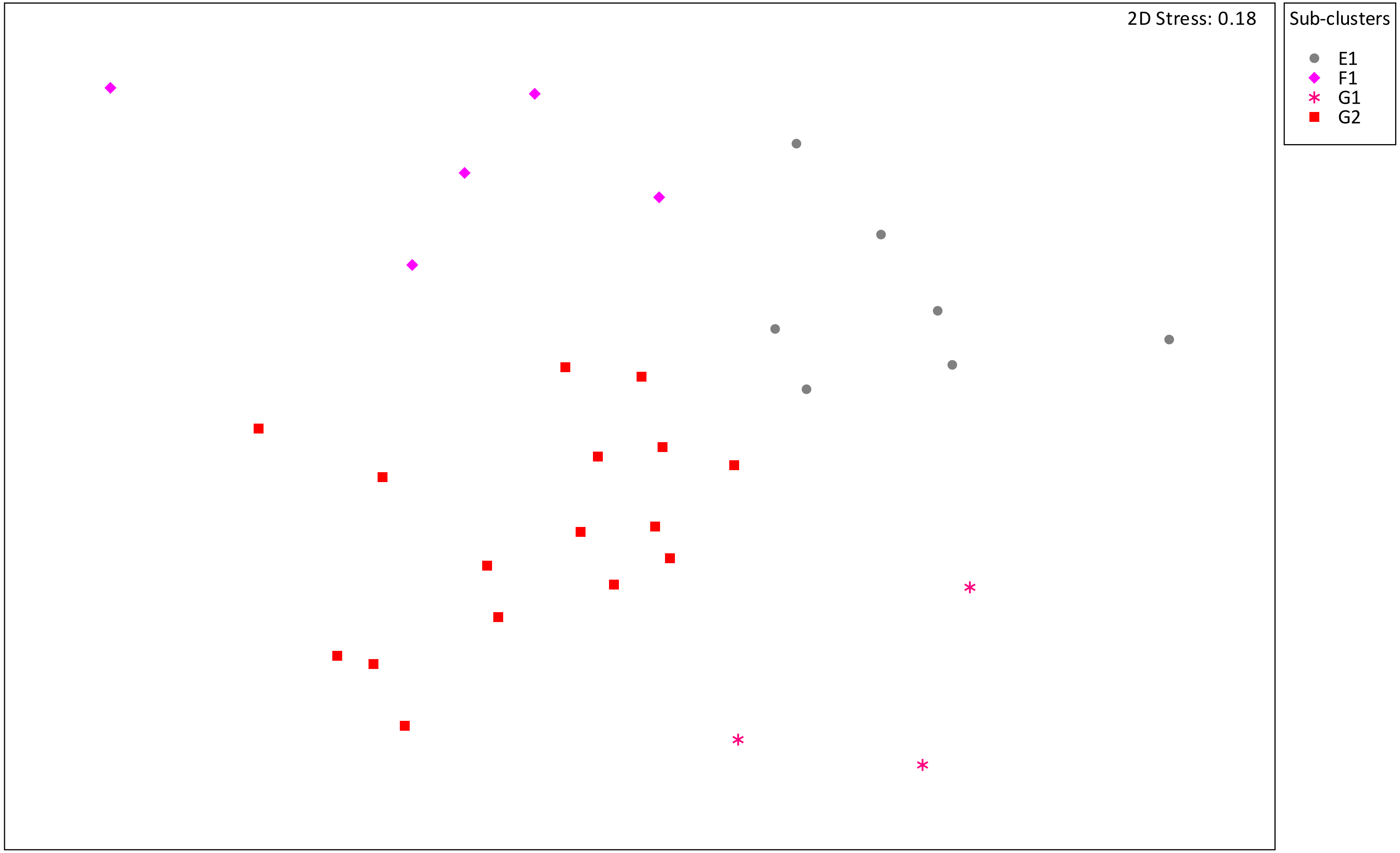


Figure A.7: 2D NMDS of sub-clusters: Group 2.

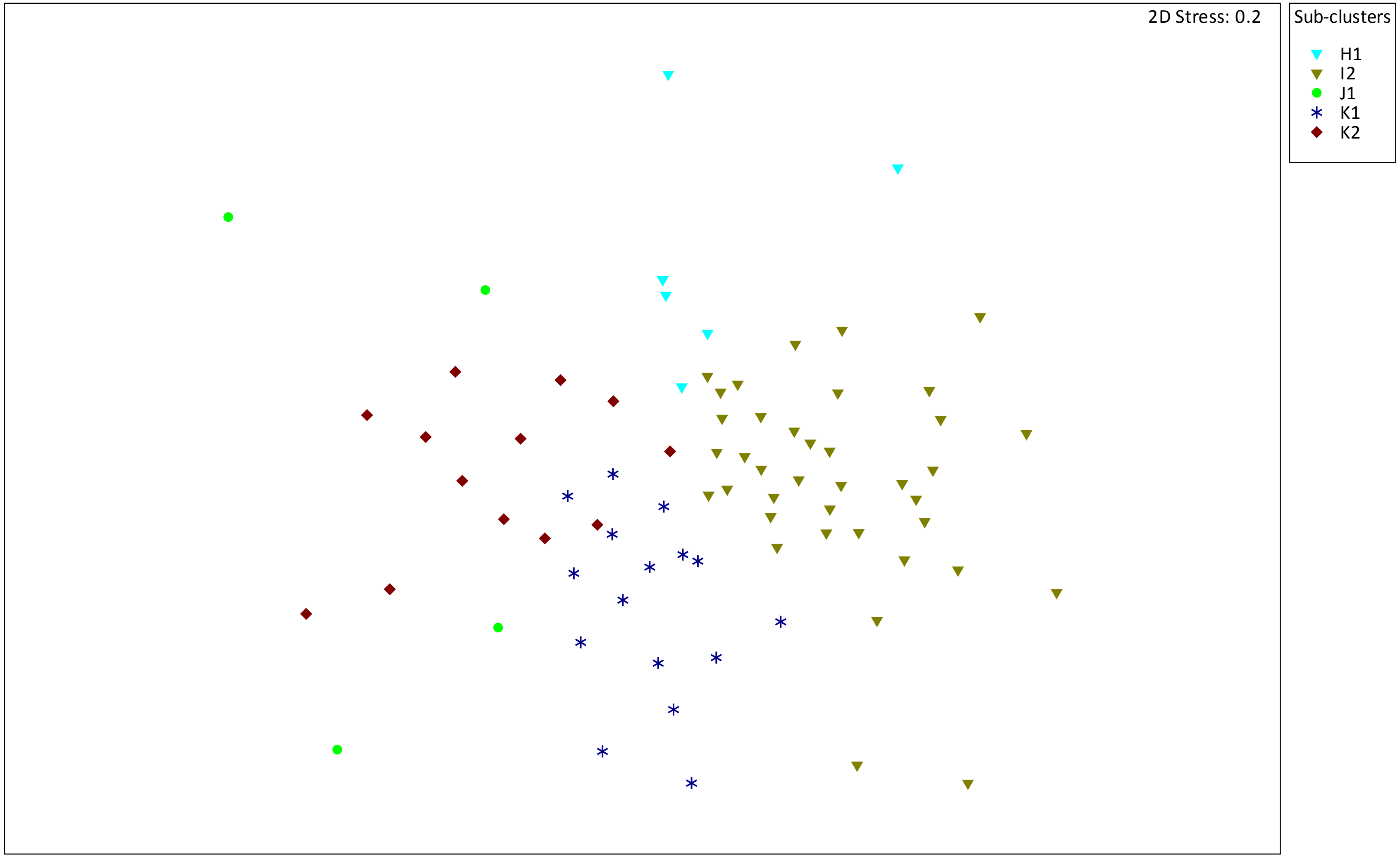


Figure A.8: 2D NMDS of sub-clusters: Group 3.

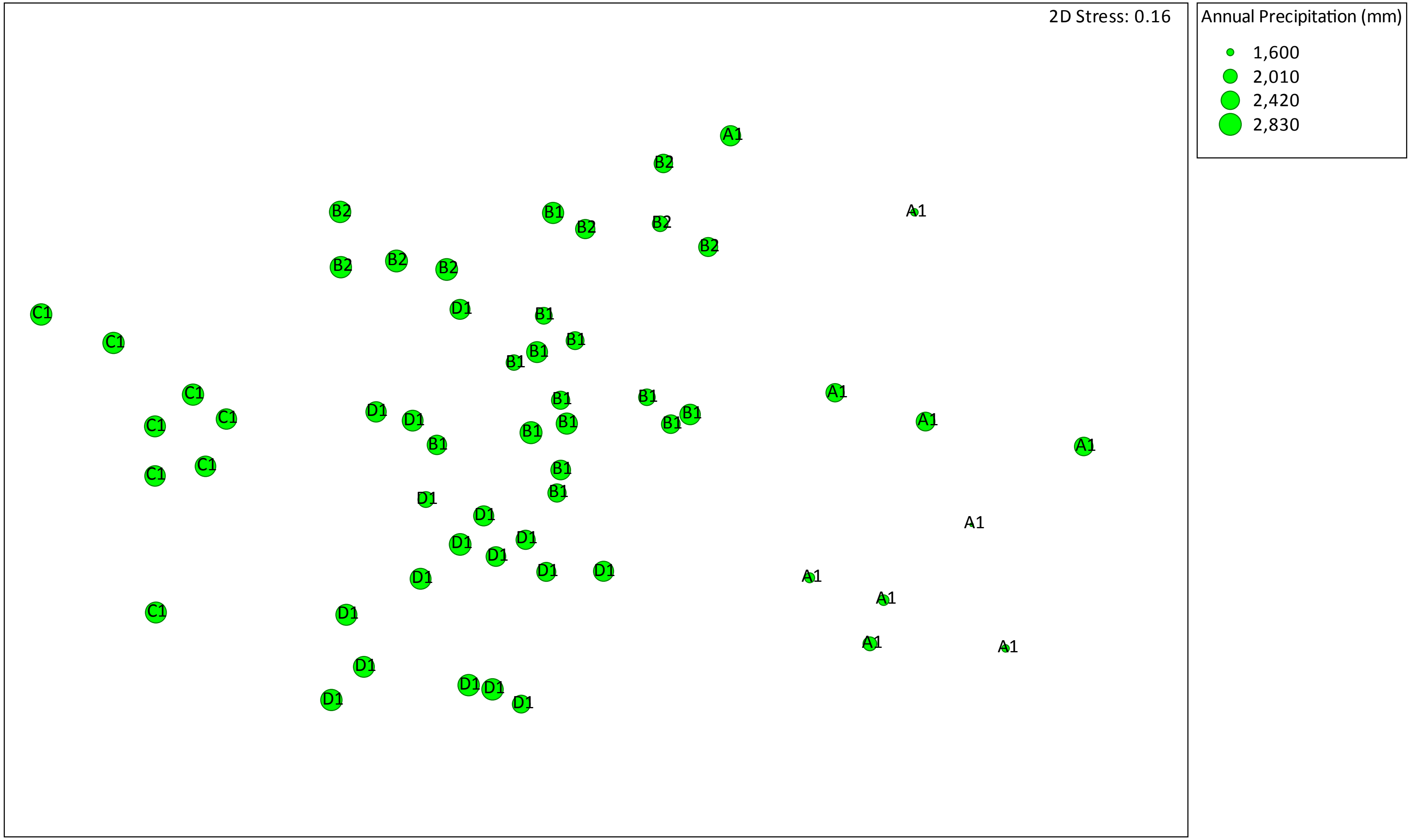


Figure A.9: 2D NMDS of sub-clusters (Group 1) superimposed with a bubble plot of Annual Precipitation.

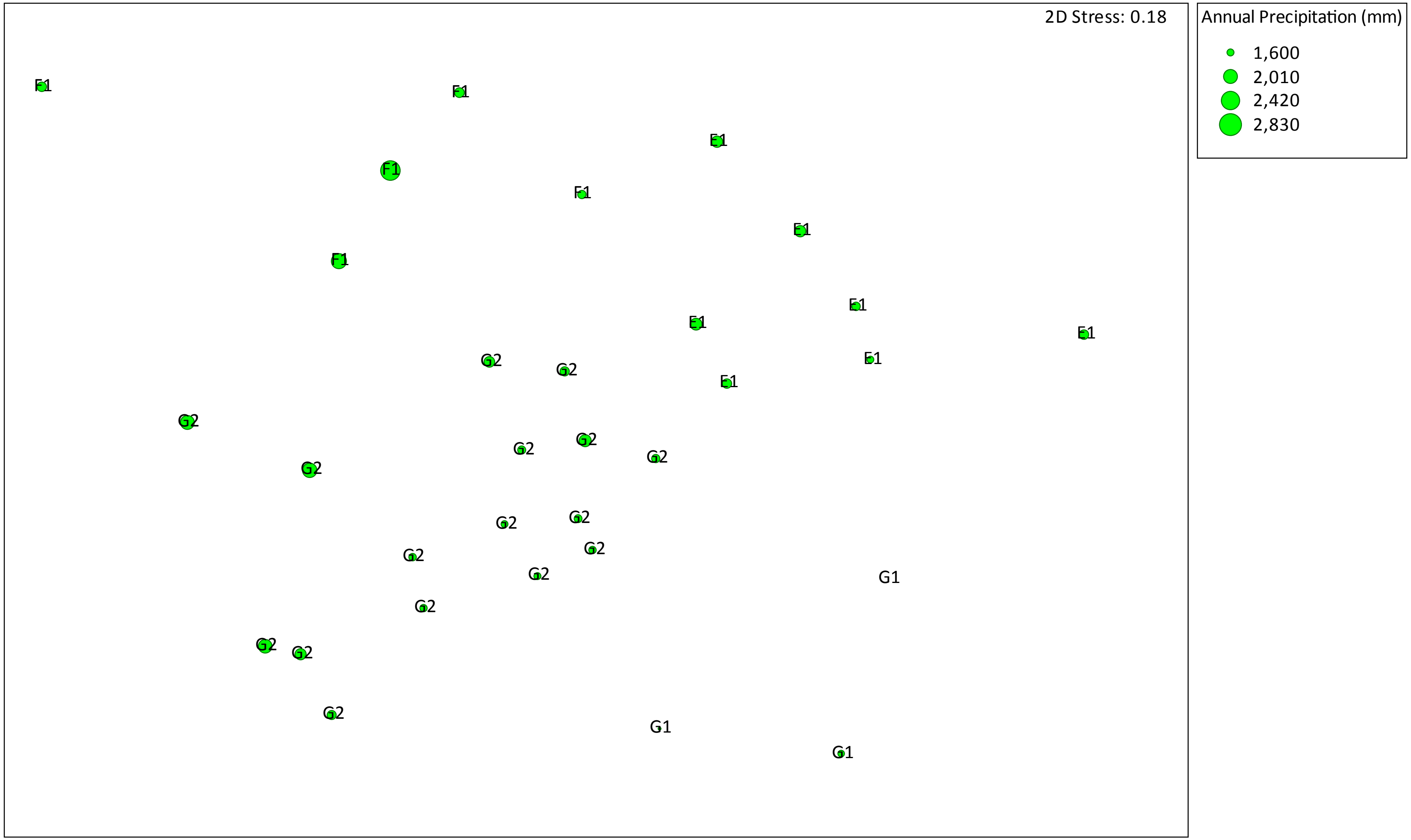


Figure A.10: 2D NMDS of sub-clusters (Group 2) superimposed with a bubble plot of Annual Precipitation.

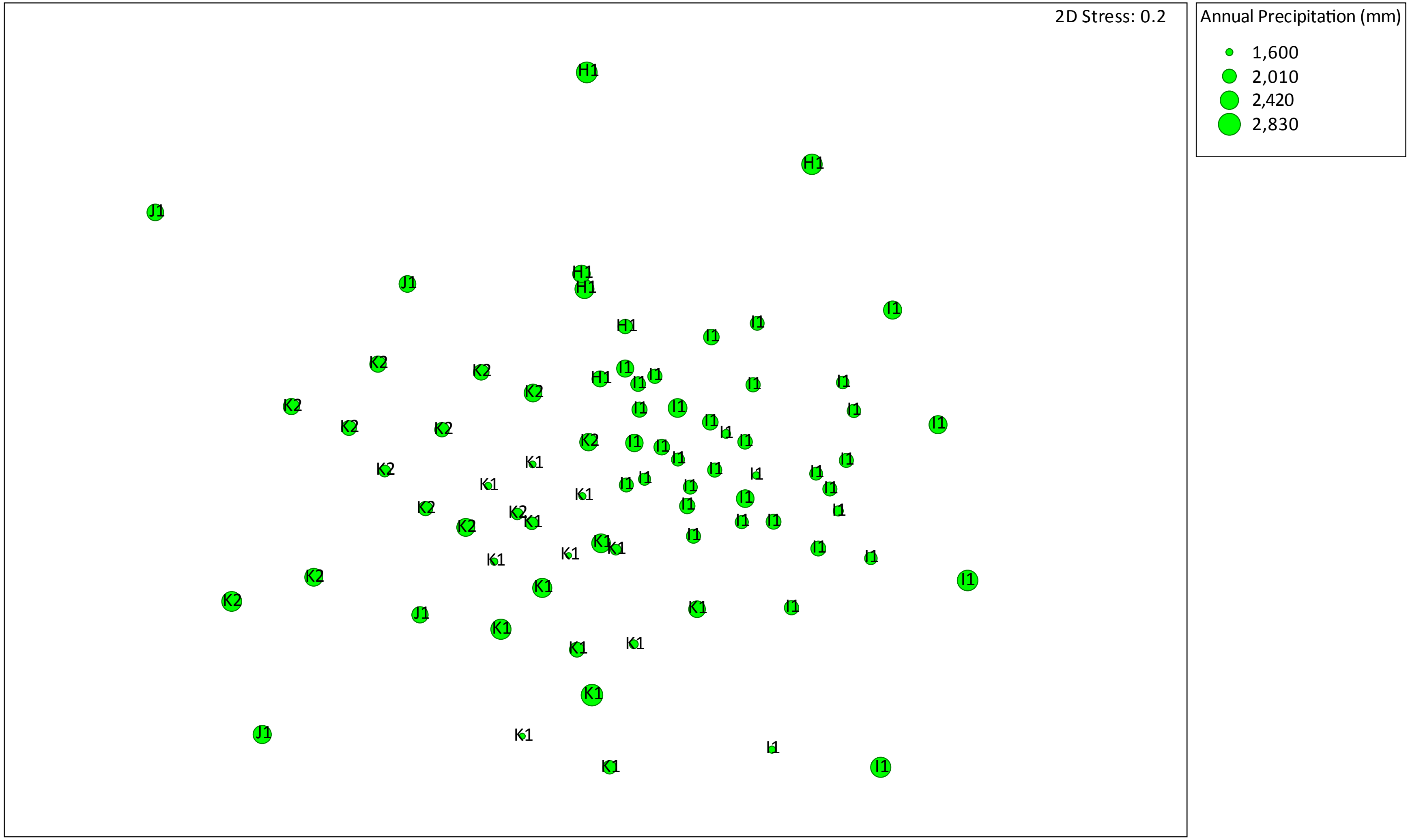


Figure A.11: 2D NMDS of sub-clusters (Group 3) superimposed with a bubble plot of Annual Precipitation.

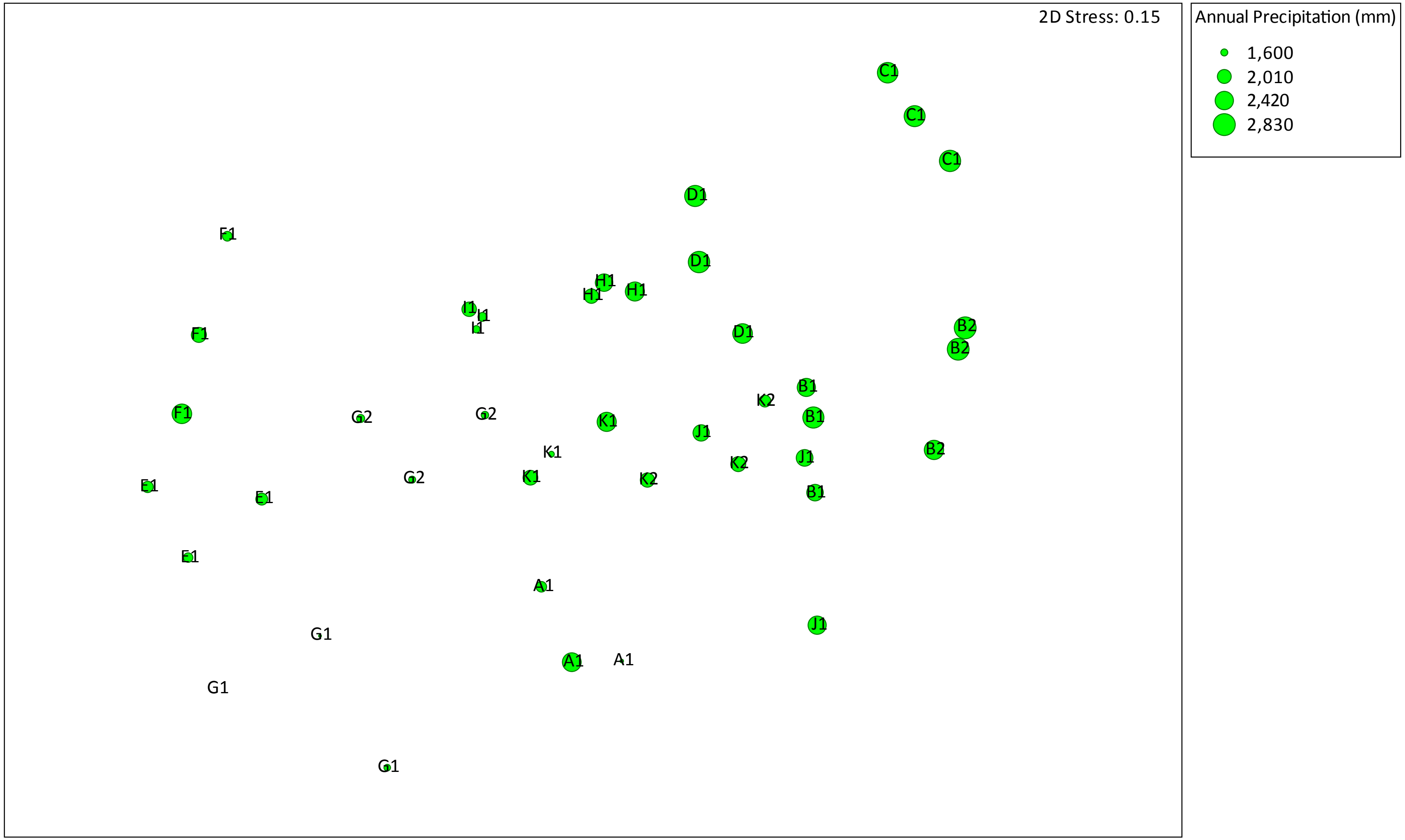


Figure A.12: 2D NMDS: central representatives from all sub-clusters (Groups 1, 2 and 3) superimposed with a bubble plot of Annual Precipitation.

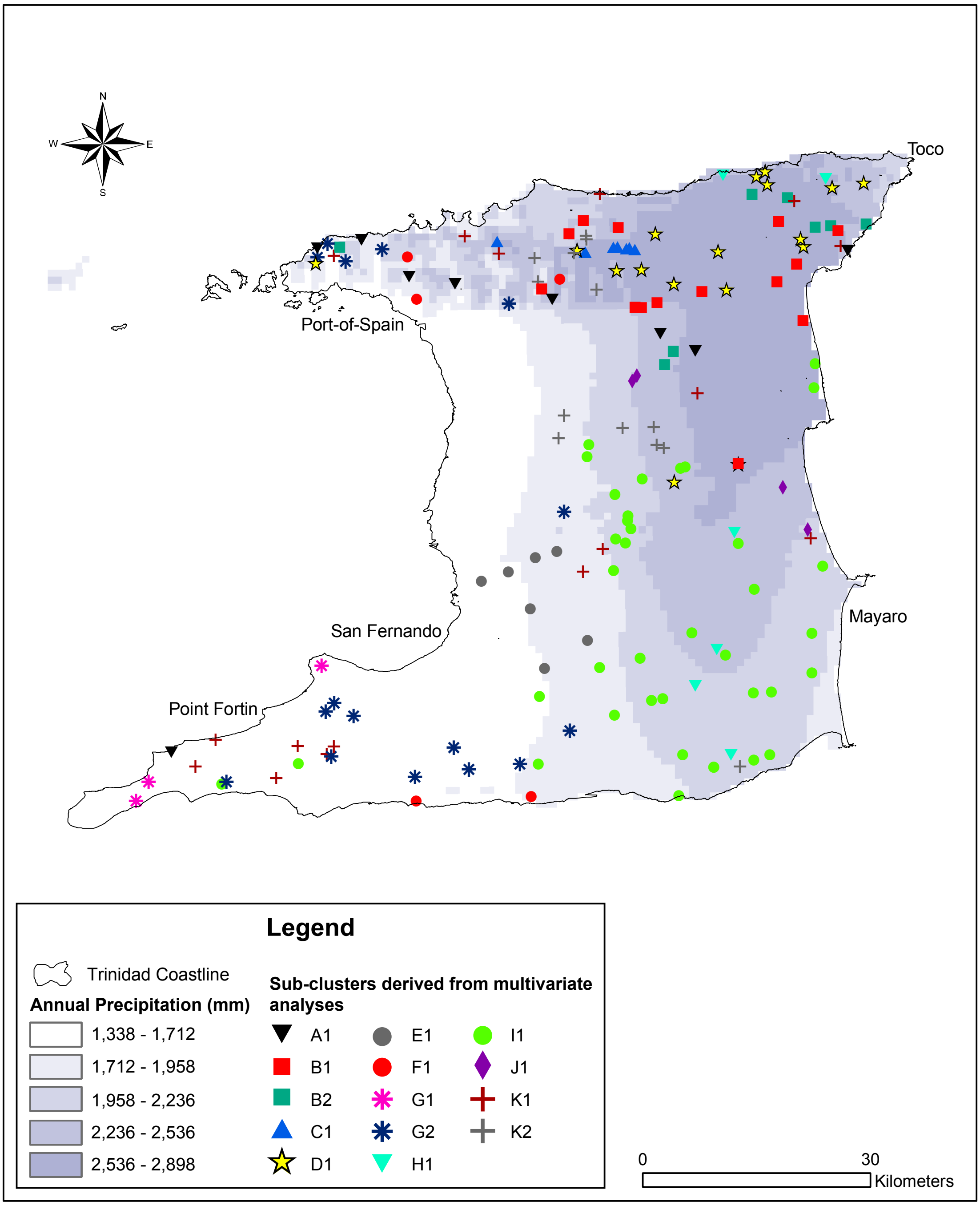


Figure A.13: Presence/Absence sub-clusters superimposed with Annual Precipitation for Trinidad.

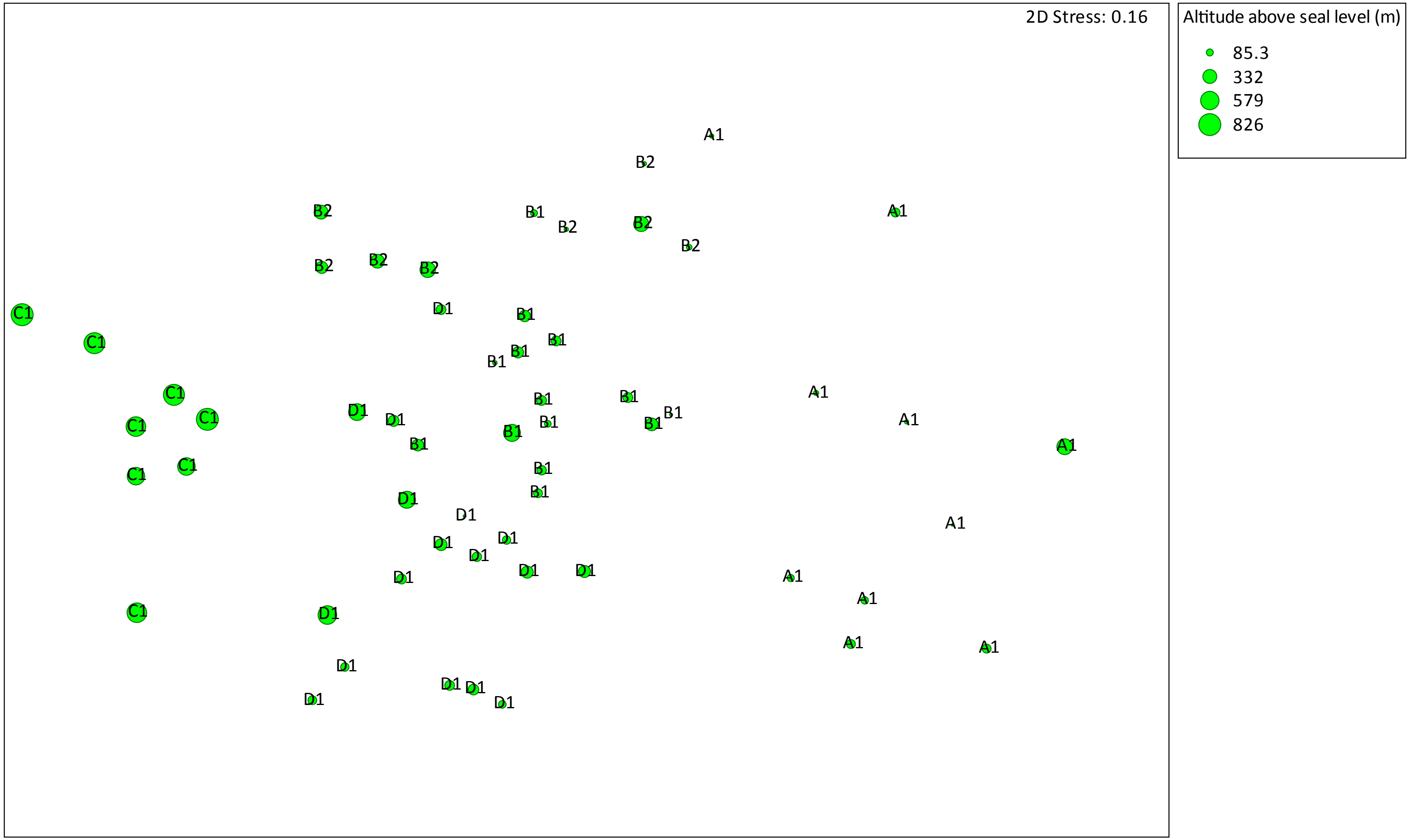


Figure A.14: 2D NMDS of sub-clusters (Group 1) superimposed with a bubble plot of Altitude above sea level.

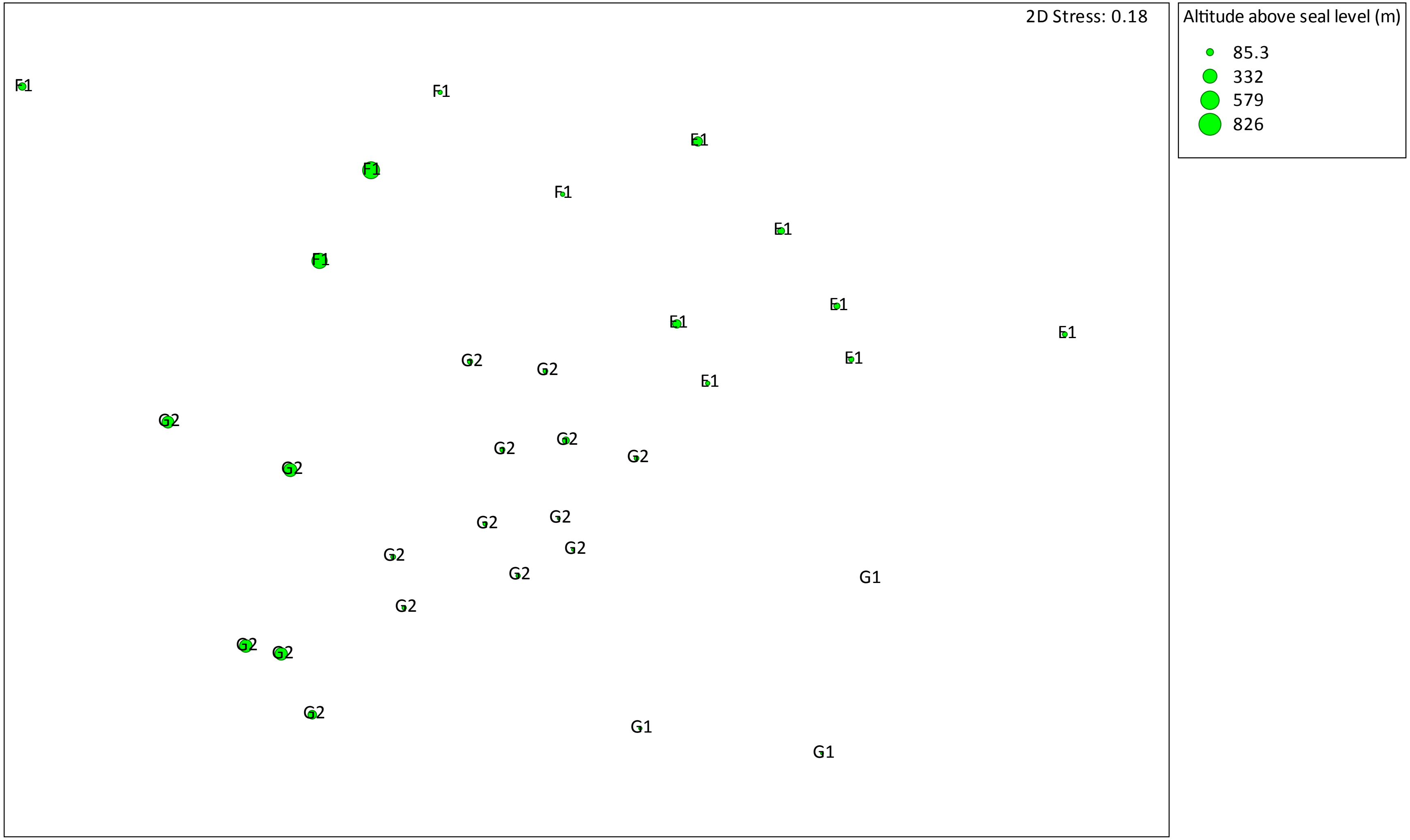


Figure A.15: 2D NMDS of sub-clusters (Group 2) superimposed with a bubble plot of Altitude above sea level.

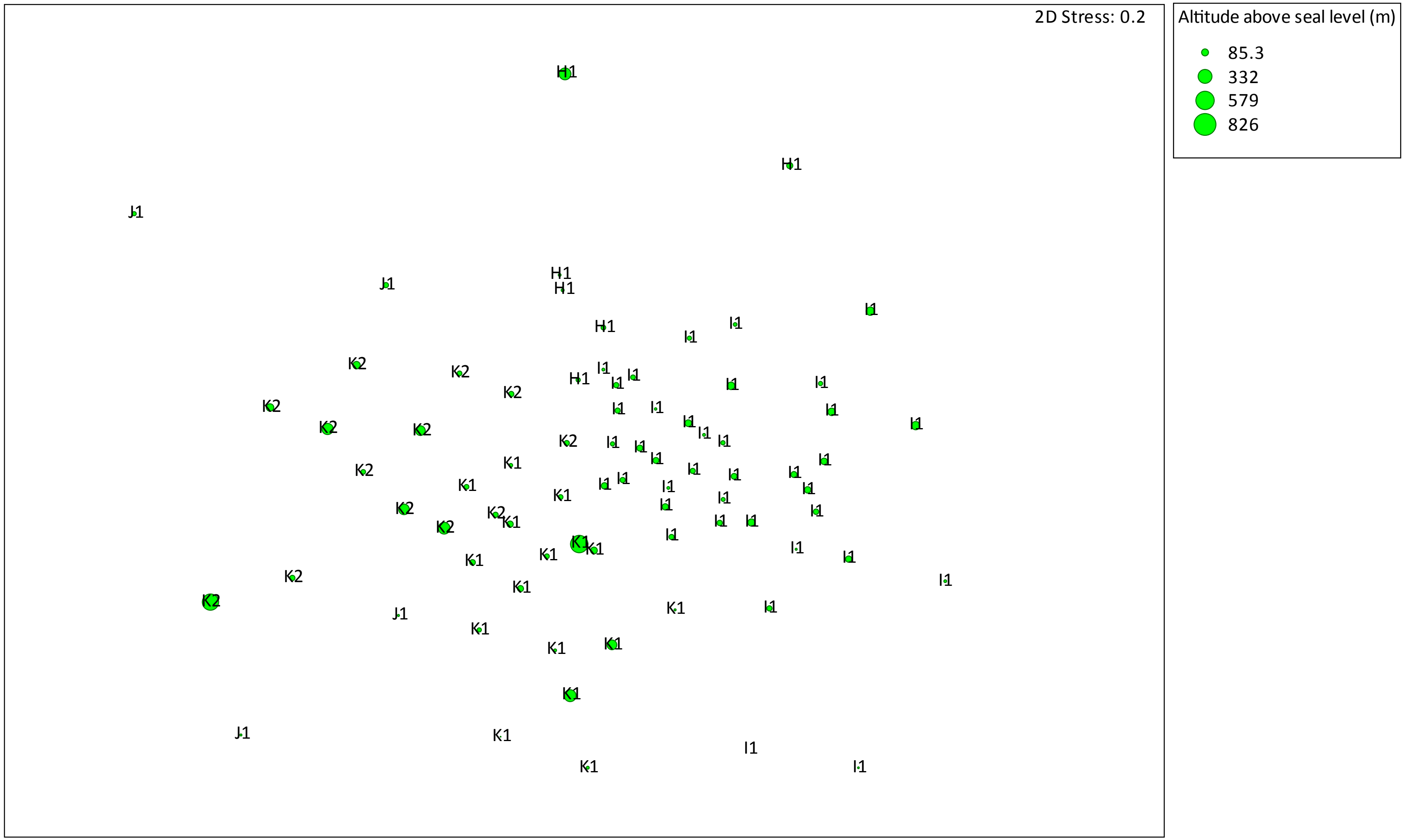


Figure A.16: 2D NMDS of sub-clusters (Group 3) superimposed with a bubble plot of Altitude above sea level.

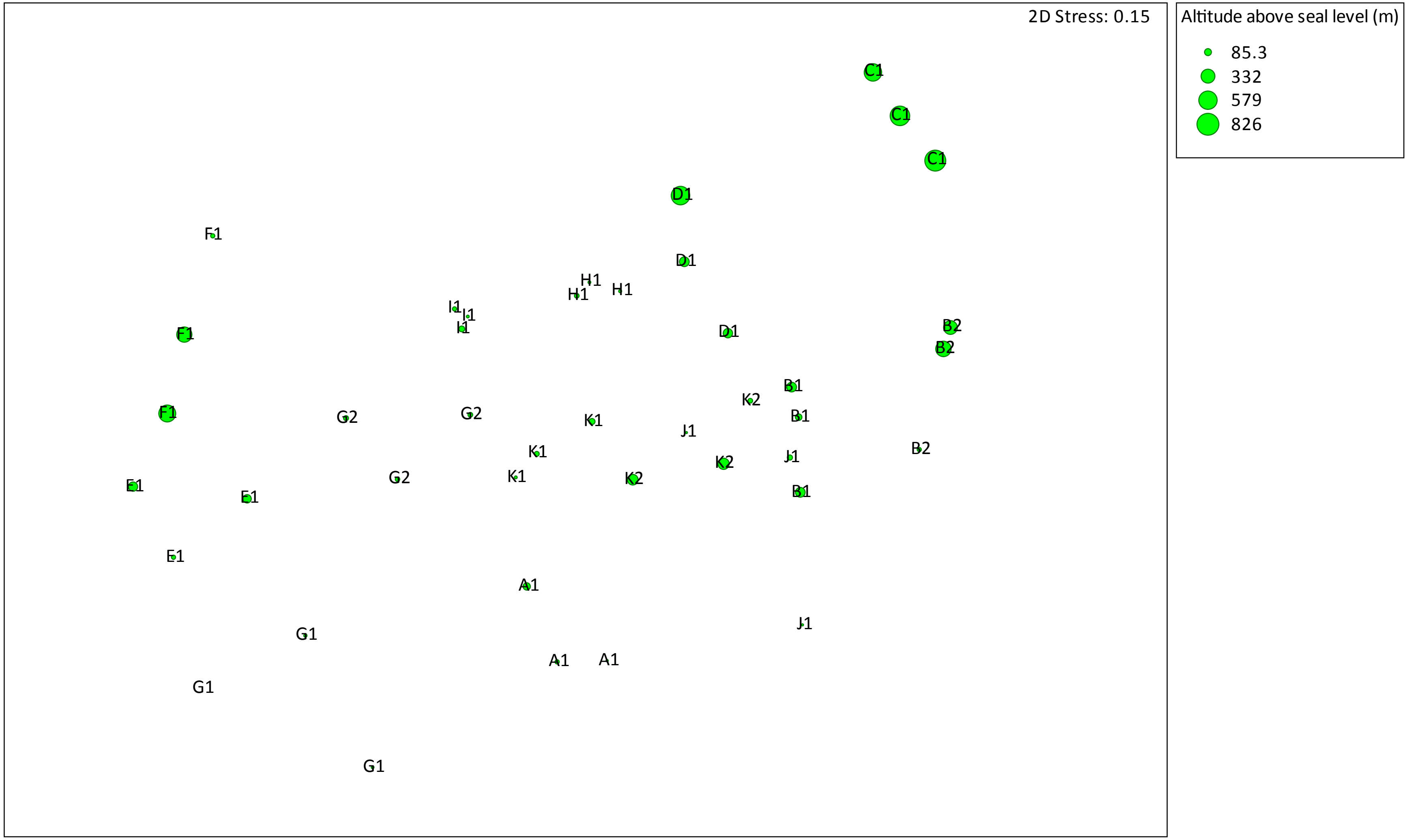


Figure A.17: 2D NMDS: central representatives from all sub-clusters (Groups 1, 2 and 3) superimposed with a bubble plot of Altitude above sea level.

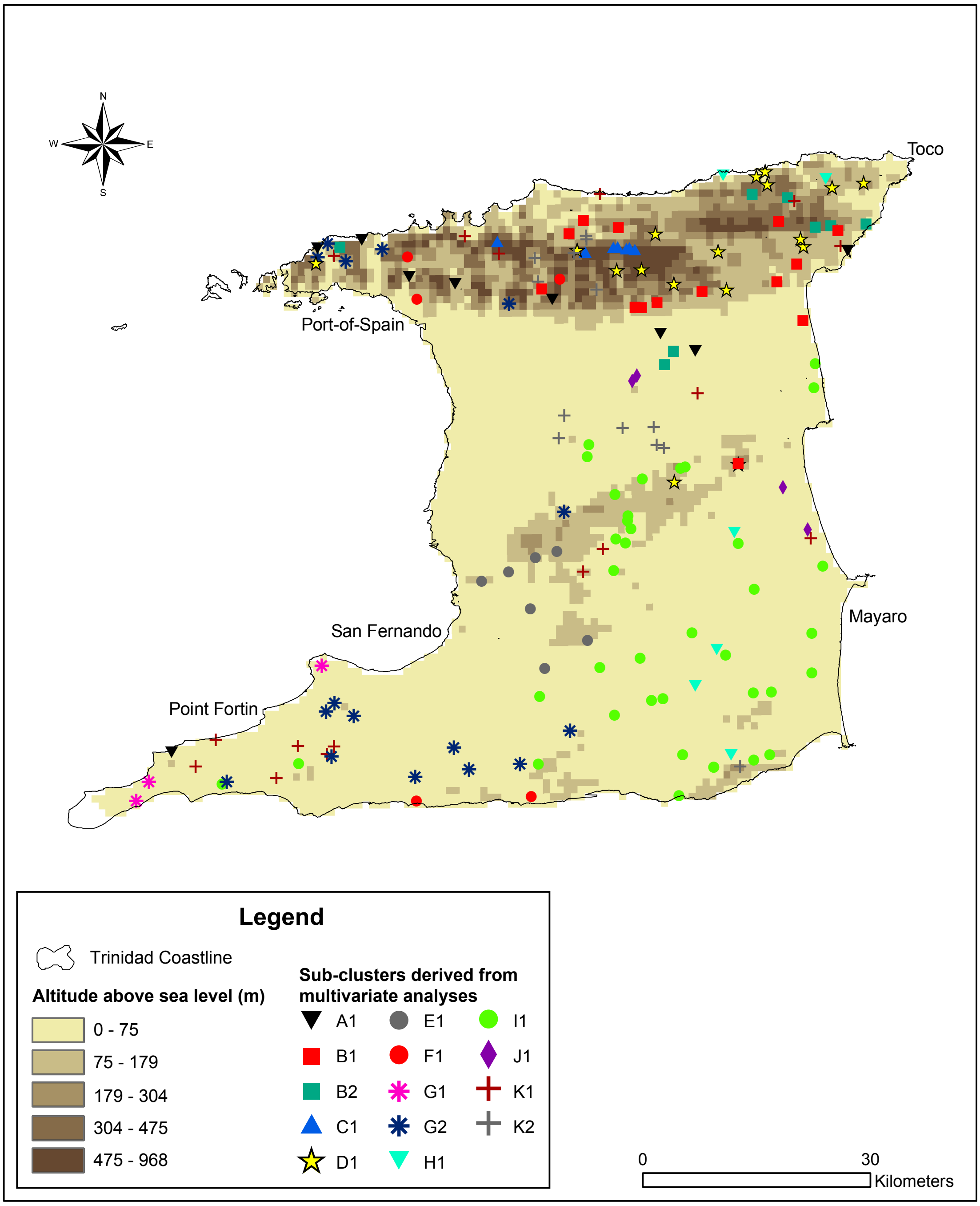


Figure A.18: Presence/Absence sub-clusters superimposed with Altitude above sea level for Trinidad.

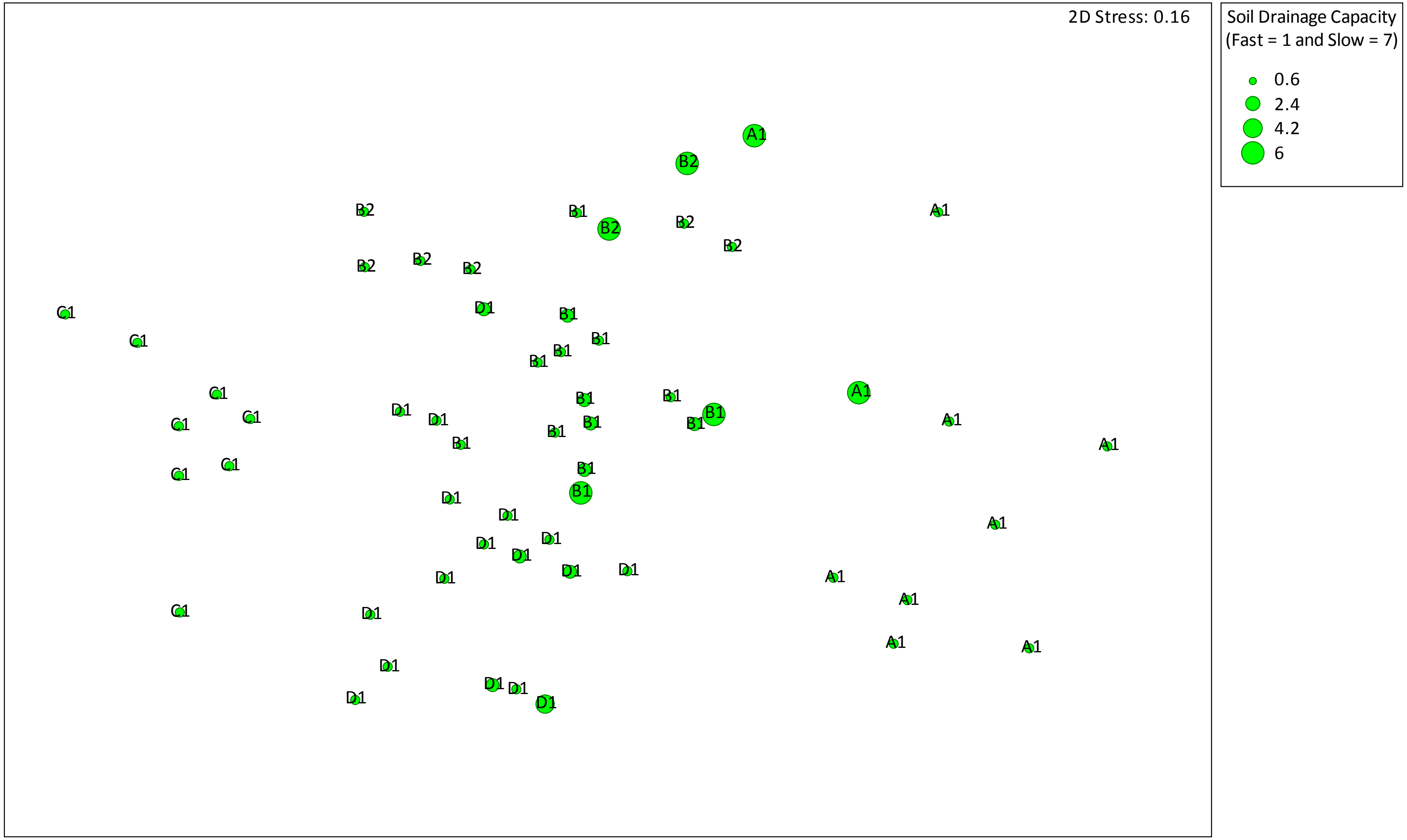


Figure A.19: 2D NMDS of sub-clusters (Group 1) superimposed with a bubble plot of Soil Drainage Capacity.

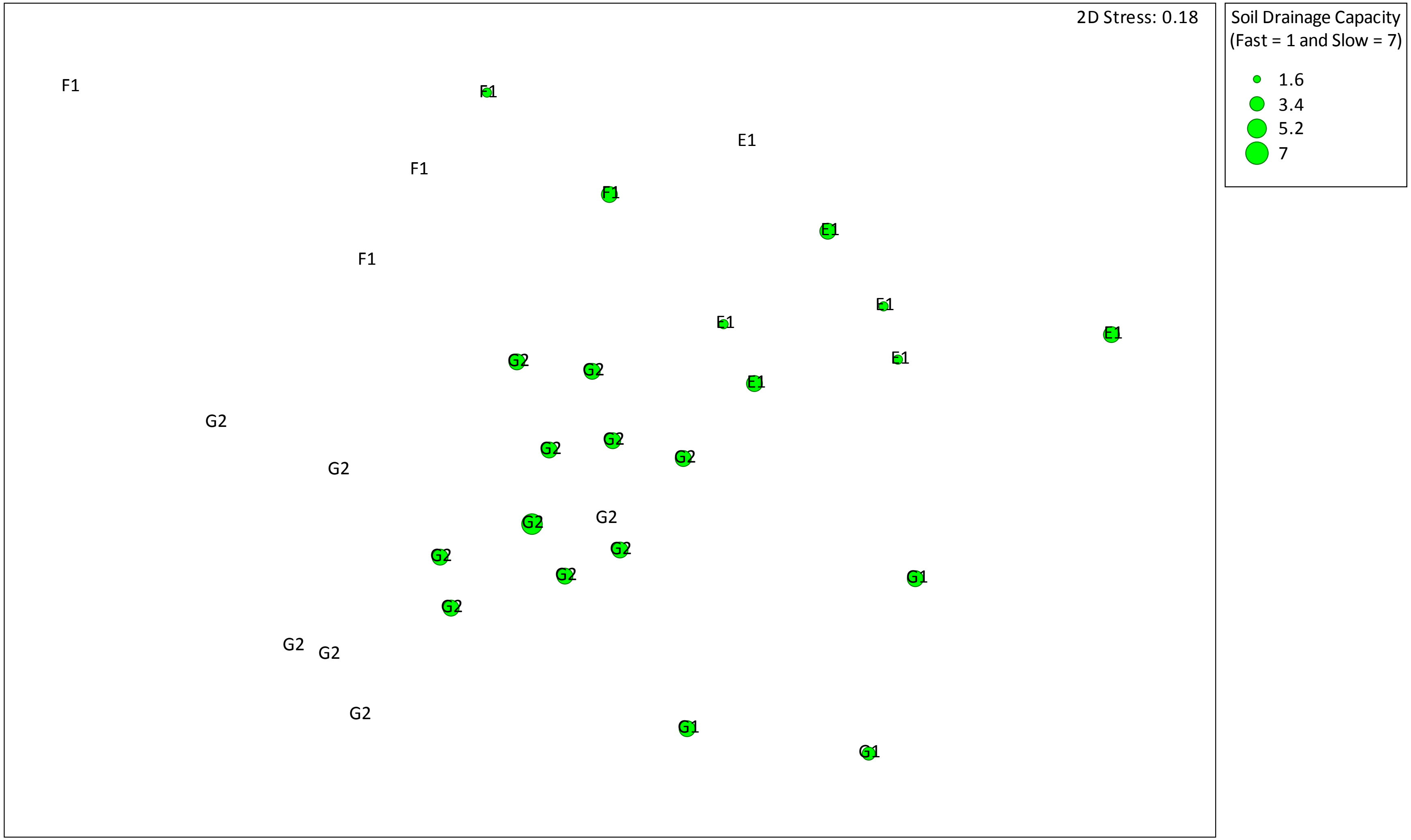


Figure A.20: 2D NMDS of sub-clusters (Group 2) superimposed with a bubble plot of Soil Drainage Capacity.

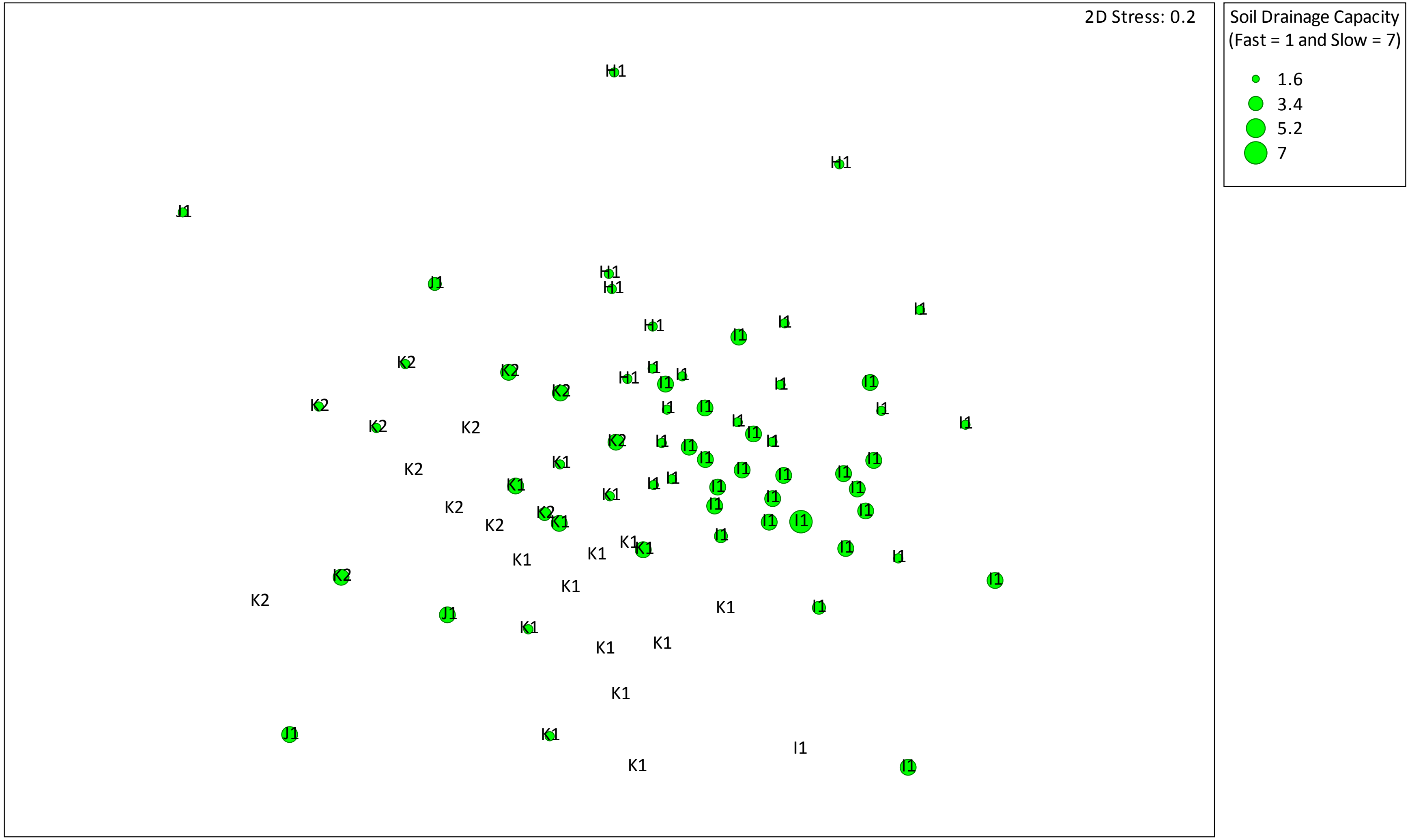


Figure A.21: 2D NMDS of sub-clusters (Group 3) superimposed with a bubble plot of Soil Drainage Capacity.

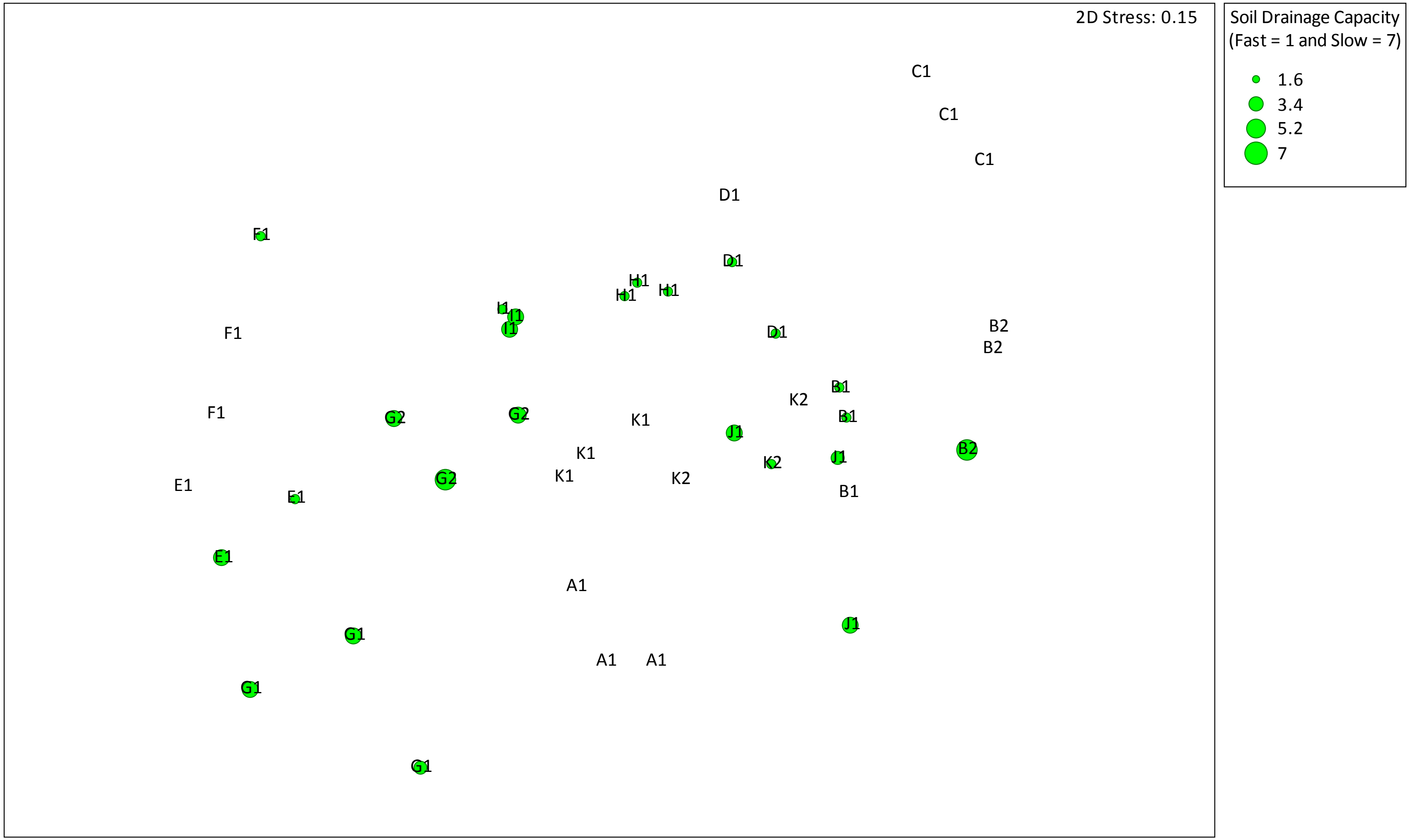


Figure A.22: 2D NMDS: central representatives from all sub-clusters (Groups 1, 2 and 3) superimposed with a bubble plot of Soil Drainage Capacity.

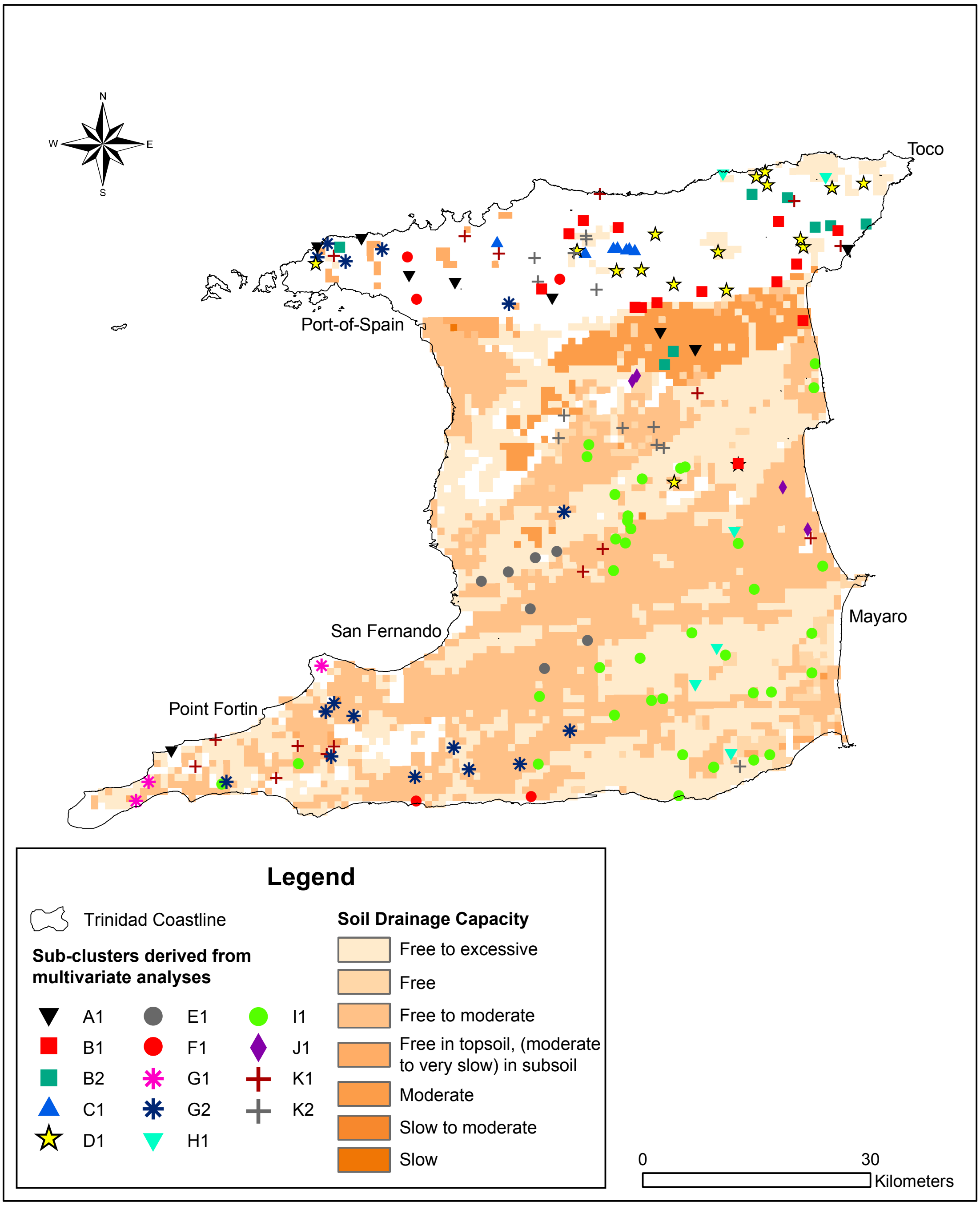


Figure A.23: Presence/Absence sub-clusters superimposed with Soil Drainage Capacity for Trinidad.

Appendix B

SIMPER analysis results of subclusters

The SIMPER analysis process breaks down the Bray-Curtis measure into its constituents, giving the values at which each family contributes to both the similarity within clusters and the dissimilarity between clusters. The analysis was set to report these contributions up to the 90% level.

Similarity within sub-clusters

The two most important categories in the similarity reports within each cluster are the Average Similarity (Av. Sim) and Similarity/Standard Deviation (Sim/SD). The Av. Sim indicates the actual average contribution of each plant species to the similarity index (derived from the modified abundance values); Sim/SD is a measure of the reliability of the species by collating the variability of counts among all the replicates of the sites in each cluster. Average Abundance (Av. Abund) refers to a simple average of the data values for each species over all samples within each sub-cluster. Contribution Percentage (Contrib%), is simply the contribution of each taxa to the overall Av. Sim values of each group. Cumulative Percentage (Cum.%) refers to the cumulative total of the Contrib% for each taxa in the results below.

Group 1A
Average similarity: 23.19

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Sterculia pruriens var. *glabrescens*	1.4	1.75	3.45	7.54	7.54
Manilkara bidentata ssp. *bidentata*	1.33	1.67	3.17	7.22	14.77
Euterpe precatoria	1.67	1.6	0.9	6.89	21.65
Virola surinamensis	1.39	1.33	0.91	5.74	27.4
Pentaclethra macroloba	1.34	1.21	0.91	5.22	32.61
Diplasia karatifolia	1.11	1.03	0.9	4.42	37.03
Manicaria saccifera	1.38	0.95	0.78	4.1	41.14
Abarema jupunba	0.97	0.92	0.9	3.98	45.12
Protium guianense	1.12	0.89	0.88	3.82	48.94
Desmoncus polyacanthos	0.94	0.82	0.87	3.52	52.46
Eschweilera subglandulosa	1	0.79	0.91	3.41	55.87
Forsteronia acouci	0.92	0.79	0.91	3.41	59.27
Mascagnia sepium ssp. *bierosa*	0.92	0.79	0.91	3.41	62.68
Tapirira guianensis	0.9	0.74	0.89	3.18	65.86
Amaioua corymbosa	0.82	0.7	0.9	3.01	68.87
Attalea maripa	1.01	0.47	0.41	2.02	70.89
Heliconia psittacorum	1.01	0.47	0.41	2.02	72.91
Philodendron ornatum	0.96	0.41	0.41	1.77	74.67
Smilax cumanensis	0.8	0.38	0.41	1.65	76.32
Monstera obliqua	0.86	0.36	0.41	1.55	77.87
Bactris simplicifrons	1.01	0.34	0.41	1.44	79.31
Philodendron acutatum	0.88	0.31	0.41	1.34	80.66
Ryania speciosa	0.78	0.31	0.41	1.34	82
Doliocarpus dentatus ssp. *dentatus*	0.72	0.29	0.41	1.27	83.26
Calophyllum lucidum	0.66	0.29	0.41	1.26	84.53
Heteropterys macrostachya	0.65	0.28	0.41	1.23	85.76
Ouratea purdieana	0.58	0.27	0.41	1.16	86.92
Rollinia exsucca	0.58	0.27	0.41	1.16	88.08
Anthurium jenmanii	0.63	0.24	0.41	1.02	89.11
Carapa guianensis	0.63	0.24	0.41	1.02	90.13

Group 7A
Average similarity: 33.35

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Brownea coccinea ssp. *capitella*	1.21	1.11	2.66	3.32	3.32
Sabal mauritiiformis	1.22	1.08	1.97	3.24	6.57
Anthurium pentaphyllum	1.09	0.91	2	2.72	9.28
Rudgea hostmanniana	1.11	0.9	1.68	2.71	11.99
Costus scaber	1	0.83	1.74	2.48	14.47
Spondias mombin	0.88	0.79	2.34	2.36	16.83
Bactris major	1.04	0.73	1.07	2.2	19.03
Macfadyena unguis-cati	0.88	0.64	1.19	1.92	20.94
Swartzia pinnata	0.87	0.63	1.27	1.88	22.83
Trichilia pallida	0.8	0.62	1.39	1.84	24.67
Heliconia spathocircinata	0.86	0.56	1	1.69	26.36
Guarea glabra	0.79	0.56	1.18	1.67	28.03
Eschweilera subglandulosa	0.82	0.55	1.04	1.64	29.67
Philodendron krugii	0.87	0.54	0.84	1.6	31.27
Desmoncus orthacanthos	0.79	0.51	0.93	1.53	32.8
Pentaclethra macroloba	0.79	0.51	0.94	1.52	34.32
Anthurium jenmanii	0.71	0.48	1.02	1.44	35.76
Carapa guianensis	0.7	0.46	1.03	1.38	37.15
Pharus latifolius	0.75	0.45	0.87	1.36	38.5
Mansoa verrucifera	0.74	0.44	0.76	1.32	39.83
Trichilia pleeana	0.68	0.42	0.93	1.27	41.09
Heliconia hirsuta	0.72	0.41	0.78	1.24	42.33
Monstera dubia	0.65	0.39	0.88	1.18	43.51
Guazuma ulmifolia	0.6	0.38	0.87	1.14	44.65
Dieffenbachia seguine	0.63	0.37	0.82	1.11	45.76
Cecropia peltata	0.61	0.37	0.87	1.1	46.86
Guapira salicifolia	0.61	0.34	0.75	1.03	47.89
Brosimum alicastrum	0.64	0.34	0.69	1.01	48.91
Roystonea oleracea	0.62	0.33	0.69	0.99	49.89
Manilkara bidentata ssp. *bidentata*	0.55	0.33	0.76	0.99	50.88
Garcinia madruno	0.56	0.32	0.76	0.96	51.84
Coccoloba fallax	0.61	0.32	0.68	0.95	52.79
Omphalea diandra	0.58	0.32	0.71	0.95	53.74
Sterculia pruriens var. *glabrescens*	0.52	0.31	0.76	0.93	54.67

Philodendron lingulatum	0.64	0.3	0.61	0.9	55.57
Drymonia serrulata	0.55	0.3	0.72	0.9	56.46
Faramea occidentalis	0.66	0.29	0.53	0.88	57.34
Ceratophytum tetragonolobum	0.59	0.29	0.57	0.86	58.2
Miconia acinodendron	0.62	0.28	0.56	0.84	59.04
Bauhinia glabra	0.63	0.28	0.56	0.84	59.88
Pterocarpus rohrii	0.5	0.28	0.71	0.84	60.72
Desmoncus polyacanthos	0.55	0.25	0.57	0.76	61.48
Calathea altissima	0.53	0.24	0.58	0.72	62.2
Sapium glandulosum	0.47	0.24	0.57	0.72	62.92
Protium sagotianum	0.48	0.23	0.62	0.7	63.62
Casearia guianensis	0.46	0.23	0.62	0.69	64.31
Mouriri rhizophoraefolia	0.48	0.23	0.61	0.68	64.99
Ceiba pentandra	0.44	0.21	0.53	0.63	65.62
Sarcoglottis metallica	0.46	0.21	0.53	0.63	66.25
Pouteria coriacea	0.45	0.21	0.57	0.62	66.87
Paullinia fuscescens	0.49	0.2	0.5	0.6	67.47
Serjania paucidentata	0.49	0.2	0.49	0.59	68.06
Philodendron fendleri	0.45	0.19	0.54	0.58	68.64
Guzmania lingulata var. *lingulata*	0.47	0.19	0.49	0.58	69.22
Andira inermis	0.43	0.19	0.53	0.58	69.79
Psychotria cuspidata	0.49	0.19	0.46	0.57	70.36
Bravaisia integerrima	0.44	0.19	0.53	0.56	70.92
Piresia sympodica	0.51	0.19	0.46	0.56	71.48
Heliconia bihai	0.51	0.18	0.4	0.54	72.02
Philodendron scandens	0.47	0.18	0.5	0.54	72.57
Clathrotropis brachypetala	0.47	0.18	0.44	0.53	73.1
Swartzia simplex	0.42	0.17	0.53	0.52	73.62
Asplenium serratum	0.43	0.17	0.5	0.51	74.14
Zanthoxylum pentandrum	0.39	0.16	0.45	0.49	74.63
Coccoloba latifolia	0.38	0.16	0.5	0.49	75.12
Erythrina pallida	0.39	0.16	0.5	0.49	75.61
Myrciaria floribunda	0.39	0.16	0.5	0.47	76.09
Gonzalagunia spicata	0.43	0.16	0.45	0.47	76.56
Brosimum guianense	0.38	0.16	0.5	0.47	77.03
Philodendron acutatum	0.45	0.16	0.38	0.47	77.49
Cupania americana	0.36	0.15	0.5	0.45	77.94
Phryganocydia corymbosa	0.45	0.15	0.35	0.44	78.39
Paullinia leiocarpa	0.4	0.14	0.42	0.43	78.82
Acalypha grisebachiana	0.45	0.14	0.39	0.43	79.24
Coccoloba cruegeri	0.39	0.14	0.42	0.42	79.67
Pachira aquatica	0.37	0.14	0.46	0.41	80.08

Inga laurina	0.34	0.13	0.42	0.38	80.46
Hylocereus lemairei	0.34	0.13	0.39	0.38	80.84
Thelypteris pennata	0.41	0.12	0.35	0.37	81.21
Olyra latifolia	0.43	0.12	0.28	0.36	81.57
Coccoloba venosa	0.34	0.12	0.43	0.36	81.93
Ischnosiphon arouma	0.39	0.12	0.36	0.35	82.28
Guapira cuspidata	0.33	0.11	0.43	0.34	82.62
Piper glabrescens	0.39	0.11	0.32	0.33	82.96
Xiphidium caeruleum	0.4	0.11	0.32	0.33	83.28
Chrysophyllum argenteum ssp. *argenteum*	0.33	0.11	0.39	0.32	83.6
Tabebuia chrysantha	0.33	0.1	0.39	0.31	83.92
Tabernaemontana cymosa	0.31	0.1	0.39	0.31	84.23
Miconia nervosa	0.35	0.1	0.35	0.3	84.53
Inga ingoides	0.3	0.1	0.39	0.3	84.83
Adiantum obliquum	0.37	0.1	0.33	0.3	85.13
Amphilophium paniculatum	0.36	0.1	0.31	0.3	85.42
Psychotria deflexa	0.37	0.1	0.32	0.29	85.72
Calyptranthes fasciculata	0.31	0.1	0.36	0.29	86
Paragonia pyramidata	0.36	0.09	0.32	0.28	86.28
Seguieria macrophylla	0.31	0.09	0.36	0.28	86.56
Attalea maripa	0.36	0.09	0.3	0.28	86.84
Eugenia trinervia	0.28	0.09	0.36	0.26	87.11
Smilax cumanensis	0.29	0.09	0.36	0.26	87.37
Protium guianense	0.31	0.08	0.33	0.24	87.61
Hura crepitans	0.33	0.08	0.26	0.24	87.85
Adiantum petiolatum	0.29	0.08	0.3	0.24	88.09
Genipa americana	0.31	0.08	0.28	0.23	88.32
Casearia sylvestris	0.28	0.07	0.29	0.22	88.54
Coursetia ferruginea	0.26	0.07	0.3	0.21	88.75
Maranta gibba	0.29	0.07	0.26	0.2	88.95
Tillandsia fasciculata var. *fasciculata*	0.27	0.07	0.27	0.2	89.14
Terminalia amazonia	0.24	0.06	0.3	0.19	89.33
Talisia hexaphylla	0.25	0.06	0.3	0.19	89.51
Mesechites trifida	0.27	0.06	0.26	0.18	89.69
Monstera obliqua	0.31	0.06	0.2	0.18	89.87
Hymenocallis tubiflora	0.28	0.06	0.23	0.17	90.04

Group 4A

Average similarity: 32.34

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Carapa guianensis	1.15	1.1	4.89	3.4	3.4
Philodendron lingulatum	1.21	1.07	2.16	3.32	6.72
Sterculia pruriens var. *glabrescens*	0.91	0.96	8.91	2.97	9.7
Psychotria muscosa	1.05	0.9	1.69	2.79	12.48
Philodendron ornatum	1.08	0.87	1.3	2.7	15.18
Heliconia hirsuta	1.03	0.87	1.63	2.68	17.86
Brownea coccinea ssp. *capitella*	1.08	0.82	1.27	2.54	20.39
Eschweilera subglandulosa	0.91	0.76	1.72	2.35	22.74
Costus scaber	0.95	0.74	1.33	2.29	25.03
Miconia nervosa	0.83	0.65	1.36	2.02	27.05
Virola surinamensis	0.79	0.64	1.39	1.99	29.04
Terminalia amazonia	0.74	0.64	1.39	1.98	31.02
Anthurium pentaphyllum	0.81	0.58	1.12	1.79	32.81
Andira inermis	0.73	0.58	1.14	1.78	34.59
Swartzia pinnata	0.76	0.56	1.14	1.72	36.31
Heliconia spathocircinata	0.83	0.54	0.9	1.66	37.97
Guzmania lingulata var. *lingulata*	0.82	0.53	0.91	1.65	39.62
Philodendron scandens	0.82	0.52	0.92	1.62	41.24
Euterpe precatoria	0.79	0.5	0.92	1.55	42.79
Miconia acinodendron	0.71	0.48	0.95	1.48	44.27
Pachira aquatica	0.66	0.47	0.96	1.45	45.72
Pentaclethra macroloba	0.82	0.46	0.68	1.43	47.15
Philodendron fendleri	0.67	0.45	0.96	1.39	48.53
Desmoncus polyacanthos	0.68	0.45	0.96	1.38	49.92
Ryania speciosa	0.81	0.44	0.68	1.36	51.28
Serjania paucidentata	0.74	0.44	0.8	1.35	52.63
Thoracocarpus bissectus	0.69	0.41	0.79	1.28	53.91
Inga ingoides	0.6	0.39	0.81	1.21	55.12
Spondias mombin	0.62	0.39	0.81	1.21	56.33
Piresia sympodica	0.76	0.39	0.57	1.2	57.53
Monotagma spicatum	0.71	0.34	0.57	1.05	58.58
Omphalea diandra	0.63	0.33	0.69	1.01	59.59
Anthurium hookeri	0.64	0.31	0.58	0.96	60.55
Becquerelia cymosa	0.63	0.3	0.55	0.93	61.49
Ischnosiphon arouma	0.65	0.3	0.57	0.92	62.41
Brosimum guianense	0.53	0.3	0.7	0.92	63.33

Clathrotropis brachypetala	0.58	0.28	0.58	0.85	64.19
Rudgea hostmanniana	0.52	0.26	0.59	0.8	64.99
Asplundia rigida	0.62	0.26	0.49	0.8	65.79
Diospyros cayennensis	0.52	0.26	0.59	0.79	66.58
Pharus latifolius	0.58	0.24	0.49	0.74	67.33
Psychotria cuspidata	0.58	0.24	0.49	0.74	68.06
Hymenocallis tubiflora	0.57	0.23	0.49	0.71	68.78
Licania heteromorpha var. *heteromorpha*	0.54	0.22	0.49	0.69	69.47
Aniba citrifolia	0.52	0.22	0.5	0.68	70.15
Polybotrya caudata	0.52	0.21	0.5	0.65	70.8
Monstera dubia	0.51	0.21	0.5	0.65	71.45
Geonoma interrupta	0.54	0.21	0.48	0.65	72.1
Psychotria poeppigiana	0.46	0.2	0.5	0.62	72.71
Dieffenbachia seguine	0.46	0.2	0.5	0.61	73.32
Garcinia madruno	0.42	0.2	0.51	0.61	73.92
Philodendron krugii	0.48	0.19	0.5	0.6	74.53
Hernandia sonora	0.42	0.19	0.5	0.58	75.1
Orthoclada laxa	0.49	0.18	0.41	0.55	75.66
Cyclanthus bipartitus	0.5	0.18	0.41	0.54	76.2
Mora excelsa	0.51	0.17	0.35	0.51	76.71
Cymbopetalum brasiliense	0.41	0.15	0.42	0.47	77.18
Tillandsia monadelpha	0.43	0.15	0.42	0.47	77.65
Abarema jupunba	0.38	0.15	0.42	0.47	78.12
Myrciaria floribunda	0.37	0.15	0.42	0.46	78.58
Protium guianense	0.4	0.15	0.42	0.45	79.03
Miconia chrysophylla	0.39	0.15	0.42	0.45	79.48
Guarea glabra	0.47	0.14	0.33	0.44	79.92
Cecropia peltata	0.38	0.14	0.42	0.43	80.35
Sarcoglottis metallica	0.39	0.14	0.42	0.42	80.77
Bauhinia glabra	0.43	0.13	0.35	0.4	81.17
Palicourea crocea	0.4	0.12	0.34	0.38	81.55
Adiantum obliquum	0.44	0.12	0.34	0.38	81.93
Philodendron simsii	0.39	0.12	0.34	0.37	82.31
Lacistema aggregatum	0.35	0.12	0.35	0.36	82.67
Doliocarpus dentatus ssp. *dentatus*	0.42	0.12	0.34	0.36	83.03
Quiina cruegeriana	0.36	0.11	0.35	0.35	83.38
Attalea maripa	0.4	0.11	0.34	0.34	83.72
Smilax cumanensis	0.39	0.11	0.34	0.34	84.06
Dioscorea cayenensis	0.32	0.11	0.35	0.34	84.4
Pachira insignis	0.36	0.11	0.35	0.33	84.73
Laetia procera	0.3	0.1	0.35	0.31	85.04
Lomariopsis japurensis	0.34	0.1	0.35	0.31	85.35

Microgramma tobagensis	0.32	0.1	0.35	0.3	85.65
Leandra rufescens	0.31	0.08	0.27	0.25	85.9
Piper demeraranum	0.35	0.08	0.27	0.25	86.15
Bactris major	0.33	0.08	0.28	0.23	86.38
Chimarrhis cymosa	0.32	0.07	0.28	0.23	86.62
Desmoncus orthacanthos	0.3	0.07	0.28	0.22	86.84
Psiguria triphylla	0.29	0.07	0.28	0.22	87.06
Euterpe oleracea	0.33	0.07	0.27	0.22	87.28
Coccoloba dussii	0.31	0.07	0.28	0.21	87.49
Hieronyma alchorneoides	0.26	0.07	0.28	0.21	87.71
Manilkara bidentata ssp. *bidentata*	0.25	0.07	0.28	0.21	87.92
Dichapetalum pedunculatum	0.28	0.07	0.28	0.21	88.13
Trichilia pallida	0.27	0.07	0.28	0.21	88.34
Symphonia globulifera	0.27	0.07	0.28	0.21	88.55
Bactris setulosa	0.3	0.07	0.28	0.21	88.76
Guapira salicifolia	0.26	0.07	0.28	0.21	88.97
Pouteria coriacea	0.26	0.07	0.28	0.21	89.18
Mouriri rhizophoraefolia	0.27	0.07	0.28	0.2	89.39
Ficus maxima	0.26	0.07	0.28	0.2	89.59
Psiguria umbrosa	0.26	0.06	0.28	0.2	89.79
Rourea surinamensis	0.27	0.06	0.28	0.2	89.99
Casearia sylvestris	0.26	0.06	0.28	0.2	90.18

Group 5A
Average similarity: 34.10

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Rudgea hostmanniana	1.16	0.98	2.07	2.87	2.87
Heliconia hirsuta	1.09	0.91	2.11	2.68	5.55
Terminalia amazonia	0.94	0.9	6.55	2.64	8.19
Sterculia pruriens var. *glabrescens*	1.03	0.85	2	2.5	10.69
Eschweilera subglandulosa	0.94	0.83	2.34	2.43	13.12
Desmoncus polyacanthos	0.88	0.78	2.37	2.27	15.4
Miconia acinodendron	1.02	0.77	1.2	2.27	17.67
Philodendron acutatum	0.93	0.75	1.6	2.2	19.86
Euterpe precatoria	0.87	0.72	1.64	2.12	21.99

Xiphidium caeruleum	1.01	0.72	1.19	2.11	24.1
Dieffenbachia seguine	0.86	0.7	1.64	2.06	26.16
Protium guianense	0.85	0.7	1.63	2.06	28.22
Scleria secans	0.96	0.67	1.14	1.95	30.17
Virola surinamensis	0.82	0.67	1.62	1.95	32.13
Byrsonima spicata	0.77	0.65	1.63	1.91	34.04
Guarea glabra	0.82	0.6	1.25	1.76	35.79
Psychotria cuspidata	0.87	0.56	1	1.65	37.45
Amaioua corymbosa	0.73	0.56	1.26	1.63	39.08
Cecropia peltata	0.71	0.55	1.27	1.62	40.69
Piresia sympodica	0.86	0.53	0.83	1.55	42.25
Miconia chrysophylla	0.85	0.52	0.81	1.51	43.76
Costus scaber	0.74	0.5	1.02	1.48	45.24
Pentaclethra macroloba	0.78	0.49	1	1.44	46.68
Scleria latifolia	0.73	0.47	1.03	1.39	48.07
Brosimum guianense	0.69	0.46	1.02	1.34	49.42
Attalea maripa	0.82	0.46	0.72	1.33	50.75
Cordia bicolor	0.58	0.37	0.85	1.1	51.85
Bauhinia glabra	0.71	0.37	0.71	1.09	52.94
Spondias mombin	0.56	0.36	0.85	1.04	53.98
Manicaria saccifera	0.7	0.34	0.59	1	54.98
Serjania paucidentata	0.67	0.32	0.68	0.95	55.93
Doliocarpus dentatus ssp. *dentatus*	0.63	0.32	0.7	0.95	56.87
Desmoncus orthacanthos	0.58	0.31	0.71	0.92	57.8
Laetia procera	0.52	0.3	0.71	0.89	58.69
Clathrotropis brachypetala	0.6	0.3	0.69	0.87	59.55
Coccoloba latifolia	0.5	0.29	0.71	0.84	60.39
Brownea coccinea ssp. *capitella*	0.56	0.29	0.71	0.84	61.23
Lygodium volubile	0.65	0.28	0.58	0.82	62.05
Rollinia exsucca	0.5	0.28	0.71	0.81	62.86
Pouteria coriacea	0.51	0.25	0.59	0.73	63.6
Ischnosiphon arouma	0.6	0.25	0.49	0.73	64.32
Heliconia spathocircinata	0.55	0.25	0.59	0.72	65.04
Psychotria poeppigiana	0.59	0.23	0.48	0.68	65.72
Inga ingoides	0.46	0.23	0.59	0.67	66.39
Psychotria deflexa	0.55	0.22	0.48	0.66	67.05
Monstera obliqua	0.54	0.22	0.49	0.64	67.69
Schefflera morototoni	0.44	0.22	0.6	0.63	68.32
Trichilia pallida	0.48	0.21	0.6	0.63	68.95
Martinella obovata	0.55	0.21	0.49	0.61	69.56
Miconia nervosa	0.54	0.2	0.49	0.59	70.14
Adiantum obliquum	0.56	0.2	0.48	0.58	70.73

Philodendron scandens	0.47	0.19	0.49	0.55	71.28
Calathea altissima	0.49	0.19	0.48	0.55	71.82
Miconia punctata	0.47	0.18	0.49	0.53	72.36
Olyra caudata	0.54	0.18	0.4	0.52	72.88
Philodendron fendleri	0.44	0.17	0.49	0.51	73.39
Cupania americana	0.4	0.17	0.49	0.5	73.9
Macfadyena unguis-cati	0.43	0.17	0.49	0.5	74.4
Carapa guianensis	0.4	0.17	0.49	0.5	74.89
Warszewiczia coccinea	0.46	0.16	0.49	0.48	75.38
Smilax cumanensis	0.39	0.16	0.49	0.47	75.85
Philodendron lingulatum	0.48	0.16	0.4	0.47	76.32
Olyra latifolia	0.48	0.16	0.4	0.47	76.78
Bactris major	0.51	0.16	0.39	0.46	77.25
Lundia corymbifera	0.46	0.15	0.4	0.44	77.69
Heliconia bihai	0.38	0.13	0.4	0.39	78.08
Sabicea villosa	0.4	0.13	0.4	0.39	78.47
Ouratea purdieana	0.35	0.13	0.4	0.38	78.85
Aristolochia rugosa	0.43	0.13	0.4	0.38	79.24
Monstera dubia	0.41	0.13	0.4	0.38	79.62
Guapira salicifolia	0.39	0.13	0.4	0.38	79.99
Pera glabrata	0.35	0.13	0.4	0.38	80.37
Abarema jupunba	0.35	0.13	0.4	0.38	80.75
Bactris simplicifrons	0.42	0.13	0.39	0.37	81.12
Genipa americana	0.42	0.13	0.39	0.37	81.48
Sarcoglottis metallica	0.34	0.12	0.4	0.35	81.84
Mascagnia sepium ssp. *bierosa*	0.35	0.12	0.4	0.35	82.18
Tabebuia chrysantha	0.35	0.12	0.4	0.34	82.53
Vismia cayennensis	0.34	0.12	0.4	0.34	82.87
Sapium glandulosum	0.33	0.11	0.4	0.33	83.2
Guazuma ulmifolia	0.33	0.11	0.4	0.33	83.53
Coussarea paniculata	0.37	0.11	0.4	0.33	83.86
Anemopaegma karstenii	0.41	0.11	0.32	0.33	84.19
Scleria melaleuca	0.4	0.11	0.32	0.33	84.51
Casearia spinescens	0.38	0.11	0.41	0.32	84.83
Piper aequale	0.41	0.1	0.32	0.3	85.14
Wulffia baccata	0.38	0.1	0.32	0.3	85.44
Manilkara bidentata ssp. *bidentata*	0.31	0.1	0.32	0.3	85.74
Paullinia fuscescens	0.38	0.1	0.32	0.29	86.03
Philodendron krugii	0.37	0.1	0.32	0.28	86.31
Lacistema aggregatum	0.32	0.09	0.32	0.26	86.57
Renealmia alpinia	0.31	0.09	0.32	0.26	86.83
Diplasia karatifolia	0.36	0.09	0.31	0.25	87.08

Guarea guidonia	0.29	0.09	0.32	0.25	87.33
Pachira insignis	0.29	0.09	0.32	0.25	87.58
Pachira aquatica	0.29	0.08	0.32	0.24	87.83
Senna undulata	0.29	0.08	0.32	0.24	88.07
Coccoloba ascendens	0.3	0.08	0.32	0.24	88.31
Ryania speciosa	0.38	0.08	0.24	0.24	88.55
Nectandra pearcei	0.29	0.08	0.32	0.24	88.79
Xylophragma seemannianum	0.29	0.08	0.32	0.24	89.03
Stigmaphyllon finlayanum	0.35	0.08	0.32	0.24	89.27
Ficus maxima	0.29	0.08	0.32	0.23	89.5
Castilla elastica ssp. *elastica*	0.28	0.08	0.32	0.23	89.73
Oeceoclades maculata	0.28	0.07	0.32	0.22	89.95
Spathiphyllum cannifolium	0.36	0.07	0.24	0.21	90.16

Group 3A
Average similarity: 36.47

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Philodendron lingulatum	1.51	1.78	6.17	4.87	4.87
Piper trigonum	1.34	1.47	4.59	4.02	8.89
Anthurium hookeri	1.38	1.34	1.57	3.68	12.58
Coccoloba ascendens	1.02	1.21	8.81	3.31	15.89
Philodendron ornatum	1.3	1.19	1.56	3.26	19.15
Psychotria muscosa	1.26	1.18	1.53	3.24	22.39
Geonoma interrupta	1.24	1.18	1.63	3.24	25.63
Becquerelia cymosa	1.25	1.17	1.6	3.22	28.84
Sterculia pruriens var. *glabrescens*	0.98	1.16	8.15	3.17	32.02
Licania heteromorpha var. *heteromorpha*	1.09	1.03	1.55	2.84	34.85
Mikania hookeriana	1.02	1.02	1.68	2.79	37.64
Marcgravia elegans	1.13	0.96	1.04	2.64	40.28
Notopleura uliginosa	1.02	0.93	1.61	2.55	42.83
Diospyros cayennensis	0.97	0.91	1.65	2.48	45.31
Piper demeraranum	1.01	0.86	1.05	2.35	47.67
Danaea leprieurii	1.06	0.83	1.03	2.29	49.95

Heliconia hirsuta	0.91	0.77	1.04	2.11	52.06
Euterpe broadwayi	0.94	0.76	1.04	2.08	54.14
Richeria grandis var. *grandis*	0.97	0.75	1.04	2.05	56.19
Ocotea eggersiana	0.87	0.7	1.04	1.93	58.11
Symphonia globulifera	0.76	0.65	1.04	1.79	59.9
Palicourea crocea	0.95	0.63	0.71	1.74	61.63
Macrolobium trinitense	0.79	0.6	1.04	1.66	63.29
Miconia chrysophylla	0.9	0.57	0.72	1.56	64.85
Miconia plukenetii	0.77	0.51	0.73	1.39	66.24
Evodianthus funifer ssp. *funifer*	0.93	0.49	0.51	1.35	67.59
Polybotrya osmundacea	0.83	0.49	0.71	1.35	68.94
Bactris setulosa	0.73	0.48	0.73	1.31	70.25
Sloanea stipitata	0.66	0.47	0.73	1.28	71.53
Salpichlaena volubilis	0.81	0.47	0.71	1.28	72.81
Plinia pinnata	0.67	0.46	0.73	1.26	74.07
Leandra clidemioides	0.78	0.42	0.51	1.14	75.21
Miconia nervosa	0.77	0.4	0.51	1.1	76.31
Guzmania lingulata var. *lingulata*	0.82	0.39	0.49	1.07	77.38
Psychotria poeppigiana	0.63	0.32	0.51	0.89	78.27
Psychotria capitata	0.68	0.32	0.51	0.88	79.15
Notopleura guadalupensis	0.65	0.31	0.51	0.85	80.01
Prestoea pubigera	0.61	0.31	0.51	0.84	80.85
Quiina cruegeriana	0.55	0.26	0.51	0.72	81.57
Pleurothallis ruscifolia	0.61	0.26	0.5	0.71	82.28
Cybianthus surinamensis	0.49	0.25	0.51	0.67	82.96
Eschweilera decolorans	0.49	0.24	0.51	0.65	83.61
Anthurium aripoense	0.56	0.19	0.34	0.51	84.12
Stromanthe tonckat	0.55	0.18	0.33	0.5	84.62
Richeria grandis	0.45	0.16	0.34	0.43	85.05
Trichomanes elegans	0.48	0.16	0.34	0.43	85.48
Dichapetalum pedunculatum	0.55	0.15	0.31	0.42	85.89
Peperomia emarginella	0.49	0.15	0.34	0.42	86.31
Tabebuia stenocalyx	0.4	0.15	0.34	0.4	86.71
Cestrum schlechtendahlii	0.47	0.14	0.34	0.4	87.11
Elaphoglossum longifolium	0.46	0.14	0.34	0.39	87.5
Miconia fragrans	0.46	0.14	0.34	0.37	87.87
Codonanthe caribaea	0.38	0.14	0.34	0.37	88.24
Marcgravia hartii	0.38	0.13	0.34	0.37	88.61
Swartzia trinitensis	0.39	0.13	0.34	0.37	88.98

Monotagma spicatum	0.44	0.13	0.34	0.36	89.34
Epidendrum nocturnum	0.38	0.13	0.34	0.36	89.7
Micropholis guyanensis ssp. *guyanensis*	0.38	0.13	0.34	0.36	90.06

Group 5B
Average similarity: 34.68

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Sterculia pruriens var. *glabrescens*	1.05	0.91	3.44	2.63	2.63
Ryania speciosa	1.16	0.91	1.5	2.63	5.26
Piresia sympodica	1.13	0.86	1.19	2.48	7.74
Carapa guianensis	0.92	0.85	5.51	2.44	10.18
Terminalia amazonia	0.85	0.75	2.25	2.15	12.33
Tovomita eggersii	0.98	0.73	1.36	2.09	14.43
Attalea maripa	0.99	0.68	1.12	1.96	16.38
Licania heteromorpha var. *heteromorpha*	0.85	0.68	1.56	1.95	18.34
Virola surinamensis	0.83	0.65	1.55	1.89	20.22
Psychotria capitata	0.88	0.64	1.14	1.83	22.05
Scleria secans	0.85	0.63	1.54	1.83	23.88
Laetia procera	0.73	0.61	1.55	1.77	25.66
Abarema jupunba	0.72	0.6	1.55	1.74	27.4
Simaba multiflora	0.84	0.6	1.15	1.72	29.12
Bauhinia glabra	0.84	0.58	1.18	1.67	30.79
Calliandra guildingii	0.87	0.55	0.95	1.59	32.38
Lygodium volubile	0.9	0.55	0.92	1.59	33.97
Manilkara bidentata ssp. *bidentata*	0.76	0.54	1.17	1.55	35.52
Protium guianense	0.76	0.51	1.16	1.47	36.98
Psychotria poeppigiana	0.8	0.49	0.94	1.42	38.4
Tabernaemontana undulata	0.77	0.48	0.96	1.39	39.79
Maprounea guianensis	0.64	0.48	1.21	1.38	41.17
Pera glabrata	0.65	0.45	0.97	1.3	42.48
Eugenia confusa	0.7	0.44	0.96	1.26	43.73
Heliconia hirsuta	0.76	0.42	0.77	1.2	44.93
Byrsonima spicata	0.65	0.42	0.96	1.2	46.13

Trichomanes pinnatum	0.77	0.41	0.75	1.19	47.32
Parinari campestris	0.59	0.41	0.96	1.17	48.49
Microgramma lycopodioides	0.59	0.39	0.97	1.13	49.62
Smilax cumanensis	0.68	0.38	0.78	1.09	50.71
Triplophyllum funestrum	0.71	0.37	0.76	1.06	51.78
Miconia punctata	0.67	0.36	0.77	1.04	52.81
Eschweilera subglandulosa	0.56	0.36	0.8	1.02	53.84
Oenocarpus bataua var. *oligocarpa*	0.61	0.34	0.8	0.99	54.83
Rudgea hostmanniana	0.62	0.34	0.79	0.98	55.81
Euterpe precatoria	0.61	0.34	0.79	0.97	56.78
Amaioua corymbosa	0.59	0.33	0.79	0.96	57.74
Desmoncus polyacanthos	0.59	0.33	0.79	0.96	58.71
Cnemidaria spectabilis	0.67	0.32	0.64	0.92	59.63
Brosimum guianense	0.57	0.31	0.79	0.9	60.53
Tabebuia stenocalyx	0.62	0.29	0.63	0.85	61.38
Palicourea crocea	0.61	0.29	0.65	0.84	62.23
Diplasia karatifolia	0.65	0.27	0.53	0.78	63.01
Miconia affinis	0.57	0.26	0.66	0.76	63.77
Quiina cruegeriana	0.49	0.26	0.65	0.76	64.53
Philodendron scandens	0.56	0.26	0.65	0.76	65.29
Lacistema aggregatum	0.54	0.26	0.66	0.75	66.04
Serjania paucidentata	0.55	0.26	0.64	0.75	66.79
Adiantum tetraphyllum	0.62	0.25	0.53	0.73	67.52
Monotagma spicatum	0.62	0.25	0.53	0.72	68.24
Philodendron ornatum	0.61	0.25	0.51	0.72	68.96
Brownea coccinea ssp. *capitella*	0.55	0.25	0.64	0.71	69.67
Psychotria muscosa	0.56	0.24	0.53	0.69	70.36
Miconia ciliata	0.54	0.22	0.53	0.64	71
Philodendron lingulatum	0.58	0.22	0.51	0.64	71.64
Pouteria coriacea	0.54	0.22	0.52	0.62	72.26
Doliocarpus dentatus ssp. *dentatus*	0.52	0.21	0.54	0.6	72.86
Metaxya rostrata	0.57	0.2	0.43	0.59	73.45
Symphonia globulifera	0.43	0.2	0.54	0.58	74.02
Miconia acinodendron	0.48	0.19	0.54	0.56	74.58
Calophyllum lucidum	0.47	0.19	0.53	0.54	75.13
Cordia bicolor	0.41	0.19	0.54	0.54	75.67
Hieronyma alchorneoides	0.42	0.19	0.54	0.54	76.21
Trichilia micrantha	0.41	0.18	0.54	0.53	76.74
Andira inermis	0.4	0.17	0.54	0.5	77.24
Tabebuia serratifolia	0.42	0.16	0.44	0.45	77.69

Ormosia monosperma	0.44	0.15	0.44	0.44	78.12
Miconia nervosa	0.45	0.15	0.43	0.42	78.54
Aniba panurensis	0.37	0.14	0.44	0.42	78.96
Bredemeyera lucida	0.36	0.14	0.44	0.41	79.37
Monstera obliqua	0.4	0.14	0.44	0.4	79.77
Coussarea paniculata	0.39	0.14	0.44	0.4	80.17
Swartzia pinnata	0.41	0.14	0.43	0.4	80.56
Mikania psilostachya	0.36	0.14	0.44	0.4	80.96
Dieffenbachia seguine	0.44	0.14	0.42	0.39	81.35
Warszewiczia coccinea	0.43	0.14	0.43	0.39	81.74
Calycolpus goetheanus	0.36	0.14	0.43	0.39	82.13
Costus scaber	0.44	0.13	0.43	0.39	82.52
Ischnosiphon arouma	0.43	0.13	0.42	0.38	82.9
Anthurium jenmanii	0.35	0.13	0.44	0.36	83.27
Adiantum obliquum	0.42	0.11	0.34	0.32	83.58
Guzmania lingulata var. *lingulata*	0.38	0.11	0.35	0.31	83.89
Philodendron fragrantissimum	0.38	0.11	0.35	0.31	84.2
Trichilia pleeana	0.36	0.1	0.35	0.3	84.5
Olyra caudata	0.4	0.1	0.34	0.3	84.8
Miconia prasina	0.36	0.1	0.35	0.29	85.08
Sloanea stipitata	0.37	0.1	0.34	0.28	85.36
Licania membranacea	0.35	0.1	0.34	0.28	85.64
Scleria latifolia	0.34	0.09	0.35	0.27	85.91
Ilex arimensis	0.33	0.09	0.35	0.27	86.18
Philodendron acutatum	0.36	0.09	0.34	0.26	86.44
Dipteryx odorata	0.3	0.09	0.35	0.26	86.7
Pleonotoma variabilis	0.29	0.09	0.35	0.26	86.96
Diospyros cayennensis	0.34	0.09	0.35	0.26	87.21
Licania cruegeriana	0.29	0.09	0.35	0.25	87.46
Inga pilosula	0.29	0.08	0.35	0.24	87.7
Thoracocarpus bissectus	0.29	0.08	0.35	0.24	87.94
Alchornea triplinervia	0.29	0.08	0.35	0.24	88.18
Smilax solanifolia	0.29	0.08	0.35	0.23	88.41
Coccoloba excelsa	0.34	0.08	0.26	0.22	88.64
Dicranoglossum desvauxii	0.27	0.08	0.35	0.22	88.85
Rourea surinamensis	0.36	0.07	0.26	0.22	89.07
Lindsaea lancea	0.36	0.07	0.26	0.21	89.28
Calyptrocarya glomerulata	0.36	0.07	0.25	0.2	89.48
Eugenia baileyi	0.29	0.07	0.26	0.19	89.67
Dichapetalum pedunculatum	0.3	0.07	0.26	0.19	89.87

Arrabidaea patellifera	0.31	0.06	0.26	0.18	90.05

Group 6A
Average similarity: 23.02

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Philodendron acutatum	1.04	0.98	1.99	4.28	4.28
Lygodium volubile	1.04	0.87	1.33	3.79	8.07
Protium guianense	0.99	0.82	1.36	3.56	11.63
Attalea maripa	0.96	0.81	1.38	3.51	15.14
Terminalia amazonia	0.87	0.73	1.36	3.16	18.3
Coccoloba latifolia	0.82	0.72	1.38	3.15	21.45
Rollinia exsucca	0.8	0.6	1.06	2.61	24.06
Olyra latifolia	0.87	0.6	0.84	2.59	26.65
Scleria secans	0.89	0.56	0.84	2.44	29.09
Wulffia baccata	0.86	0.53	0.82	2.32	31.4
Miconia acinodendron	0.83	0.48	0.67	2.08	33.48
Rhynchospora cephalotes	0.85	0.45	0.66	1.95	35.43
Rudgea hostmanniana	0.68	0.42	0.83	1.83	37.27
Andira inermis	0.68	0.42	0.81	1.83	39.09
Ryania speciosa	0.68	0.36	0.63	1.56	40.65
Euterpe precatoria	0.66	0.35	0.67	1.51	42.16
Heliconia psittacorum	0.7	0.34	0.53	1.49	43.65
Costus scaber	0.67	0.33	0.65	1.45	45.1
Tabebuia serratifolia	0.56	0.32	0.67	1.39	46.49
Bromelia plumieri	0.56	0.31	0.67	1.33	47.81
Palicourea crocea	0.6	0.28	0.52	1.2	49.02
Smilax cumanensis	0.57	0.27	0.53	1.16	50.18
Ilex arimensis	0.6	0.26	0.51	1.12	51.3
Cecropia peltata	0.52	0.25	0.53	1.1	52.4
Heliconia hirsuta	0.59	0.25	0.52	1.09	53.49
Amaioua corymbosa	0.53	0.24	0.53	1.06	54.56
Lacistema aggregatum	0.48	0.24	0.53	1.02	55.58
Macfadyena unguis-cati	0.5	0.23	0.53	1.02	56.59
Byrsonima spicata	0.47	0.23	0.53	1	57.6
Pera glabrata	0.47	0.23	0.53	1	58.6
Cordia bicolor	0.48	0.22	0.53	0.94	59.54
Chelonanthus alatus	0.46	0.18	0.41	0.78	60.31
Renealmia alpinia	0.44	0.17	0.41	0.74	61.05

Miconia prasina	0.5	0.17	0.41	0.74	61.79
Virola surinamensis	0.46	0.17	0.41	0.73	62.52
Cordia curassavica	0.45	0.16	0.41	0.71	63.23
Dioclea guianensis	0.5	0.16	0.31	0.7	63.92
Oeceoclades maculata	0.45	0.16	0.41	0.69	64.62
Lygodium venustum	0.48	0.16	0.4	0.69	65.3
Manilkara bidentata ssp. *bidentata*	0.42	0.16	0.41	0.68	65.99
Desmoncus polyacanthos	0.48	0.15	0.42	0.67	66.65
Pharus latifolius	0.39	0.15	0.41	0.67	67.32
Bredemeyera lucida	0.46	0.15	0.41	0.65	67.97
Guazuma ulmifolia	0.38	0.15	0.42	0.65	68.62
Schefflera morototoni	0.4	0.15	0.41	0.64	69.26
Swartzia simplex	0.45	0.15	0.41	0.64	69.9
Merremia macrocalyx	0.4	0.14	0.41	0.61	70.51
Adiantum tetraphyllum	0.47	0.14	0.31	0.61	71.12
Casearia guianensis	0.37	0.14	0.42	0.61	71.73
Genipa americana	0.42	0.14	0.42	0.59	72.32
Pleonotoma variabilis	0.36	0.14	0.42	0.59	72.91
Brosimum guianense	0.36	0.13	0.42	0.58	73.49
Abarema jupunba	0.35	0.13	0.42	0.56	74.05
Miconia ciliata	0.46	0.12	0.3	0.53	74.58
Scleria melaleuca	0.43	0.11	0.31	0.49	75.07
Roupala montana	0.34	0.11	0.31	0.48	75.54
Calliandra guildingii	0.39	0.11	0.31	0.48	76.02
Mangifera indica	0.4	0.11	0.31	0.47	76.49
Rourea surinamensis	0.44	0.11	0.3	0.47	76.96
Passiflora auriculata	0.37	0.11	0.31	0.47	77.43
Doliocarpus dentatus ssp. *dentatus*	0.4	0.11	0.3	0.47	77.9
Lantana camara	0.37	0.1	0.31	0.44	78.34
Olyra caudata	0.4	0.1	0.31	0.43	78.77
Solanum asperum	0.39	0.1	0.3	0.42	79.19
Pachira insignis	0.32	0.1	0.31	0.42	79.61
Ischnosiphon arouma	0.38	0.1	0.3	0.41	80.02
Vismia cayennensis	0.31	0.09	0.31	0.41	80.43
Protium sagotianum	0.39	0.09	0.31	0.41	80.84
Trichilia pallida	0.31	0.09	0.31	0.4	81.24
Psychotria gracilenta	0.35	0.09	0.31	0.4	81.64
Ficus guianensis	0.33	0.09	0.31	0.39	82.04
Warszewiczia coccinea	0.37	0.09	0.3	0.39	82.42
Calophyllum lucidum	0.3	0.09	0.31	0.38	82.8
Swartzia pinnata	0.38	0.09	0.31	0.38	83.17
Eschweilera subglandulosa	0.31	0.09	0.31	0.37	83.55

Brownea coccinea ssp. *capitella*	0.3	0.09	0.31	0.37	83.91
Dieffenbachia seguine	0.31	0.08	0.31	0.37	84.28
Scleria bracteata	0.41	0.08	0.21	0.35	84.64
Sterculia pruriens var. *glabrescens*	0.35	0.08	0.31	0.35	84.98
Mandevilla hirsuta	0.38	0.08	0.22	0.34	85.32
Psychotria capitata	0.4	0.08	0.22	0.34	85.67
Clidemia pustulata	0.35	0.08	0.22	0.33	85.99
Tetracera costata ssp. *costata*	0.35	0.07	0.22	0.31	86.3
Chiococca alba	0.37	0.06	0.21	0.28	86.58
Ormosia monosperma	0.29	0.06	0.22	0.27	86.85
Clidemia sericea	0.31	0.06	0.21	0.27	87.13
Panicum maximum	0.36	0.06	0.21	0.27	87.4
Calea solidaginea	0.29	0.06	0.22	0.27	87.67
Davilla kunthii	0.34	0.06	0.2	0.26	87.93
Guapira cuspidata	0.3	0.05	0.22	0.24	88.17
Licania cruegeriana	0.25	0.05	0.22	0.23	88.4
Lundia corymbifera	0.28	0.05	0.21	0.22	88.62
Cassipourea guianensis	0.25	0.05	0.21	0.22	88.84
Enicostema verticillatum	0.27	0.05	0.22	0.22	89.07
Inga ingoides	0.23	0.05	0.22	0.22	89.28
Cupania rubiginosa	0.29	0.05	0.22	0.21	89.5
Ceratophytum tetragonolobum	0.31	0.05	0.21	0.21	89.71
Psychotria cuspidata	0.3	0.05	0.21	0.21	89.92
Chrysophyllum argenteum ssp. *argenteum*	0.29	0.05	0.22	0.21	90.13

Group 8B
Average similarity: 29.96

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Brownea coccinea ssp. *capitella*	1.02	0.88	1.86	2.94	2.94
Costus scaber	1.02	0.86	1.79	2.88	5.81
Dieffenbachia seguine	1.11	0.85	1.19	2.83	8.65
Heliconia hirsuta	1.09	0.83	1.15	2.76	11.41
Protium guianense	0.94	0.81	1.9	2.7	14.11

Gonzalagunia spicata	0.92	0.66	1.21	2.2	16.32
Swartzia pinnata	0.87	0.63	1.2	2.12	18.43
Desmoncus polyacanthos	0.78	0.61	1.26	2.04	20.47
Tectaria incisa	0.9	0.57	0.86	1.9	22.37
Adiantum tetraphyllum	0.94	0.56	0.69	1.87	24.24
Attalea maripa	0.87	0.54	0.86	1.8	26.04
Rudgea hostmanniana	0.84	0.51	0.87	1.71	27.76
Sarcoglottis metallica	0.76	0.51	0.91	1.7	29.45
Swartzia simplex	0.77	0.51	0.91	1.69	31.14
Chrysophyllum argenteum ssp. *argenteum*	0.83	0.51	0.86	1.69	32.83
Sterculia pruriens var. *glabrescens*	0.82	0.5	0.88	1.68	34.51
Trichilia pallida	0.82	0.5	0.89	1.66	36.17
Cupania americana	0.63	0.45	0.92	1.51	37.68
Philodendron acutatum	0.78	0.41	0.65	1.38	39.06
Warszewiczia coccinea	0.77	0.41	0.67	1.35	40.41
Xiphidium caeruleum	0.72	0.38	0.68	1.27	41.68
Ischnosiphon arouma	0.71	0.38	0.68	1.27	42.95
Macfadyena unguis-cati	0.73	0.36	0.66	1.22	44.17
Cyclopeltis semicordata	0.7	0.36	0.67	1.19	45.36
Monstera adansonii	0.59	0.35	0.7	1.18	46.55
Guazuma ulmifolia	0.55	0.34	0.7	1.15	47.7
Castilla elastica ssp. *elastica*	0.66	0.34	0.69	1.15	48.85
Tabebuia serratifolia	0.55	0.34	0.7	1.12	49.97
Ceratophytum tetragonolobum	0.66	0.34	0.68	1.12	51.09
Wulffia baccata	0.63	0.33	0.69	1.11	52.2
Philodendron krugii	0.62	0.33	0.69	1.09	53.29
Pouteria multiflora	0.54	0.33	0.69	1.08	54.37
Schefflera morototoni	0.54	0.32	0.69	1.08	55.46
Rourea surinamensis	0.54	0.32	0.69	1.08	56.53
Terminalia amazonia	0.54	0.32	0.7	1.06	57.59
Spondias mombin	0.53	0.32	0.7	1.05	58.64
Miconia nervosa	0.63	0.26	0.51	0.86	59.5
Miconia acinodendron	0.62	0.26	0.52	0.85	60.35
Guarea guidonia	0.56	0.25	0.52	0.83	61.18
Pachira aquatica	0.57	0.24	0.51	0.79	61.97
Paragonia pyramidata	0.53	0.24	0.53	0.78	62.75
Mangifera indica	0.46	0.23	0.53	0.77	63.52
Casearia guianensis	0.58	0.23	0.51	0.77	64.29
Simaba multiflora	0.59	0.23	0.51	0.77	65.06
Pleonotoma variabilis	0.52	0.23	0.53	0.76	65.82

Guarea glabra	0.58	0.22	0.5	0.75	66.57
Lygodium volubile	0.55	0.22	0.52	0.74	67.31
Serjania paucidentata	0.57	0.22	0.51	0.74	68.05
Licania cruegeriana	0.46	0.22	0.53	0.74	68.79
Psiguria umbrosa	0.52	0.22	0.52	0.74	69.53
Pterocarpus rohrii	0.46	0.22	0.52	0.73	70.26
Cecropia peltata	0.46	0.22	0.52	0.73	70.98
Oeceoclades maculata	0.51	0.22	0.53	0.72	71.7
Heliconia spathocircinata	0.51	0.21	0.52	0.72	72.42
Drymonia serrulata	0.45	0.21	0.53	0.71	73.13
Pharus latifolius	0.45	0.21	0.53	0.71	73.85
Ficus yoponensis	0.48	0.21	0.53	0.71	74.55
Protium sagotianum	0.51	0.21	0.53	0.69	75.24
Faramea occidentalis	0.44	0.21	0.53	0.69	75.94
Piper dilatatum	0.58	0.2	0.37	0.65	76.59
Theobroma cacao	0.53	0.16	0.37	0.55	77.14
Psychotria cuspidata	0.53	0.16	0.37	0.53	77.67
Olyra caudata	0.47	0.15	0.38	0.49	78.15
Anthurium pentaphyllum	0.37	0.14	0.39	0.47	78.62
Eschweilera subglandulosa	0.38	0.14	0.39	0.47	79.09
Miconia virescens	0.37	0.14	0.39	0.47	79.56
Virola surinamensis	0.37	0.14	0.39	0.46	80.02
Pera glabrata	0.37	0.14	0.39	0.46	80.48
Zanthoxylum pentandrum	0.37	0.14	0.39	0.46	80.95
Olyra latifolia	0.44	0.14	0.39	0.46	81.41
Hymenocallis tubiflora	0.45	0.14	0.39	0.46	81.87
Hymenaea courbaril	0.37	0.14	0.39	0.46	82.33
Ceiba pentandra	0.37	0.14	0.39	0.45	82.78
Cedrela odorata	0.36	0.13	0.39	0.45	83.23
Brosimum guianense	0.41	0.13	0.39	0.45	83.67
Coccoloba latifolia	0.44	0.13	0.39	0.45	84.12
Manilkara bidentata ssp. *bidentata*	0.36	0.13	0.39	0.44	84.56
Anthurium jenmanii	0.4	0.13	0.39	0.43	84.99
Dioscorea bulbifera	0.36	0.13	0.39	0.43	85.42
Chiococca alba	0.43	0.13	0.39	0.43	85.85
Smilax cumanensis	0.36	0.13	0.39	0.42	86.26
Calyptranthes fasciculata	0.36	0.12	0.39	0.41	86.67
Inga ingoides	0.35	0.12	0.39	0.41	87.08
Eugenia trinervia	0.42	0.12	0.39	0.4	87.48
Piper hispidum	0.47	0.11	0.26	0.36	87.84
Garcinia macrophylla	0.42	0.09	0.25	0.3	88.14
Heliconia bihai	0.41	0.09	0.25	0.29	88.44
Cyclanthus bipartitus	0.4	0.09	0.26	0.29	88.72

Philodendron lingulatum	0.41	0.08	0.25	0.28	89
Maranta gibba	0.4	0.08	0.26	0.27	89.28
Philodendron scandens	0.38	0.08	0.26	0.27	89.55
Piper marginatum	0.4	0.08	0.25	0.26	89.81
Hura crepitans	0.35	0.08	0.26	0.25	90.06

Group 4B
Average similarity: 30.57

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Heliconia hirsuta	1.19	1.11	3.64	3.64	3.64
Sterculia pruriens var. *glabrescens*	1.03	1.02	9.28	3.35	6.99
Miconia nervosa	0.99	0.95	6.11	3.12	10.11
Psychotria muscosa	1.04	0.8	1.35	2.62	12.73
Cnemidaria spectabilis	1.03	0.8	1.46	2.61	15.33
Tabernaemontana attenuata	1.01	0.76	1.37	2.5	17.83
Piper trigonum	0.95	0.76	1.51	2.49	20.32
Adiantum tetraphyllum	1.12	0.75	0.91	2.46	22.78
Rudgea hostmanniana	0.89	0.74	1.53	2.43	25.21
Ryania speciosa	1.11	0.73	0.91	2.4	27.61
Microgramma lycopodioides	0.78	0.67	1.48	2.18	29.79
Serjania paucidentata	0.84	0.65	1.49	2.12	31.91
Byrsonima spicata	0.77	0.65	1.49	2.11	34.02
Miconia acinodendron	0.9	0.59	0.91	1.94	35.96
Palicourea crocea	0.89	0.55	0.91	1.8	37.76
Philodendron lingulatum	0.88	0.52	0.91	1.71	39.47
Philodendron ornatum	0.88	0.52	0.89	1.7	41.18
Miconia chrysophylla	0.83	0.52	0.87	1.7	42.88
Ischnosiphon arouma	0.81	0.52	0.91	1.69	44.57
Miconia affinis	0.79	0.49	0.88	1.6	46.16
Costus scaber	0.67	0.47	0.93	1.54	47.71
Brownea coccinea ssp. *capitella*	0.64	0.47	0.93	1.52	49.23
Dichapetalum pedunculatum	0.76	0.45	0.89	1.48	50.71
Geonoma interrupta	0.69	0.44	0.93	1.45	52.16

Licania heteromorpha var. *heteromorpha*	0.69	0.44	0.93	1.45	53.61
Tovomita eggersii	0.69	0.44	0.9	1.45	55.06
Terminalia amazonia	0.65	0.43	0.91	1.42	56.48
Diospyros cayennensis	0.71	0.42	0.91	1.39	57.87
Notopleura uliginosa	0.64	0.42	0.91	1.39	59.26
Virola surinamensis	0.64	0.42	0.91	1.39	60.65
Euterpe precatoria	0.7	0.42	0.91	1.36	62.01
Pera glabrata	0.71	0.41	0.91	1.35	63.36
Sloanea stipitata	0.7	0.34	0.6	1.12	64.48
Bauhinia glabra	0.69	0.32	0.61	1.06	65.54
Elaphoglossum luridum	0.63	0.29	0.61	0.96	66.5
Swartzia pinnata	0.54	0.29	0.62	0.95	67.45
Tabebuia stenocalyx	0.69	0.29	0.57	0.95	68.4
Tabebuia serratifolia	0.61	0.28	0.62	0.93	69.33
Philodendron krugii	0.6	0.28	0.62	0.93	70.26
Polybotrya osmundacea	0.58	0.28	0.61	0.92	71.18
Andira inermis	0.51	0.27	0.62	0.89	72.07
Hieronyma alchorneoides var. *alchorneoides*	0.51	0.27	0.62	0.89	72.96
Cybianthus surinamensis	0.56	0.26	0.6	0.86	73.82
Cecropia peltata	0.48	0.24	0.61	0.79	74.61
Alchornea triplinervia	0.49	0.24	0.61	0.78	75.39
Brosimum guianense	0.49	0.24	0.61	0.78	76.17
Monotagma spicatum	0.64	0.21	0.39	0.68	76.84
Psychotria capitata	0.63	0.19	0.38	0.61	77.45
Piper glabrescens	0.57	0.18	0.39	0.58	78.03
Mollinedia ovata	0.53	0.16	0.39	0.54	78.57
Pinzona coriacea	0.51	0.16	0.4	0.53	79.1
Ocotea oblonga	0.48	0.16	0.39	0.52	79.62
Philodendron scandens	0.54	0.16	0.39	0.52	80.14
Becquerelia cymosa	0.46	0.15	0.4	0.48	80.62
Eschweilera subglandulosa	0.42	0.15	0.4	0.48	81.1
Miconia splendens	0.53	0.15	0.36	0.48	81.58
Anthurium pentaphyllum	0.49	0.15	0.4	0.48	82.06
Arrabidaea inaequalis	0.45	0.14	0.4	0.47	82.53
Desmoncus polyacanthos	0.41	0.14	0.4	0.47	83
Myrcia amazonica	0.41	0.14	0.4	0.47	83.48
Simaba multiflora	0.41	0.14	0.4	0.47	83.95
Smilax solanifolia	0.48	0.14	0.4	0.47	84.42
Codonanthe crassifolia	0.39	0.14	0.4	0.47	84.88
Marcgravia hartii	0.43	0.14	0.4	0.46	85.35
Sarcoglottis metallica	0.38	0.14	0.4	0.46	85.81
Guarea glabra	0.38	0.14	0.4	0.46	86.26

Thoracocarpus bissectus	0.43	0.14	0.4	0.45	86.72
Guzmania lingulata var. *lingulata*	0.5	0.14	0.4	0.45	87.17
Hernandia sonora	0.39	0.14	0.4	0.44	87.61
Piper demeraranum	0.47	0.13	0.38	0.43	88.04
Anemopaegma karstenii	0.39	0.13	0.39	0.41	88.45
Miconia prasina	0.39	0.13	0.39	0.41	88.86
Cordia bicolor	0.39	0.12	0.39	0.4	89.26
Licania membranacea	0.5	0.12	0.39	0.39	89.66
Miconia multispicata	0.45	0.12	0.39	0.38	90.04

Group 2A
Average similarity: 30.58

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Ryania speciosa	1.5	1.59	4.02	5.21	5.21
Eugenia confusa	1.31	1.24	1.89	4.06	9.28
Psychotria muscosa	1.21	1.08	1.52	3.53	12.81
Tabebuia stenocalyx	1.04	0.99	1.54	3.25	16.06
Cassipourea guianensis	1.08	0.98	1.43	3.21	19.27
Ronabea latifolia	0.99	0.91	1.21	2.96	22.24
Sterculia pruriens var. *glabrescens*	0.94	0.87	1.49	2.84	25.08
Palicourea crocea	0.98	0.84	1.15	2.76	27.83
Psychotria capitata	1.05	0.79	0.95	2.58	30.41
Manilkara bidentata ssp. *bidentata*	0.95	0.78	1.11	2.54	32.95
Licania heteromorpha var. *heteromorpha*	0.83	0.66	0.96	2.15	35.1
Eschweilera subglandulosa	0.83	0.62	0.94	2.02	37.12
Philodendron lingulatum	0.82	0.61	0.96	2.01	39.12
Virola surinamensis	0.81	0.58	0.92	1.9	41.03
Miconia ciliata	0.86	0.55	0.65	1.79	42.82
Philodendron ornatum	0.81	0.53	0.77	1.73	44.55
Amaioua corymbosa	0.66	0.47	0.78	1.53	46.08
Smilax cumanensis	0.74	0.44	0.64	1.42	47.51
Protium guianense	0.67	0.43	0.79	1.41	48.92
Calliandra guildingii	0.77	0.41	0.63	1.35	50.27
Euterpe precatoria	0.78	0.41	0.62	1.34	51.61

Diplasia karatifolia	0.79	0.41	0.53	1.33	52.93
Diospyros cayennensis	0.62	0.37	0.64	1.22	54.16
Philodendron acutatum	0.74	0.37	0.52	1.19	55.35
Ormosia monosperma	0.57	0.35	0.66	1.15	56.5
Rourea surinamensis	0.69	0.35	0.53	1.13	57.63
Licania membranacea	0.61	0.34	0.65	1.12	58.75
Mora excelsa	0.74	0.33	0.44	1.08	59.82
Doliocarpus dentatus ssp. *dentatus*	0.65	0.33	0.53	1.07	60.9
Terminalia amazonia	0.55	0.32	0.65	1.06	61.96
Anthurium jenmanii	0.56	0.32	0.66	1.06	63.01
Psychotria poeppigiana	0.56	0.31	0.54	1.02	64.03
Pinzona coriacea	0.62	0.3	0.54	0.98	65.01
Becquerelia cymosa	0.71	0.3	0.44	0.97	65.98
Scleria latifolia	0.62	0.29	0.43	0.94	66.92
Calophyllum lucidum	0.52	0.28	0.53	0.93	67.85
Tovomita eggersii	0.59	0.28	0.53	0.91	68.76
Metaxya rostrata	0.64	0.27	0.43	0.89	69.64
Marlierea ferruginea	0.58	0.26	0.52	0.86	70.5
Tabernaemontana attenuata	0.55	0.26	0.53	0.84	71.34
Philodendron scandens	0.53	0.24	0.54	0.79	72.13
Guzmania lingulata var. *lingulata*	0.5	0.24	0.54	0.78	72.92
Coccoloba ascendens	0.58	0.23	0.42	0.74	73.66
Tapirira guianensis	0.47	0.22	0.44	0.71	74.37
Byrsonima spicata	0.45	0.2	0.43	0.67	75.04
Carapa guianensis	0.46	0.2	0.43	0.64	75.68
Scleria secans	0.52	0.19	0.34	0.61	76.29
Garcinia madruno	0.47	0.19	0.43	0.61	76.89
Eugenia baileyi	0.41	0.17	0.44	0.57	77.46
Cybianthus surinamensis	0.42	0.17	0.44	0.57	78.03
Heliconia hirsuta	0.41	0.17	0.44	0.55	78.58
Pouteria coriacea	0.4	0.17	0.44	0.55	79.13
Miconia affinis	0.46	0.16	0.35	0.52	79.64
Monotagma spicatum	0.5	0.15	0.34	0.49	80.13
Miconia fragrans	0.44	0.15	0.35	0.48	80.61
Manicaria saccifera	0.49	0.14	0.33	0.46	81.08
Parinari campestris	0.38	0.13	0.34	0.44	81.52
Mikania hookeriana	0.4	0.13	0.34	0.42	81.94
Microgramma lycopodioides	0.36	0.13	0.35	0.41	82.35
Guapira eggersiana	0.4	0.12	0.34	0.41	82.75

Brownea coccinea ssp. *capitella*	0.42	0.12	0.34	0.4	83.16
Ilex arimensis	0.36	0.12	0.35	0.4	83.56
Quiina cruegeriana	0.34	0.12	0.35	0.38	83.94
Philodendron fendleri	0.35	0.12	0.35	0.38	84.32
Hirtella racemosa	0.35	0.11	0.35	0.37	84.69
Symphonia globulifera	0.33	0.11	0.35	0.36	85.05
Andira inermis	0.33	0.11	0.35	0.35	85.4
Isertia parviflora	0.41	0.11	0.26	0.35	85.75
Clathrotropis brachypetala	0.42	0.11	0.26	0.34	86.09
Lacistema aggregatum	0.36	0.1	0.26	0.34	86.43
Podocarpus trinitensis	0.4	0.1	0.26	0.31	86.75
Piresia sympodica	0.42	0.09	0.26	0.29	87.04
Clidemia involucrata	0.34	0.09	0.26	0.29	87.34
Oenocarpus bataua var. *oligocarpa*	0.39	0.09	0.26	0.29	87.62
Codonanthe caribaea	0.31	0.09	0.26	0.28	87.9
Philodendron fragrantissimum	0.36	0.08	0.25	0.27	88.18
Abarema jupunba	0.31	0.08	0.26	0.27	88.45
Anemopaegma karstenii	0.36	0.08	0.26	0.27	88.72
Coccoloba marginata	0.38	0.08	0.25	0.27	88.99
Lindsaea lancea	0.35	0.08	0.26	0.26	89.25
Leandra rufescens	0.36	0.08	0.26	0.26	89.51
Bauhinia glabra	0.33	0.08	0.26	0.26	89.76
Mikania psilostachya	0.36	0.08	0.24	0.25	90.02

Group 8A
Average similarity: 33.92

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Sabal mauritiiformis	0.94	0.85	4.99	2.51	2.51
Desmoncus orthacanthos	0.92	0.76	1.8	2.25	4.76
Costus scaber	0.96	0.73	1.8	2.16	6.91
Macfadyena unguis-cati	0.92	0.72	1.87	2.12	9.03
Cecropia peltata	0.86	0.71	1.84	2.1	11.13
Piper marginatum	1.01	0.71	1.24	2.1	13.23
Spondias mombin	0.9	0.69	1.82	2.04	15.27
Zanthoxylum martinicense	0.8	0.68	1.84	2	17.27

Heliconia bihai	0.97	0.65	1.18	1.91	19.18
Trichilia pallida	0.82	0.65	1.9	1.91	21.09
Andira inermis	0.76	0.63	1.93	1.86	22.94
Faramea occidentalis	0.76	0.63	1.93	1.86	24.8
Sapium glandulosum	0.76	0.63	1.93	1.86	26.66
Casearia spinescens	0.81	0.56	1.18	1.64	28.3
Monstera dubia	0.75	0.53	1.21	1.56	29.86
Guapira salicifolia	0.74	0.52	1.24	1.55	31.41
Lygodium venustum	0.76	0.51	1.23	1.52	32.92
Rudgea hostmanniana	0.7	0.51	1.22	1.5	34.42
Cupania americana	0.68	0.5	1.24	1.48	35.9
Dieffenbachia seguine	0.73	0.5	1.24	1.47	37.37
Casearia sylvestris	0.68	0.49	1.25	1.46	38.82
Tabebuia chrysantha	0.71	0.49	1.24	1.45	40.27
Heliconia spathocircinata	0.85	0.49	0.85	1.44	41.72
Ceiba pentandra	0.65	0.48	1.26	1.41	43.13
Piper tuberculatum	0.65	0.41	0.89	1.22	44.34
Urera baccifera	0.7	0.41	0.91	1.2	45.54
Tabernaemontana cymosa	0.62	0.39	0.9	1.15	46.69
Guazuma ulmifolia	0.63	0.39	0.91	1.15	47.84
Olyra latifolia	0.75	0.38	0.69	1.11	48.95
Protium guianense	0.64	0.37	0.91	1.1	50.05
Swartzia pinnata	0.59	0.37	0.91	1.09	51.14
Guapira cuspidata	0.6	0.37	0.92	1.08	52.22
Calathea lutea	0.75	0.36	0.67	1.05	53.27
Brosimum guianense	0.56	0.35	0.92	1.04	54.31
Gouania polygama	0.73	0.35	0.67	1.04	55.35
Xiphidium caeruleum	0.7	0.34	0.67	0.99	56.34
Monstera obliqua	0.7	0.33	0.67	0.96	57.3
Pharus latifolius	0.63	0.31	0.68	0.9	58.2
Miconia acinodendron	0.63	0.3	0.66	0.9	59.1
Attalea maripa	0.65	0.3	0.69	0.89	59.99
Bactris major	0.68	0.3	0.66	0.89	60.88
Entada polystachya	0.57	0.29	0.68	0.87	61.75
Coccoloba latifolia	0.53	0.28	0.69	0.82	62.57
Castilla elastica ssp. *elastica*	0.58	0.28	0.69	0.82	63.39
Eschweilera subglandulosa	0.54	0.27	0.68	0.8	64.19
Prionostemma aspera	0.57	0.27	0.69	0.79	64.98
Inga ingoides	0.51	0.27	0.69	0.79	65.76
Cordia collococca	0.51	0.26	0.69	0.77	66.54
Wulffia baccata	0.63	0.26	0.52	0.77	67.3
Phryganocydia corymbosa	0.63	0.25	0.53	0.75	68.05
Rollinia exsucca	0.49	0.25	0.7	0.75	68.8

Oeceoclades maculata	0.54	0.25	0.69	0.75	69.55
Cordia bicolor	0.48	0.25	0.7	0.74	70.29
Martinella obovata	0.59	0.23	0.51	0.67	70.96
Sterculia pruriens var. *glabrescens*	0.53	0.22	0.51	0.66	71.62
Panicum pilosum	0.59	0.22	0.52	0.63	72.26
Brosimum alicastrum	0.54	0.21	0.52	0.62	72.87
Casearia guianensis	0.53	0.21	0.52	0.61	73.48
Paullinia fuscescens	0.51	0.2	0.51	0.6	74.08
Hylocereus lemairei	0.52	0.2	0.52	0.58	74.66
Cordia curassavica	0.49	0.19	0.53	0.56	75.22
Sarcoglottis metallica	0.44	0.18	0.53	0.54	75.76
Euterpe precatoria	0.51	0.18	0.51	0.54	76.3
Roystonea oleracea	0.48	0.18	0.52	0.54	76.84
Adiantum obliquum	0.56	0.18	0.39	0.52	77.36
Flemingia strobilifera	0.46	0.18	0.53	0.52	77.88
Schefflera morototoni	0.42	0.17	0.52	0.51	78.39
Warszewiczia coccinea	0.42	0.17	0.53	0.5	78.88
Ficus maxima	0.42	0.17	0.53	0.49	79.38
Trichilia pleeana	0.41	0.17	0.53	0.49	79.86
Brownea coccinea ssp. *capitella*	0.39	0.16	0.53	0.48	80.34
Clathrotropis brachypetala	0.39	0.16	0.53	0.48	80.82
Protium sagotianum	0.39	0.16	0.53	0.48	81.3
Thelypteris poiteana	0.45	0.15	0.38	0.44	81.74
Stachytarpheta cayennensis	0.48	0.15	0.38	0.43	82.17
Hymenocallis tubiflora	0.46	0.14	0.37	0.42	82.59
Prestonia quinquangularis	0.41	0.13	0.38	0.39	82.98
Ceratophytum tetragonolobum	0.45	0.13	0.38	0.39	83.37
Tournefortia hirsutissima	0.44	0.13	0.38	0.39	83.76
Paullinia pinnata	0.47	0.12	0.38	0.37	84.12
Psiguria umbrosa	0.38	0.12	0.39	0.37	84.49
Smilax cumanensis	0.37	0.12	0.39	0.34	84.83
Momordica charantia	0.43	0.12	0.37	0.34	85.18
Lundia corymbifera	0.43	0.12	0.38	0.34	85.52
Cissus verticillata	0.38	0.12	0.38	0.34	85.86
Coccoloba venosa	0.37	0.11	0.39	0.34	86.2
Scleria latifolia	0.41	0.11	0.38	0.33	86.52
Philodendron acutatum	0.38	0.11	0.38	0.32	86.84
Bromelia plumieri	0.35	0.11	0.39	0.32	87.16
Gonzalagunia spicata	0.33	0.11	0.39	0.32	87.47
Guarea guidonia	0.35	0.11	0.38	0.31	87.79

Desmoncus polyacanthos	0.35	0.11	0.39	0.31	88.1
Pterocarpus rohrii	0.34	0.11	0.39	0.31	88.41
Erythrina poeppigiana	0.35	0.1	0.38	0.31	88.72
Solanum stramoniifolium	0.33	0.1	0.39	0.3	89.02
Genipa americana	0.33	0.1	0.39	0.29	89.31
Nectandra pearcei	0.31	0.1	0.39	0.28	89.59
Cyperus simplex	0.41	0.09	0.26	0.26	89.85
Orthoclada laxa	0.43	0.09	0.26	0.25	90.1

Group 9A
Average similarity: 22.78

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Piper marginatum	1.1	0.89	1.46	3.91	3.91
Paullinia leiocarpa	1.06	0.88	1.48	3.88	7.79
Brosimum alicastrum	1.02	0.77	0.82	3.37	11.16
Spondias mombin	0.82	0.73	1.46	3.19	14.35
Phryganocydia corymbosa	1.02	0.69	0.88	3.02	17.38
Olyra latifolia	1.02	0.68	0.78	2.97	20.35
Oeceoclades maculata	1.1	0.67	0.82	2.92	23.27
Melicoccus bijugatus	0.91	0.61	0.82	2.66	25.93
Trichilia pallida	0.85	0.58	0.89	2.57	28.5
Coursetia ferruginea	0.89	0.54	0.82	2.37	30.86
Cordia panamensis	0.81	0.49	0.86	2.14	33
Psiguria umbrosa	0.74	0.46	0.9	2.04	35.04
Cupania americana	0.62	0.42	0.9	1.83	36.87
Maranta gibba	0.73	0.42	0.9	1.83	38.71
Bromelia plumieri	0.78	0.42	0.59	1.83	40.54
Sabal mauritiiformis	0.74	0.35	0.61	1.55	42.08
Cordia curassavica	0.66	0.34	0.57	1.51	43.59
Mansoa verrucifera	0.69	0.33	0.61	1.44	45.03
Arrabidaea patellifera	0.7	0.31	0.61	1.38	46.41
Gouania polygama	0.7	0.31	0.61	1.38	47.79
Hura crepitans	0.59	0.31	0.59	1.35	49.14
Anthurium jenmanii	0.7	0.3	0.59	1.32	50.46
Lygodium venustum	0.7	0.29	0.59	1.29	51.76
Chiococca alba	0.68	0.29	0.39	1.29	53.05
Cecropia peltata	0.54	0.29	0.6	1.29	54.34
Macfadyena unguis-cati	0.64	0.29	0.59	1.29	55.63

Smilax cumanensis	0.54	0.29	0.6	1.28	56.91
Maclura tinctoria	0.53	0.29	0.6	1.27	58.18
Cedrela odorata	0.53	0.28	0.6	1.23	59.41
Ceiba pentandra	0.53	0.28	0.6	1.22	60.63
Protium sagotianum	0.57	0.26	0.59	1.16	61.79
Hiraea reclinata	0.53	0.26	0.61	1.15	62.94
Casearia guianensis	0.53	0.26	0.6	1.15	64.09
Croton gossypiifolius	0.63	0.26	0.38	1.14	65.22
Cordia collococca	0.49	0.24	0.61	1.05	66.27
Genipa americana	0.54	0.23	0.61	1.02	67.3
Guazuma ulmifolia	0.48	0.23	0.61	1.02	68.32
Zanthoxylum martinicense	0.48	0.23	0.61	1.02	69.34
Hamelia patens	0.61	0.19	0.39	0.85	70.18
Cyperus simplex	0.57	0.18	0.39	0.78	70.97
Casearia spinescens	0.5	0.18	0.39	0.78	71.74
Bactris major	0.52	0.17	0.39	0.73	72.47
Lasiacis anomala	0.52	0.17	0.4	0.73	73.2
Rudgea hostmanniana	0.53	0.16	0.39	0.72	73.92
Adiantum villosum	0.45	0.16	0.4	0.71	74.63
Hymenaea courbaril	0.51	0.16	0.37	0.7	75.33
Desmoncus orthacanthos	0.5	0.15	0.4	0.66	75.99
Dieffenbachia seguine	0.46	0.15	0.38	0.65	76.64
Wulffia baccata	0.51	0.14	0.38	0.64	77.27
Erythrina poeppigiana	0.41	0.14	0.39	0.64	77.91
Costus scaber	0.4	0.14	0.38	0.63	78.54
Diospyros inconstans	0.52	0.14	0.38	0.6	79.14
Scleria melaleuca	0.41	0.13	0.39	0.58	79.72
Bursera simaruba	0.38	0.13	0.39	0.57	80.29
Guapira salicifolia	0.38	0.13	0.39	0.57	80.86
Passiflora tuberosa	0.37	0.13	0.39	0.55	81.41
Commelina obliqua	0.44	0.12	0.39	0.55	81.96
Adiantum petiolatum	0.45	0.12	0.39	0.54	82.5
Lantana camara	0.44	0.12	0.22	0.53	83.02
Swartzia simplex	0.43	0.12	0.39	0.52	83.55
Morisonia americana	0.39	0.12	0.4	0.52	84.06
Nectandra martinicensis	0.37	0.12	0.4	0.51	84.57
Tabernaemontana cymosa	0.37	0.12	0.4	0.51	85.07
Aphelandra pulcherrima	0.52	0.11	0.22	0.49	85.56
Guapira cuspidata	0.36	0.11	0.4	0.49	86.05
Capparis hastata	0.34	0.11	0.4	0.48	86.53
Sapium glandulosum	0.34	0.11	0.4	0.48	87.01
Adiantum lucidum	0.42	0.1	0.22	0.46	87.47
Prionostemma aspera	0.49	0.09	0.22	0.4	87.87

Cissus verticillata	0.45	0.08	0.22	0.35	88.21
Randia armata	0.45	0.07	0.22	0.31	88.53
Machaerium robiniifolium	0.45	0.07	0.22	0.3	88.83
Securidaca lophosoma	0.45	0.07	0.22	0.3	89.14
Serjania caracasana	0.43	0.07	0.22	0.29	89.43
Bredemeyera lucida	0.45	0.07	0.22	0.29	89.72
Petrea volubilis	0.51	0.07	0.22	0.29	90.01

Group 10A
Average similarity: 23.53

Species	**Av. Abund**	**Av. Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Cissus verticillata	1.08	0.97	1.88	4.12	4.12
Smilax cumanensis	1	0.9	1.81	3.81	7.93
Spondias mombin	0.93	0.76	1.17	3.25	11.17
Flemingia strobilifera	1.01	0.76	1.2	3.24	14.41
Cecropia peltata	0.98	0.76	1.16	3.23	17.65
Bromelia plumieri	0.87	0.73	1.25	3.12	20.77
Cordia curassavica	0.83	0.69	1.2	2.94	23.71
Andira inermis	0.78	0.59	0.91	2.51	26.22
Psidium guajava	0.84	0.58	0.9	2.47	28.68
Cordia collococca	0.78	0.54	0.91	2.3	30.99
Casearia guianensis	0.73	0.52	0.88	2.21	33.2
Piper marginatum	0.79	0.51	0.88	2.18	35.37
Oeceoclades maculata	0.78	0.51	0.89	2.17	37.55
Solanum hirtum	0.72	0.51	0.89	2.16	39.7
Wulffia baccata	0.8	0.42	0.68	1.78	41.48
Tabebuia chrysantha	0.66	0.41	0.69	1.72	43.2
Acroceras zizanioides	0.67	0.39	0.69	1.66	44.86
Sabal mauritiiformis	0.73	0.39	0.69	1.65	46.52
Senna bacillaris	0.66	0.38	0.67	1.6	48.12
Guapira salicifolia	0.62	0.37	0.67	1.57	49.69
Blechum pyramidatum	0.64	0.36	0.67	1.54	51.23
Costus scaber	0.61	0.36	0.68	1.53	52.76
Genipa americana	0.6	0.35	0.68	1.49	54.25
Sapium glandulosum	0.6	0.35	0.68	1.48	55.73
Phryganocydia corymbosa	0.76	0.34	0.51	1.45	57.19
Heliconia bihai	0.67	0.31	0.52	1.33	58.51
Scleria melaleuca	0.62	0.3	0.52	1.29	59.8

Roystonea oleracea	0.57	0.27	0.52	1.14	60.95
Cissampelos pareira	0.5	0.25	0.53	1.05	62
Cupania americana	0.52	0.24	0.51	1	63
Gouania polygama	0.57	0.23	0.51	1	64
Piper tuberculatum	0.5	0.23	0.51	0.98	64.98
Desmodium incanum	0.55	0.23	0.51	0.97	65.95
Guazuma ulmifolia	0.5	0.22	0.51	0.95	66.9
Diospyros inconstans	0.53	0.22	0.51	0.95	67.85
Desmoncus orthacanthos	0.54	0.22	0.52	0.94	68.79
Paspalum fasciculatum	0.65	0.22	0.38	0.94	69.72
Stachytarpheta cayennensis	0.47	0.21	0.52	0.91	70.63
Panicum maximum	0.57	0.19	0.39	0.8	71.43
Casearia sylvestris	0.45	0.17	0.39	0.73	72.16
Mimosa pigra	0.49	0.17	0.39	0.72	72.88
Sapindus saponaria	0.48	0.16	0.39	0.69	73.57
Stigmaphyllon finlayanum	0.49	0.16	0.39	0.69	74.26
Prestonia quinquangularis	0.43	0.15	0.37	0.66	74.91
Lygodium venustum	0.42	0.15	0.39	0.65	75.56
Lantana trifolia	0.43	0.15	0.37	0.63	76.19
Lasiacis anomala	0.45	0.13	0.37	0.57	76.76
Malachra fasciata	0.4	0.13	0.38	0.57	77.32
Mangifera indica	0.4	0.13	0.38	0.56	77.89
Passiflora foetida	0.38	0.13	0.38	0.55	78.44
Albizia niopoides var. *niopoides*	0.38	0.13	0.38	0.55	78.98
Brosimum alicastrum	0.4	0.13	0.38	0.54	79.53
Casearia spinescens	0.39	0.13	0.38	0.54	80.07
Enicostema verticillatum	0.37	0.12	0.38	0.52	80.59
Corchorus siliquosus	0.35	0.1	0.26	0.41	80.99
Heliconia psittacorum	0.42	0.09	0.26	0.4	81.39
Rottboellia cochinchinensis	0.39	0.09	0.26	0.4	81.79
Adiantum obliquum	0.41	0.09	0.26	0.39	82.18
Ochroma pyramidale	0.35	0.09	0.26	0.38	82.57
Stachytarpheta jamaicensis	0.35	0.09	0.26	0.38	82.94
Merremia umbellata	0.38	0.09	0.26	0.36	83.31
Adiantum villosum	0.33	0.08	0.26	0.36	83.67
Solanum stramoniifolium	0.33	0.08	0.26	0.35	84.02
Vismia cayennensis	0.33	0.08	0.26	0.35	84.37
Rhynchosia minima	0.4	0.08	0.26	0.35	84.72
Justicia secunda	0.33	0.08	0.26	0.35	85.07

Zanthoxylum martinicense	0.33	0.08	0.26	0.35	85.42
Trema micrantha	0.33	0.08	0.26	0.34	85.76
Chromolaena odorata	0.32	0.08	0.26	0.34	86.1
Tabebuia rosea	0.31	0.08	0.26	0.33	86.43
Mandevilla subsagittata	0.32	0.08	0.26	0.33	86.76
Lasiacis ligulata	0.37	0.08	0.26	0.33	87.09
Commelina erecta	0.39	0.08	0.26	0.33	87.42
Cedrela odorata	0.31	0.08	0.26	0.32	87.74
Lonchocarpus domingensis	0.3	0.08	0.26	0.32	88.06
Borreria remota	0.33	0.07	0.26	0.32	88.38
Hura crepitans	0.31	0.07	0.26	0.31	88.69
Maclura tinctoria	0.3	0.07	0.26	0.31	89
Paullinia pinnata	0.31	0.07	0.26	0.31	89.31
Tabernaemontana cymosa	0.32	0.07	0.25	0.3	89.6
Macfadyena unguis-cati	0.32	0.07	0.26	0.29	89.89
Ruellia tuberosa	0.3	0.07	0.26	0.28	90.18

Table B.1: SIMPER analysis results for the RBS collection of vascular plants within Trinidad.

Appendix C

Present, Future and Change (from present to future) maps of Bioclim variables selected for SDM analyses

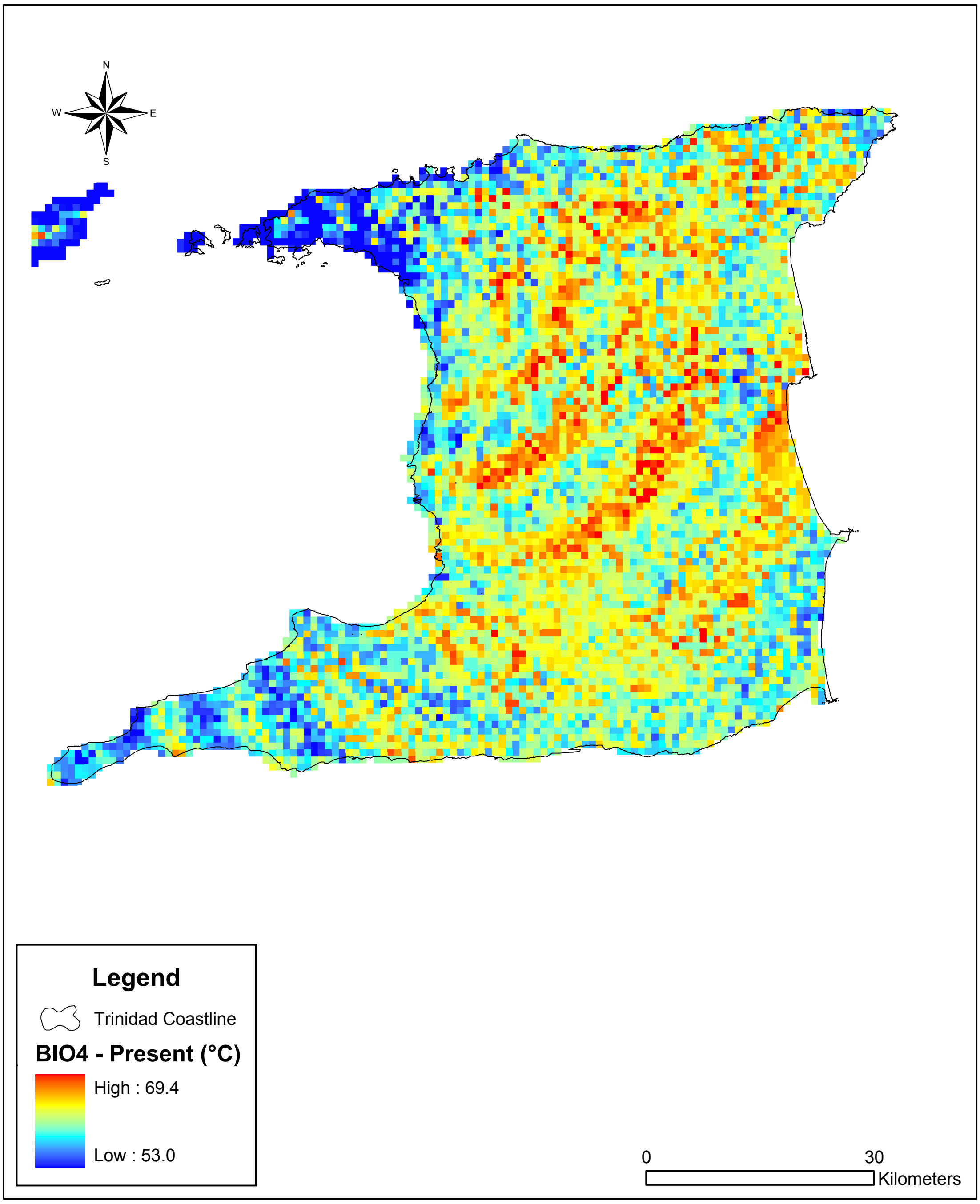


Figure C.1: BIO4 (Temperature seasonality) across Trinidad for the present climate.

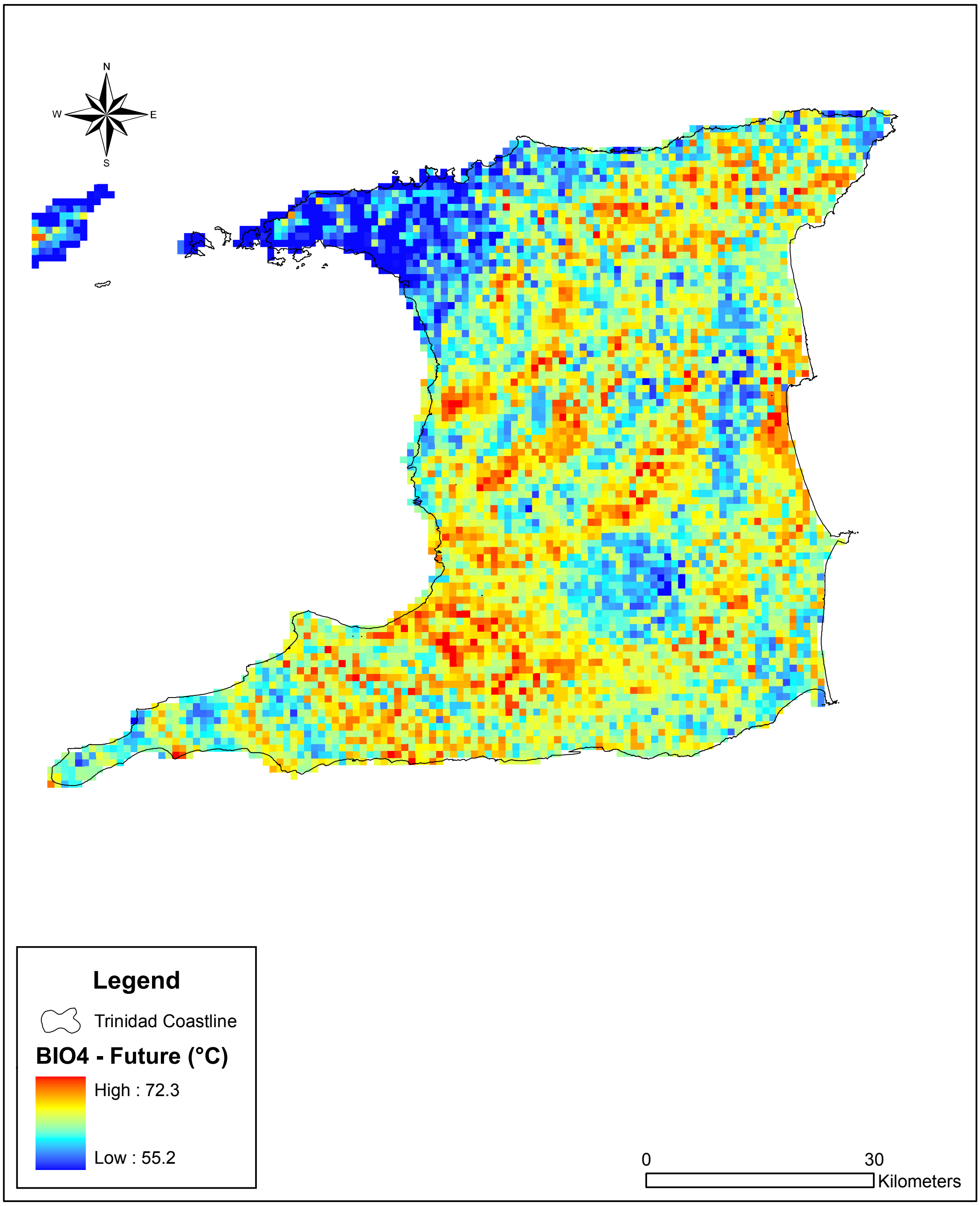


Figure C.2: BIO4 (Temperature seasonality) across Trinidad for the future (SRES A2 scenario) climate.

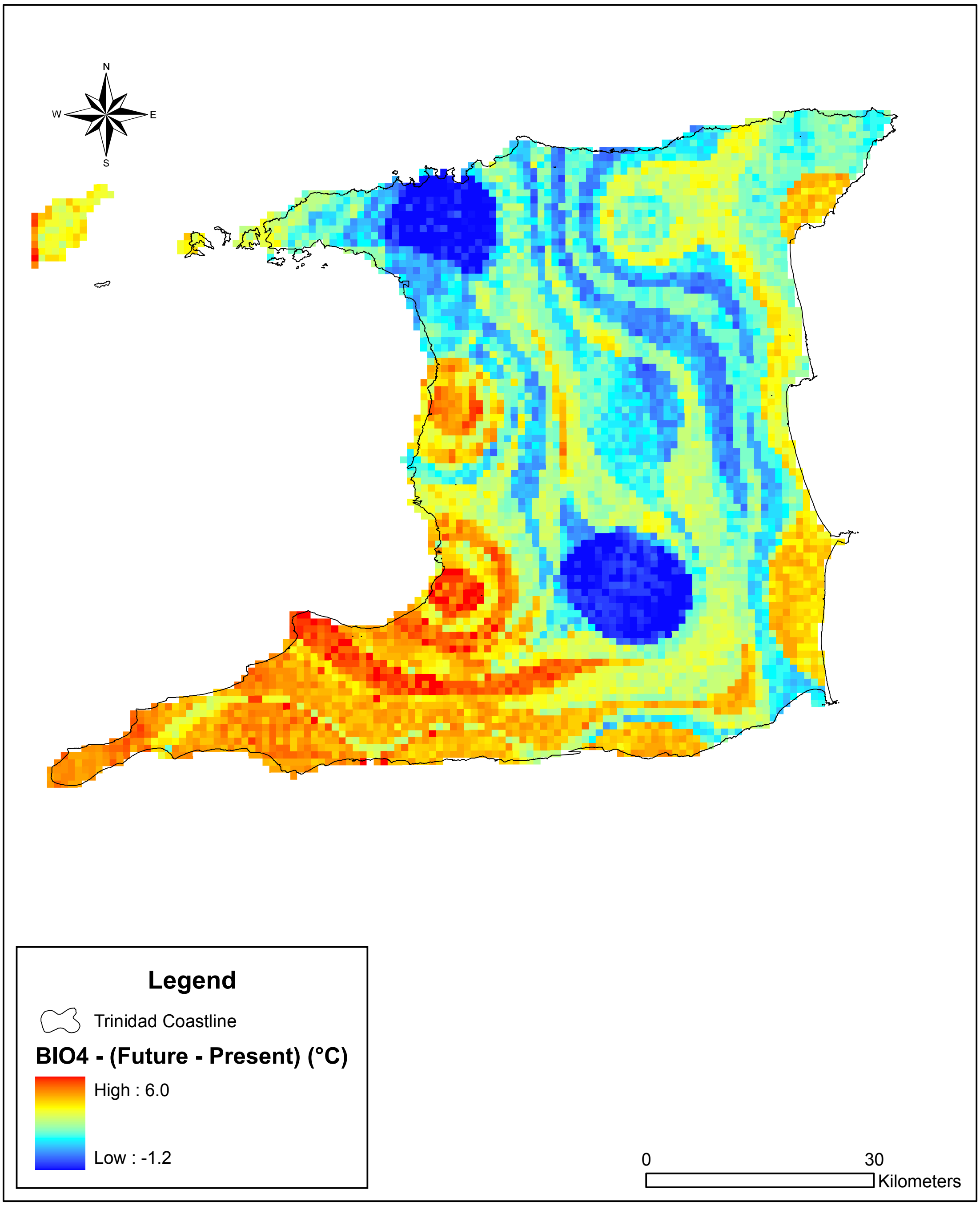


Figure C.3: Change in BIO4 (Temperature seasonality) across Trinidad between the present and future (SRES A2 scenario) climates.

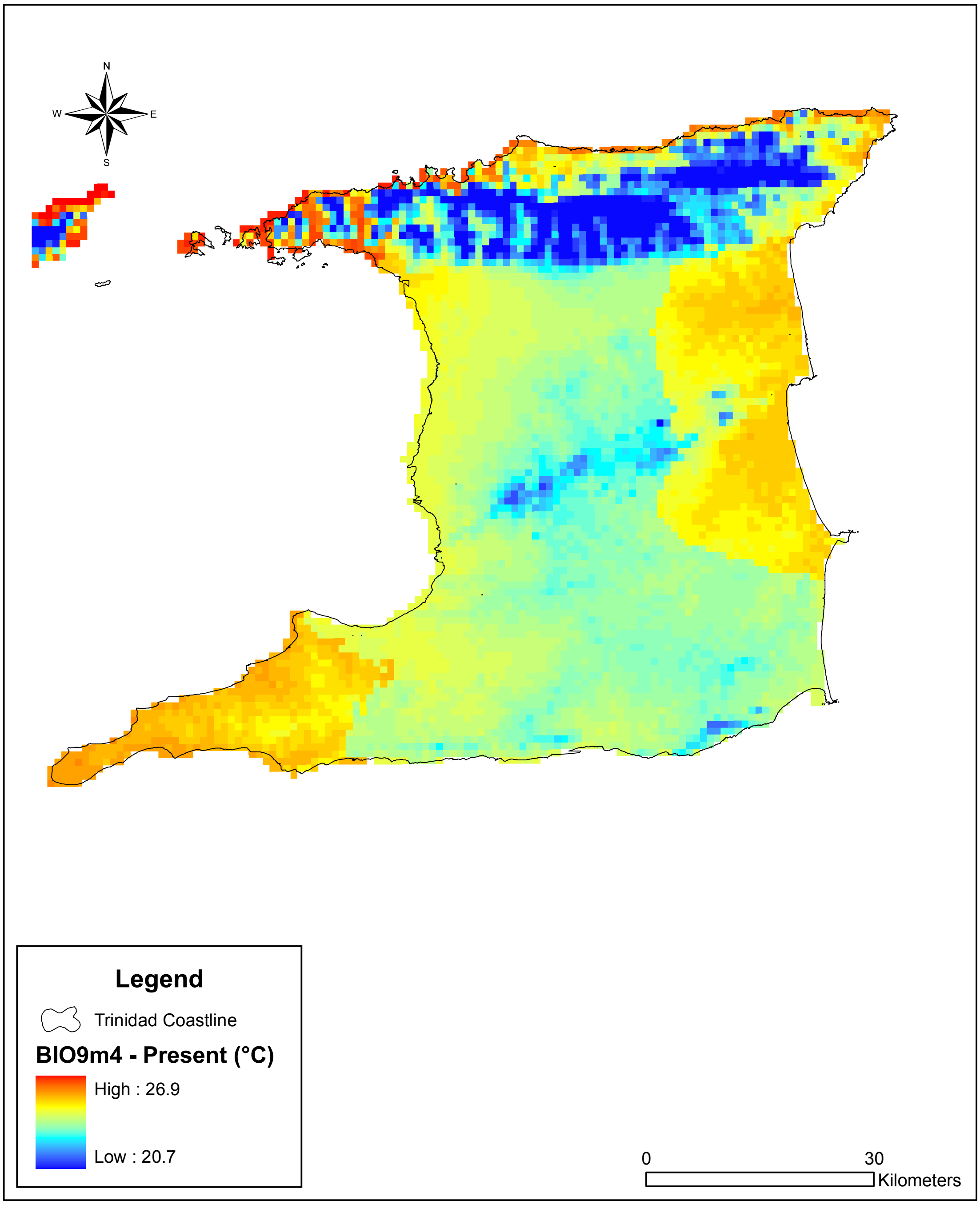


Figure C.4: BIO9m4 (Mean temperature of driest consecutive 4 month period) across Trinidad for present the climate.

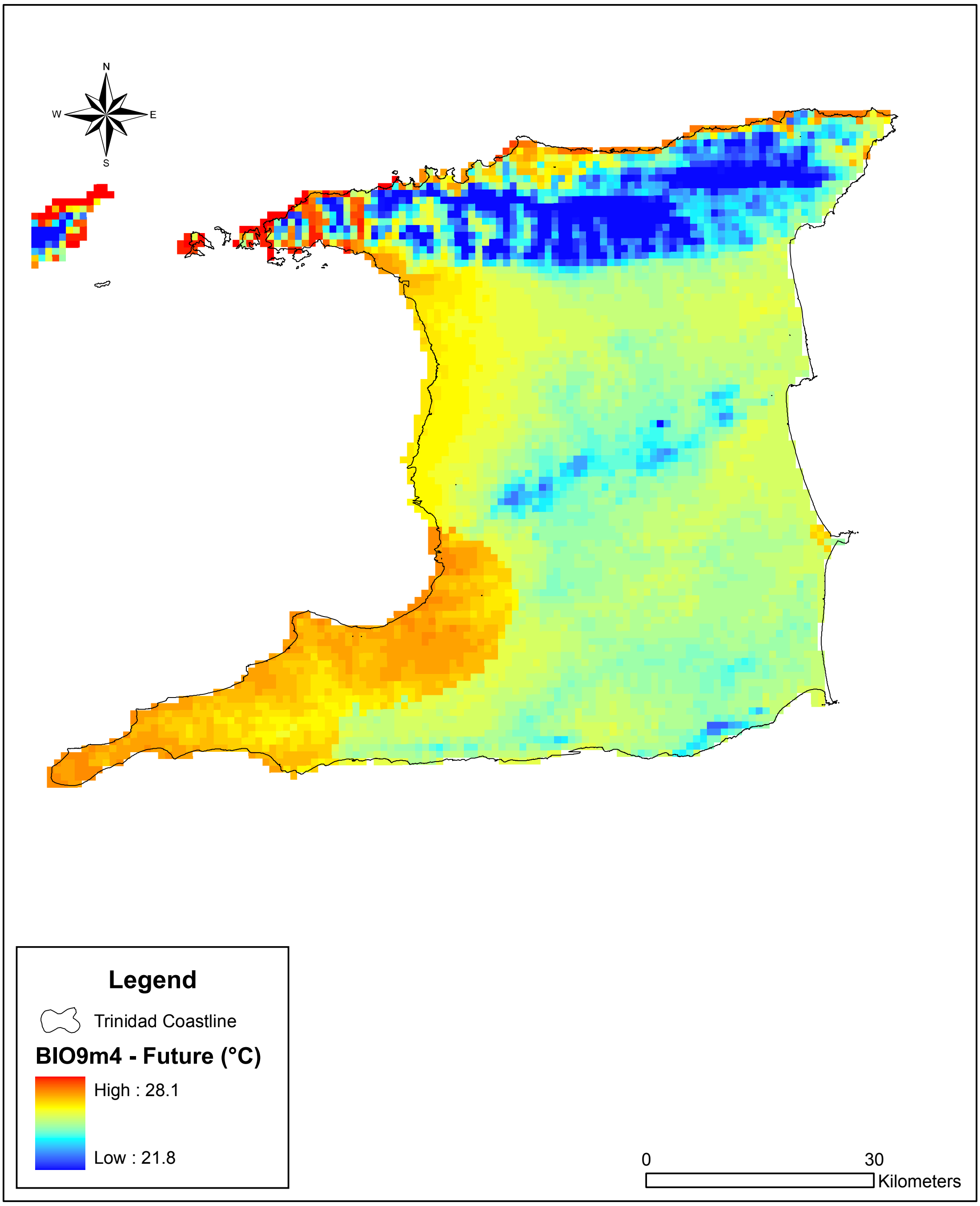


Figure C.5: BIO9m4 (Mean temperature of driest consecutive 4 month period) across Trinidad for the future (SRES A2 scenario) climate.

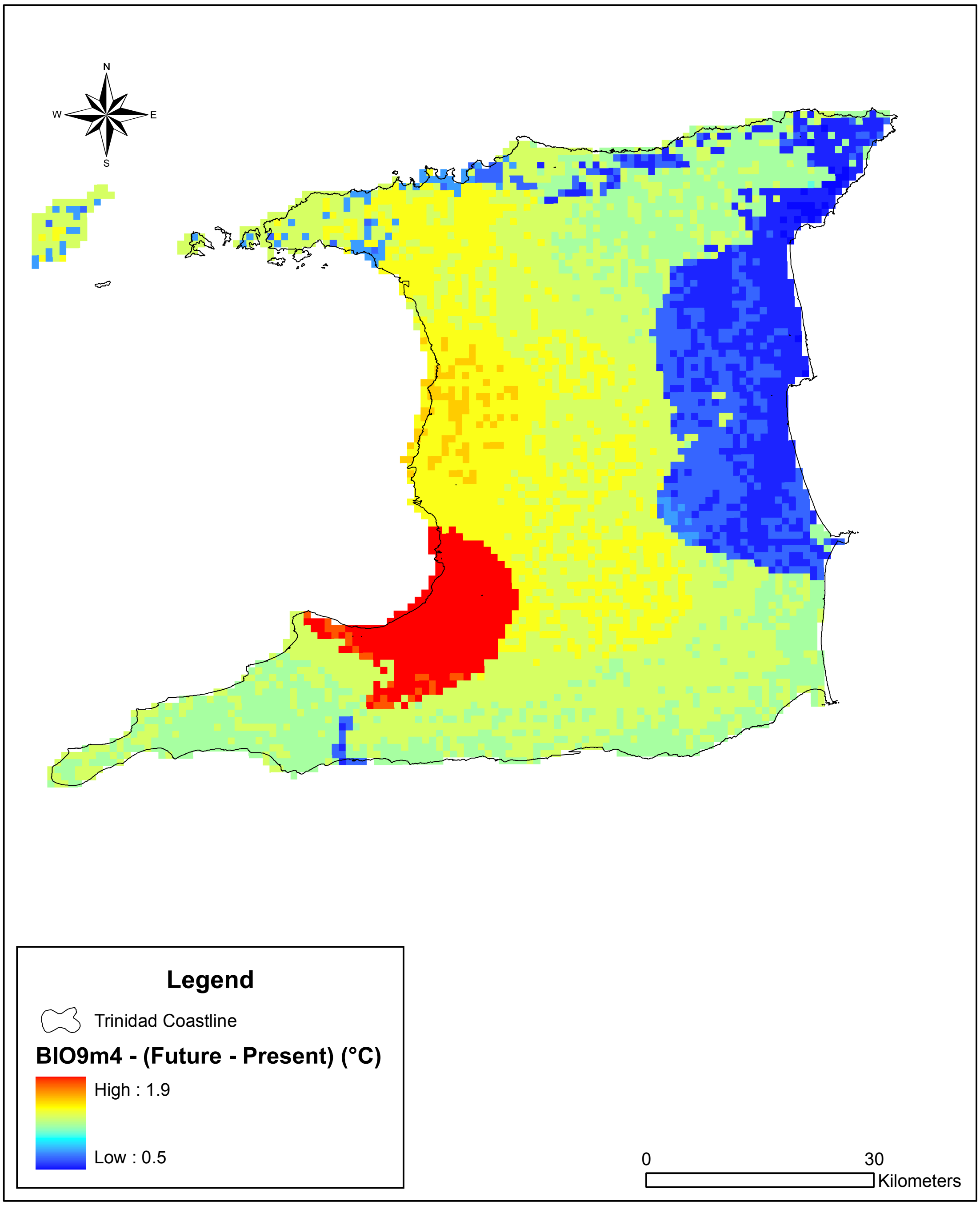


Figure C.6: Change in BIO9m4 (Mean temperature of driest consecutive 4 month period) across Trinidad between the present and future (SRES A2 scenario) climates.

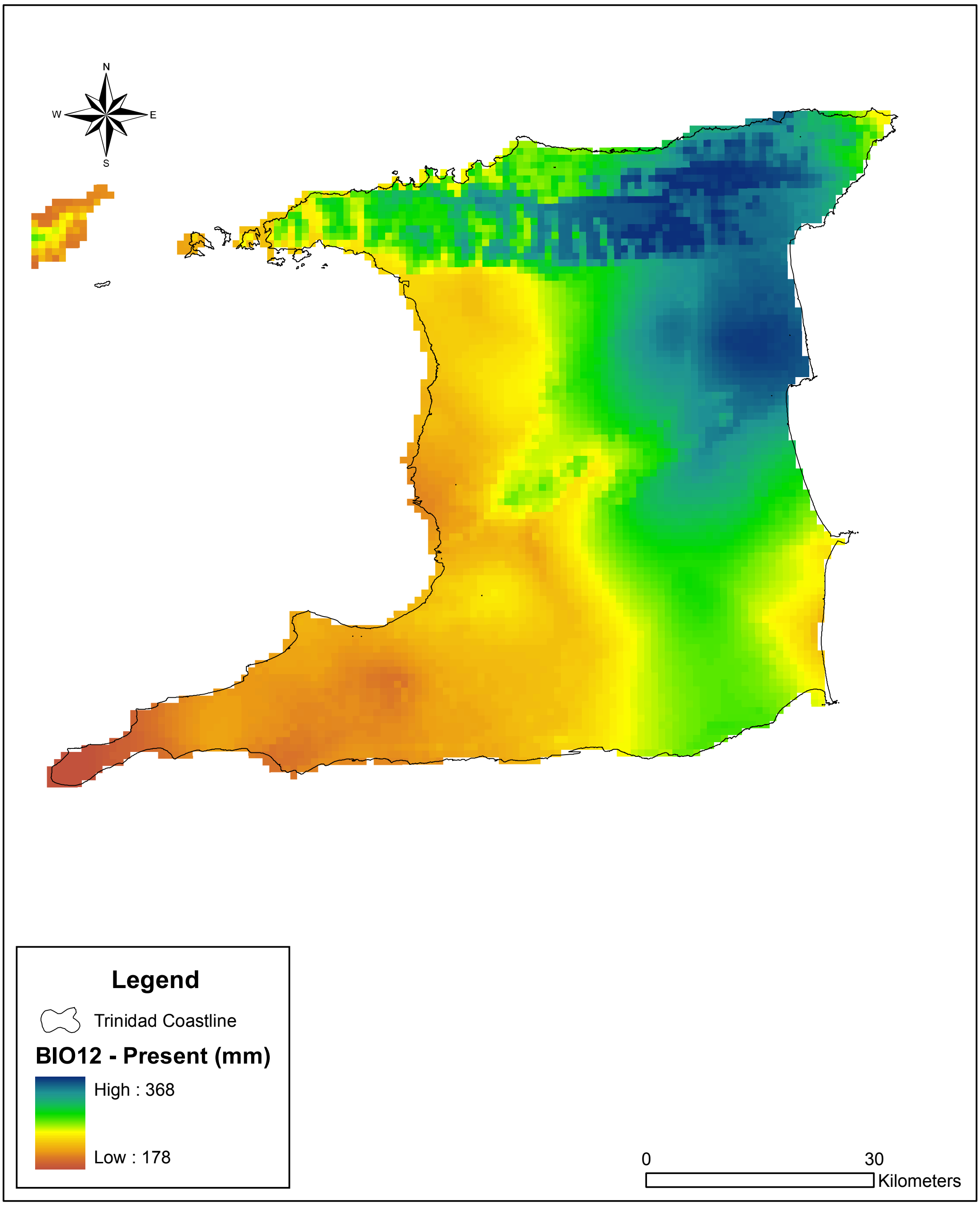


Figure C.7: BIO12 (Annual precipitation) across Trinidad for present climate.

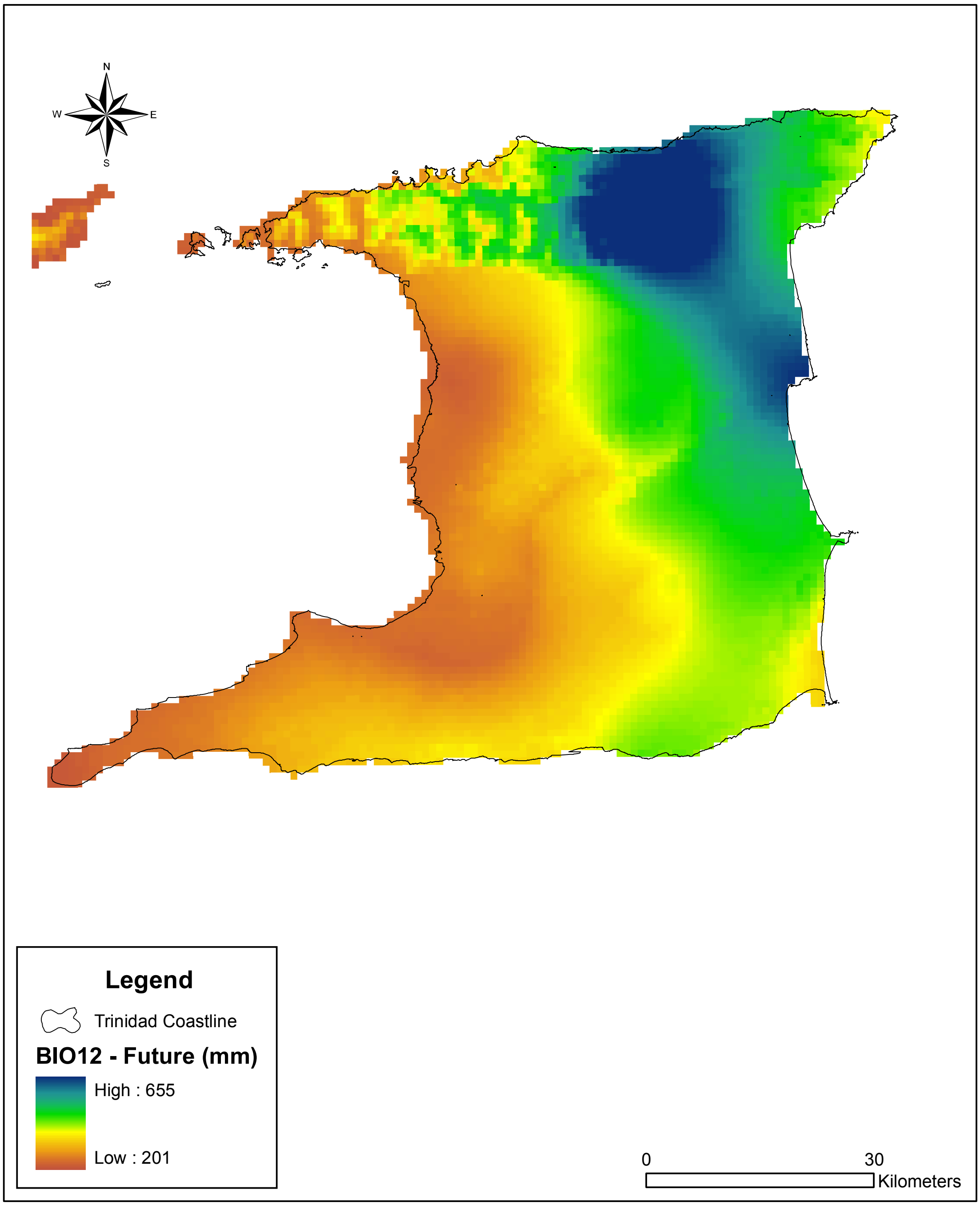


Figure C.8: BIO12 (Annual precipitation) across Trinidad for the future (SRES A2 scenario) climate.

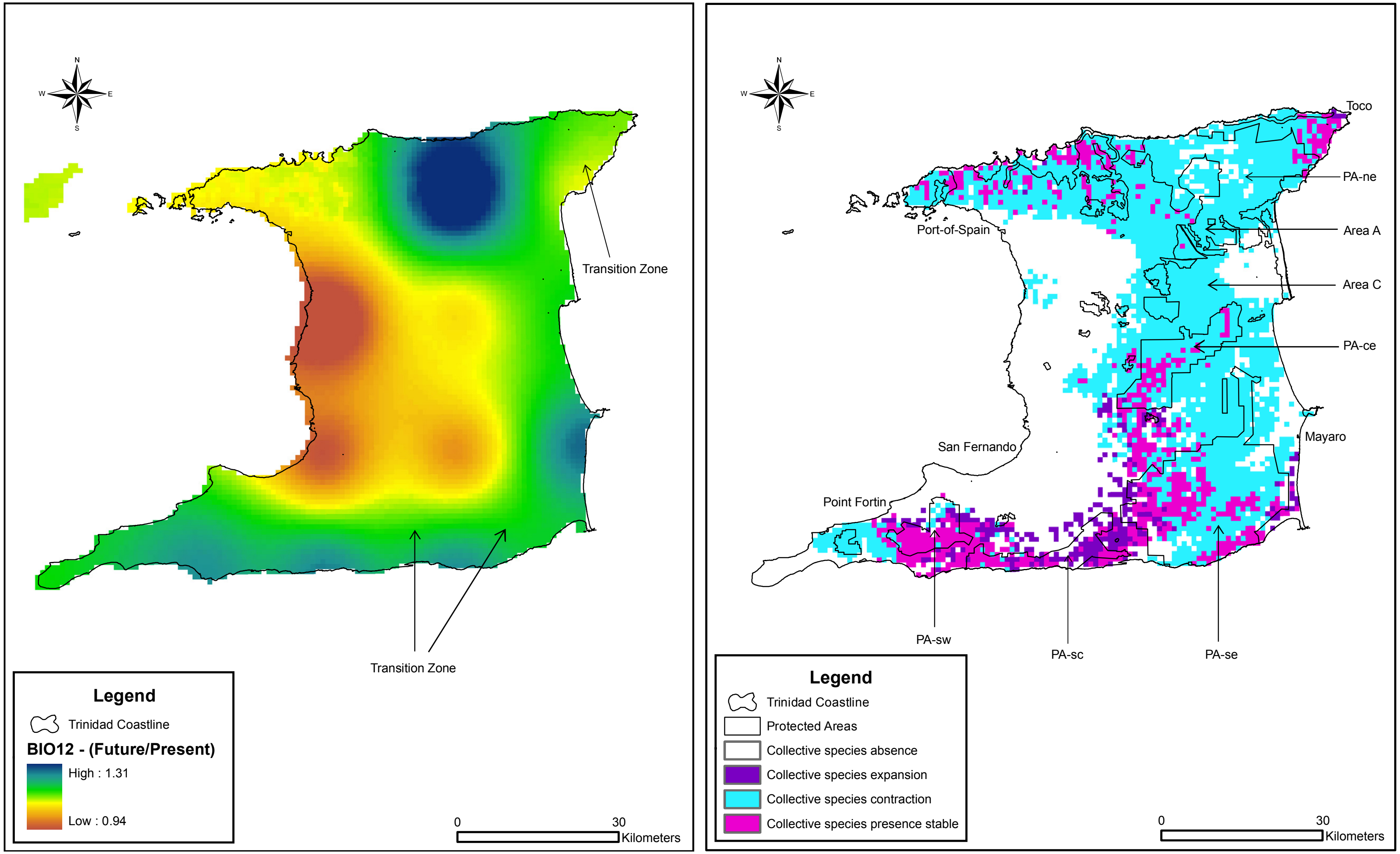


Figure C.9: Change in BIO12 (Annual precipitation) across Trinidad between the present and future (SRES A2 scenario) climates compared to Collective Species Change Map.

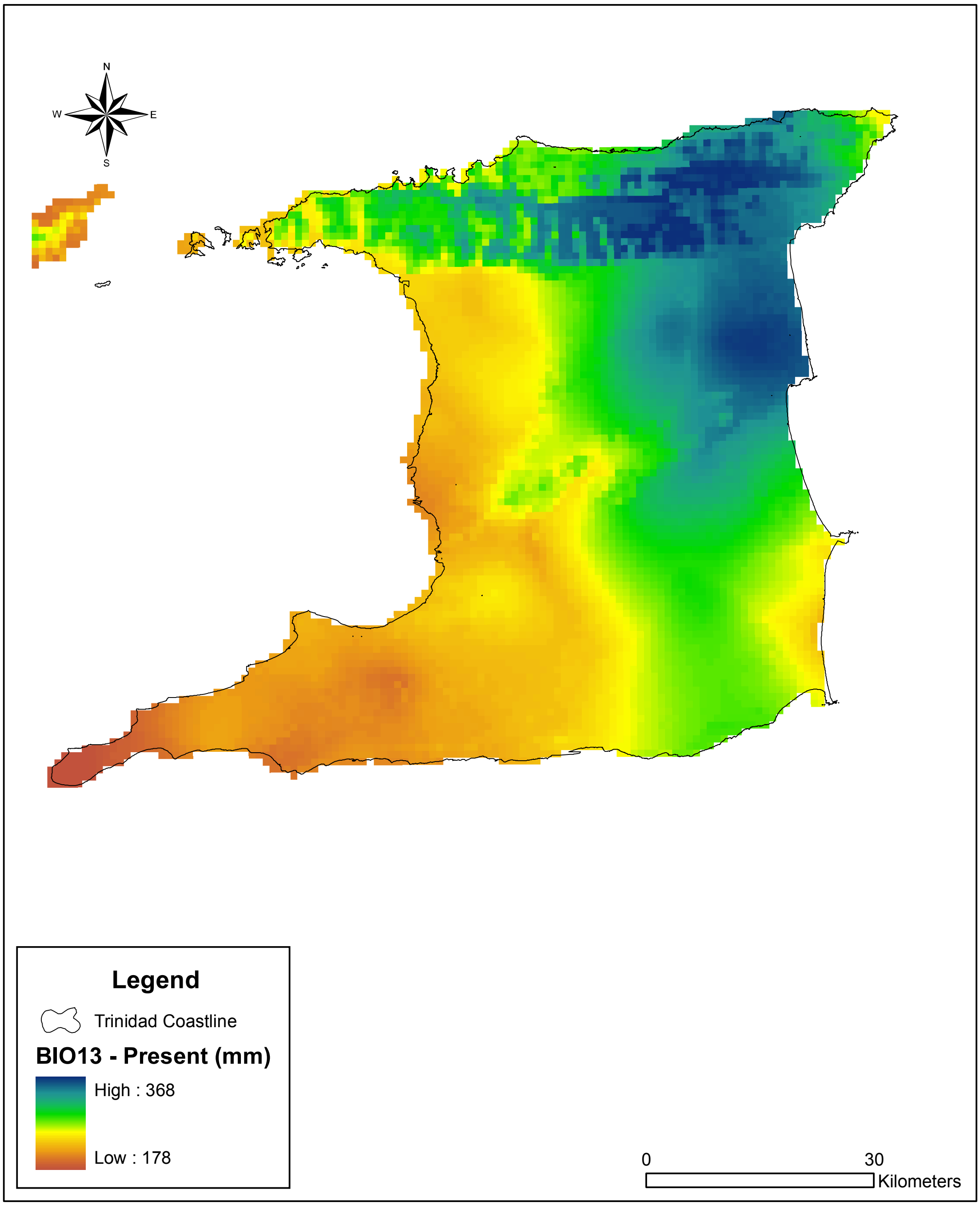


Figure C.10: BIO13 (Precipitation of wettest month) across Trinidad for present climate.

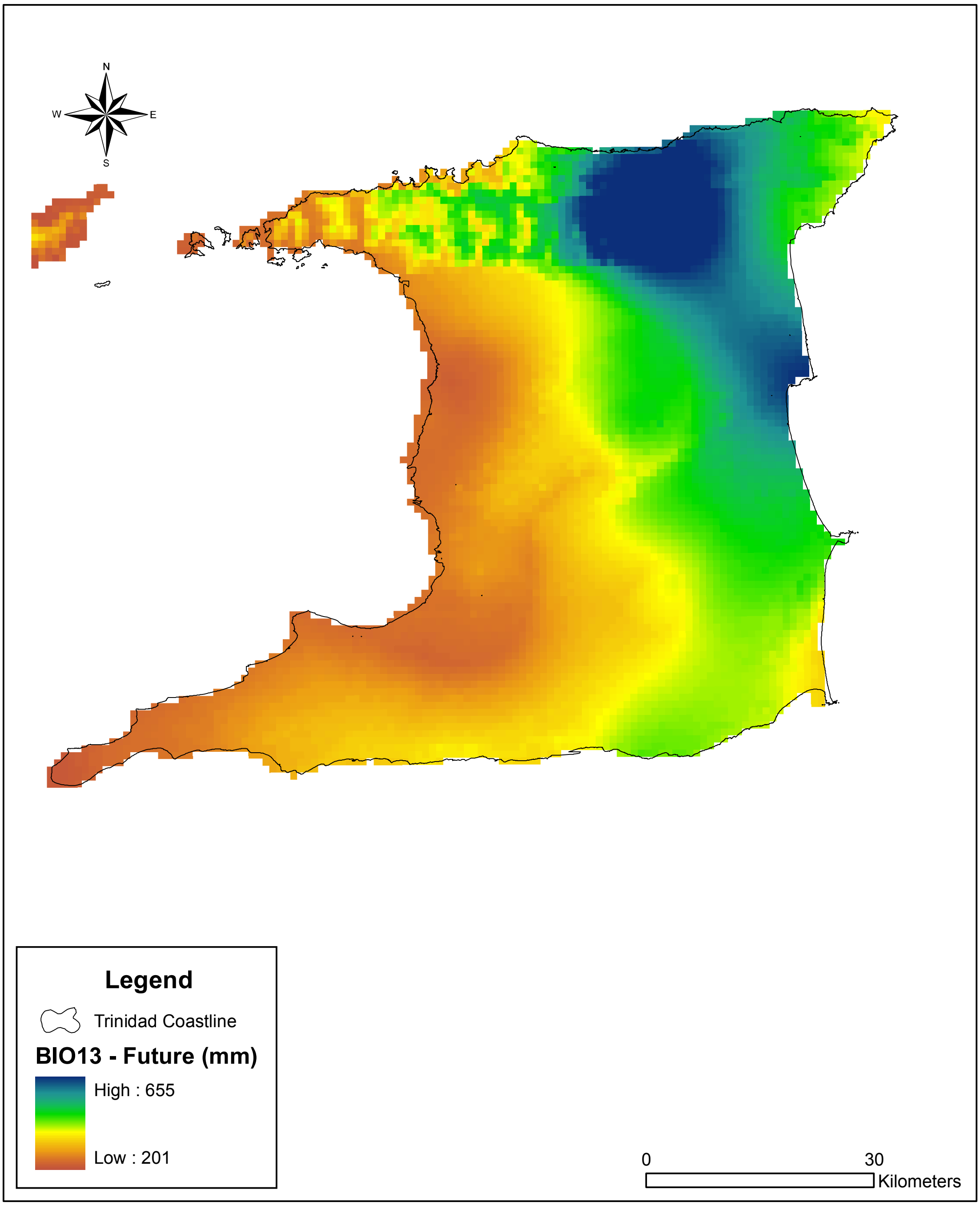


Figure C.11: BIO13 (Precipitation of wettest month) across Trinidad for the future (SRES A2 scenario) climate.

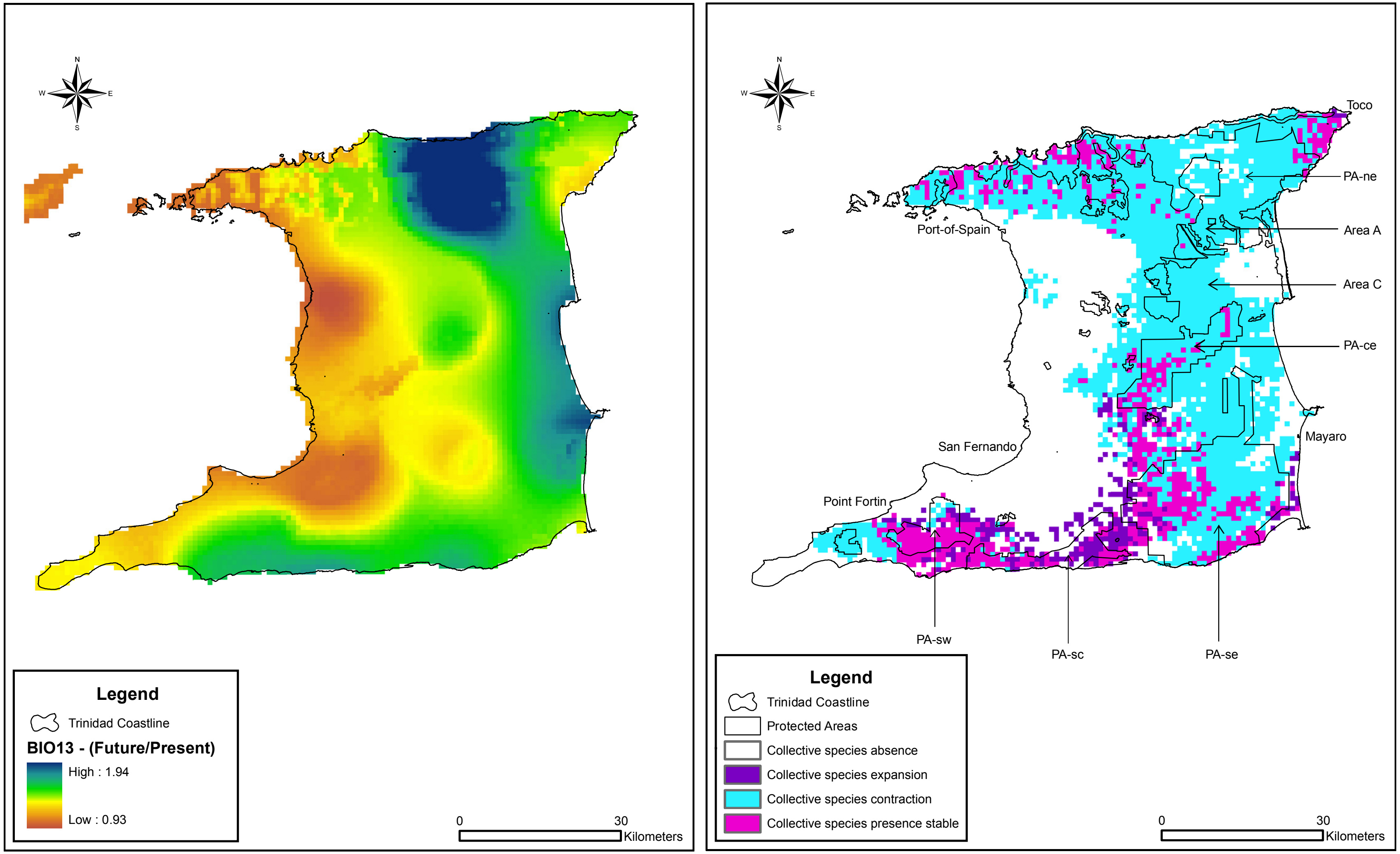


Figure C.12: Change in BIO13 (Precipitation of wettest month) across Trinidad between the present and future (SRES A2 scenario) climates compared to Collective Species Change Map.

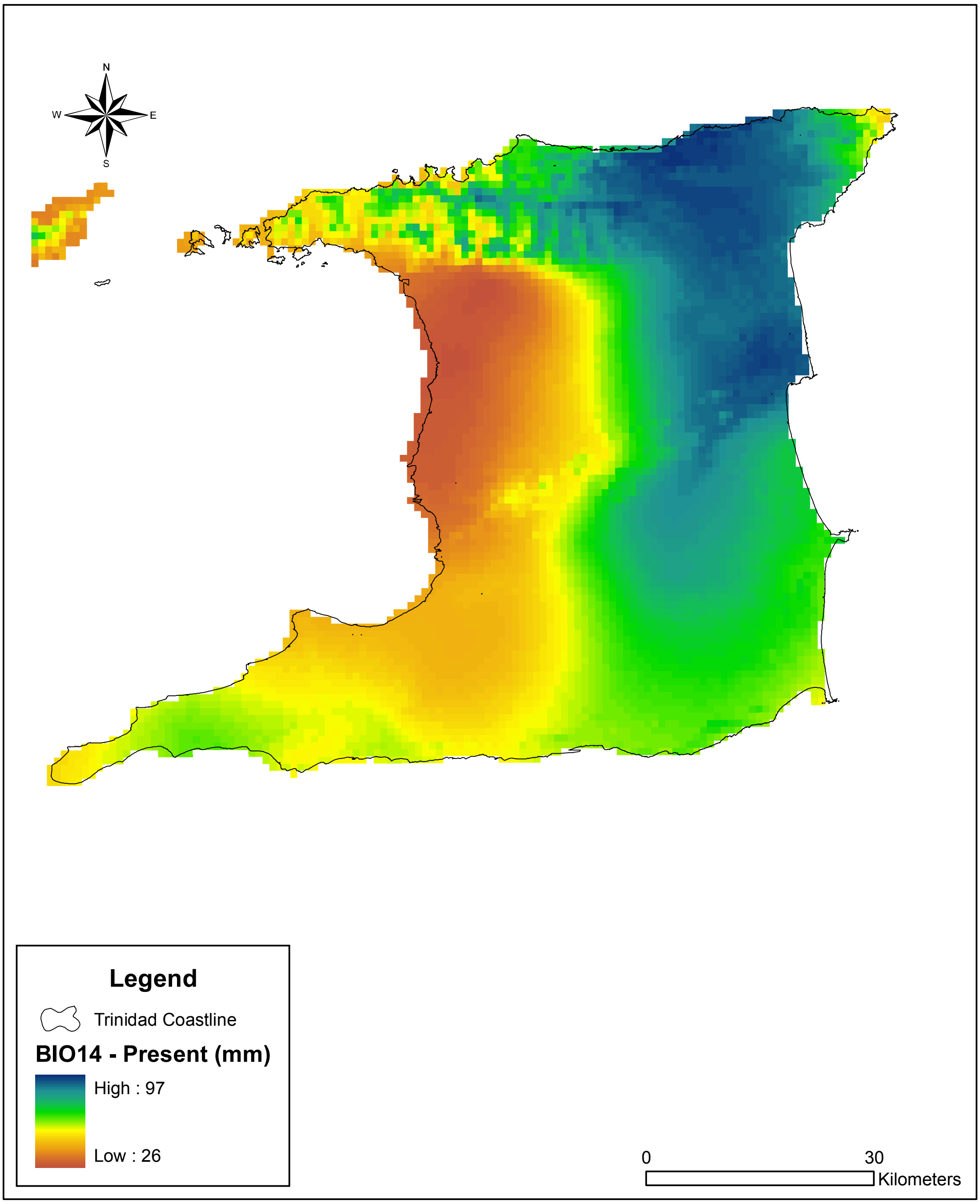


Figure C.13: BIO14 (Precipitation of driest month) across Trinidad for present climate.

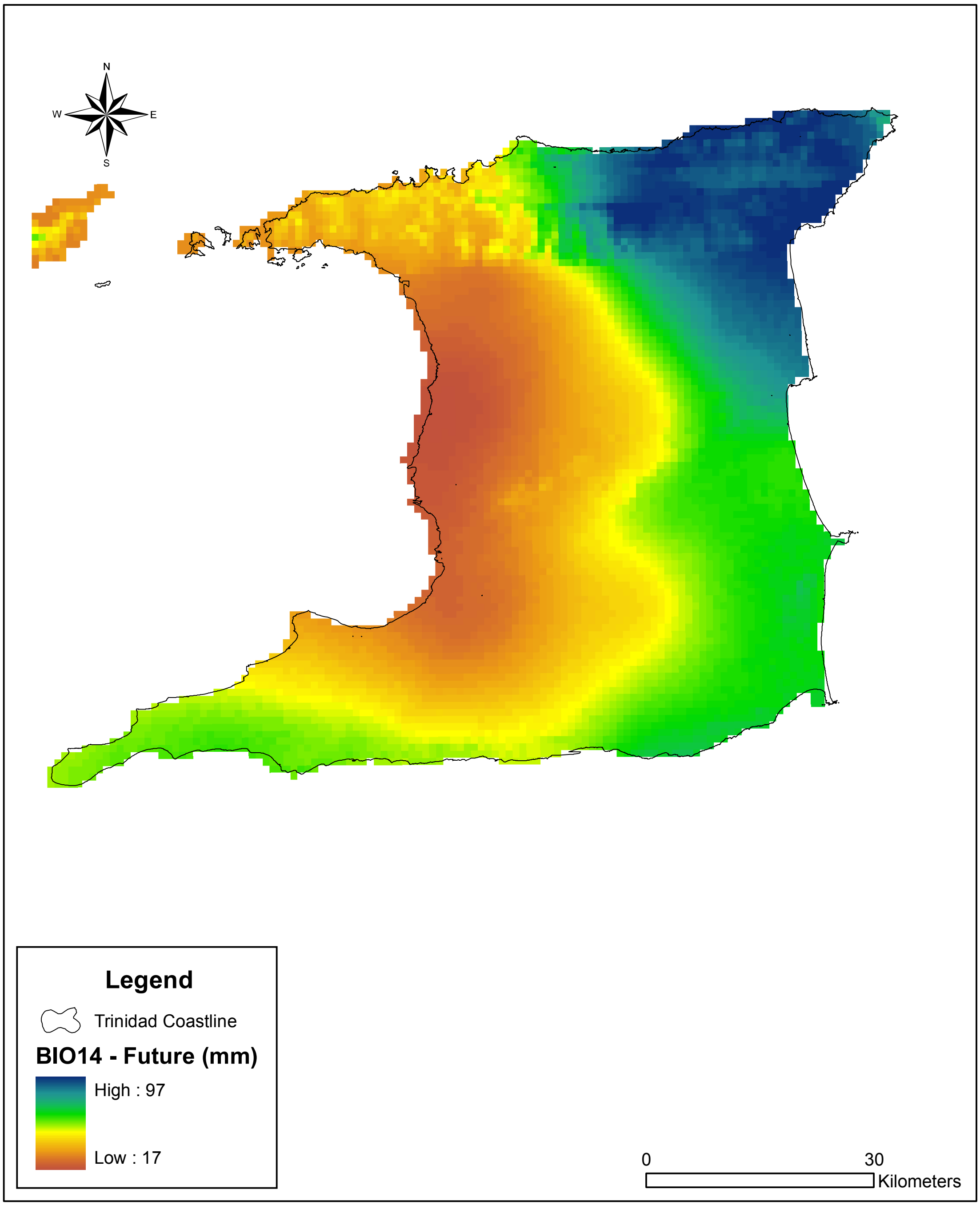


Figure C.14: BIO14 (Precipitation of driest month) across Trinidad for the future (SRES A2 scenario) climate.

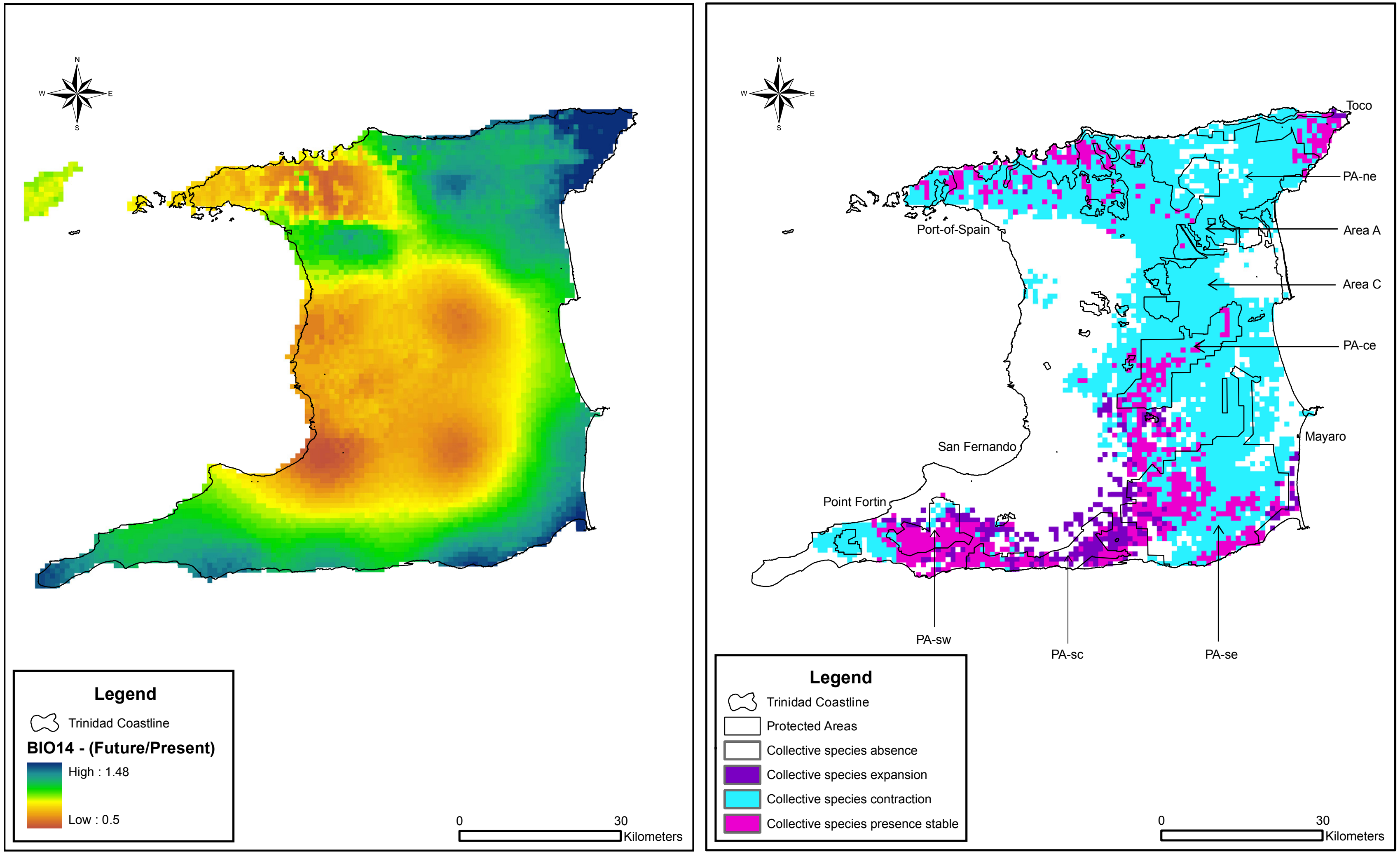


Figure C.15: Change in BIO14 (Precipitation of driest month) across Trinidad between the present and future (SRES A2 scenario) climates compared to Collective Species Change Map.

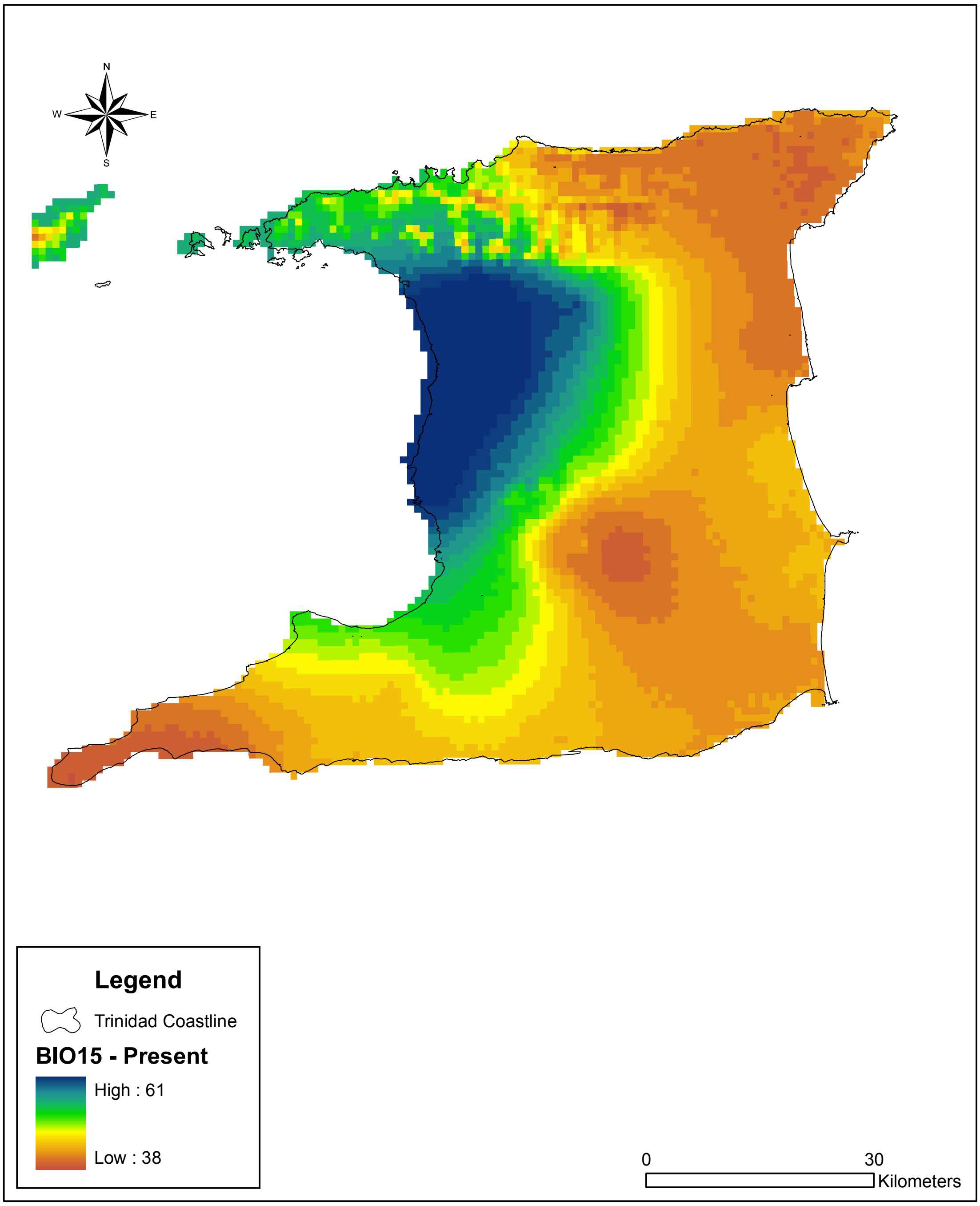


Figure C.16: BIO15 (Precipitation seasonality) across Trinidad for present climate.

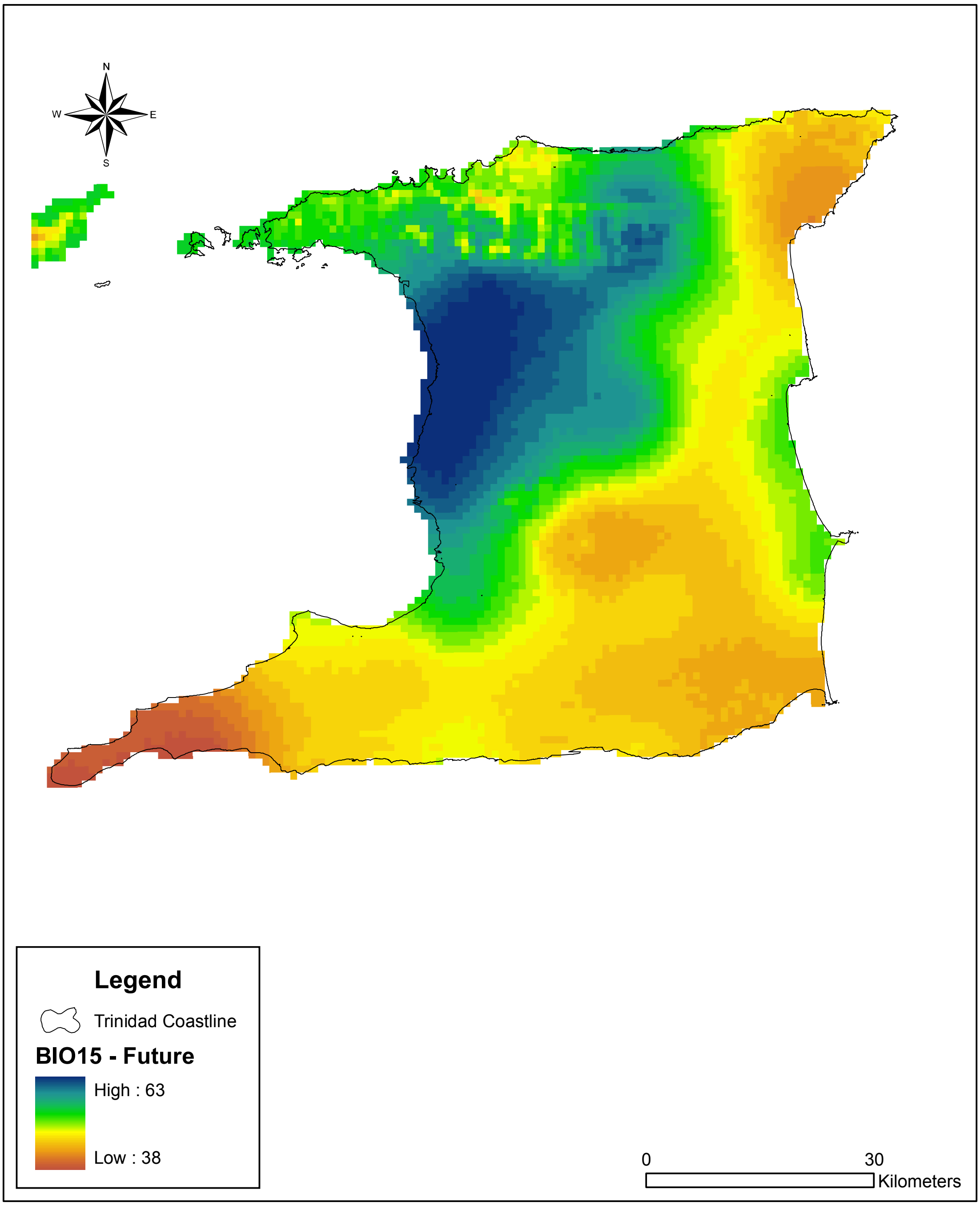


Figure C.17: BIO15 (Precipitation seasonality) across Trinidad for the future (SRES A2 scenario) climate.

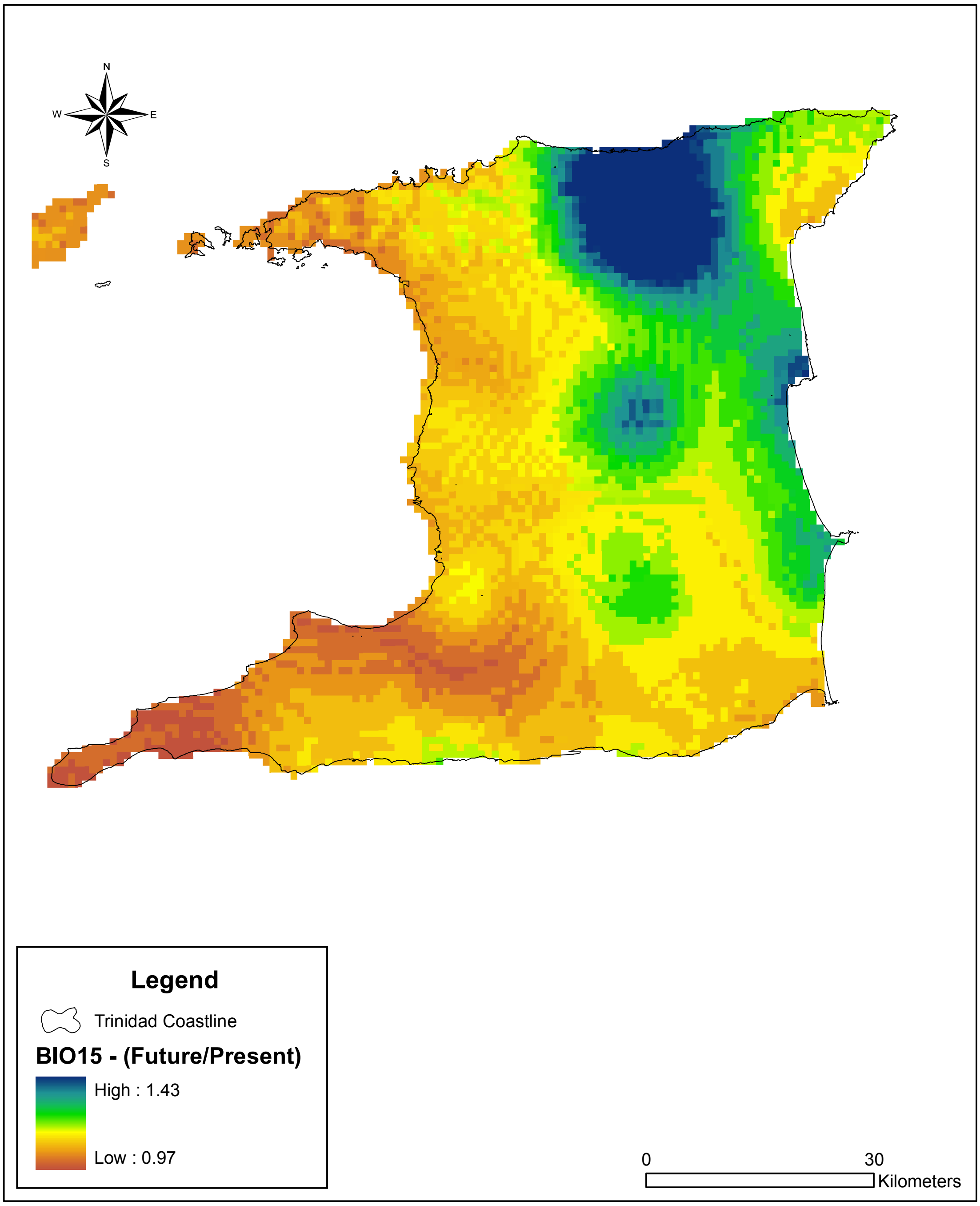


Figure C.18: Change in BIO15 (Precipitation seasonality) across Trinidad between the present and future (SRES A2 scenario) climates.

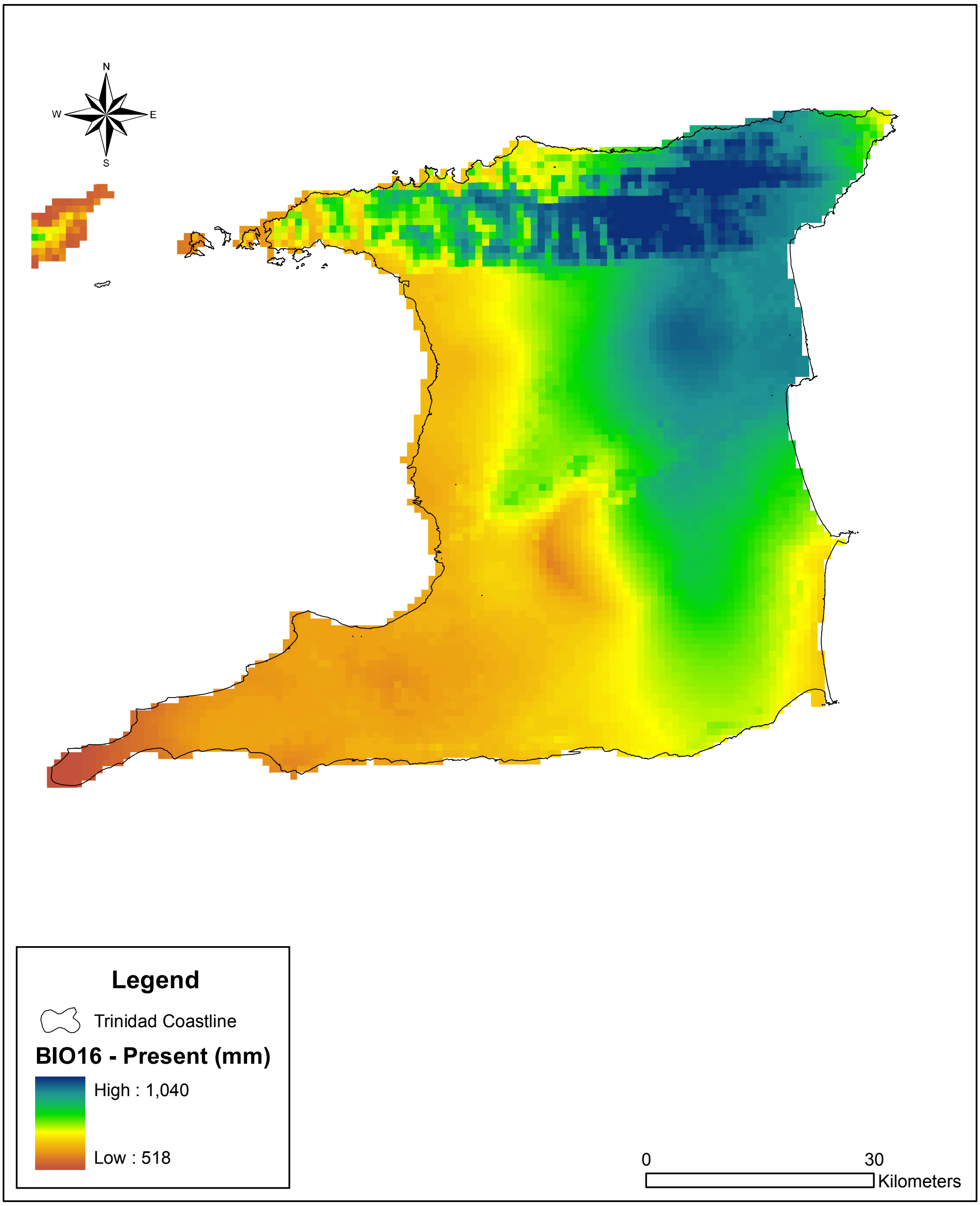


Figure C.19: BIO16 (Precipitation of wettest quarter) across Trinidad for present climate.

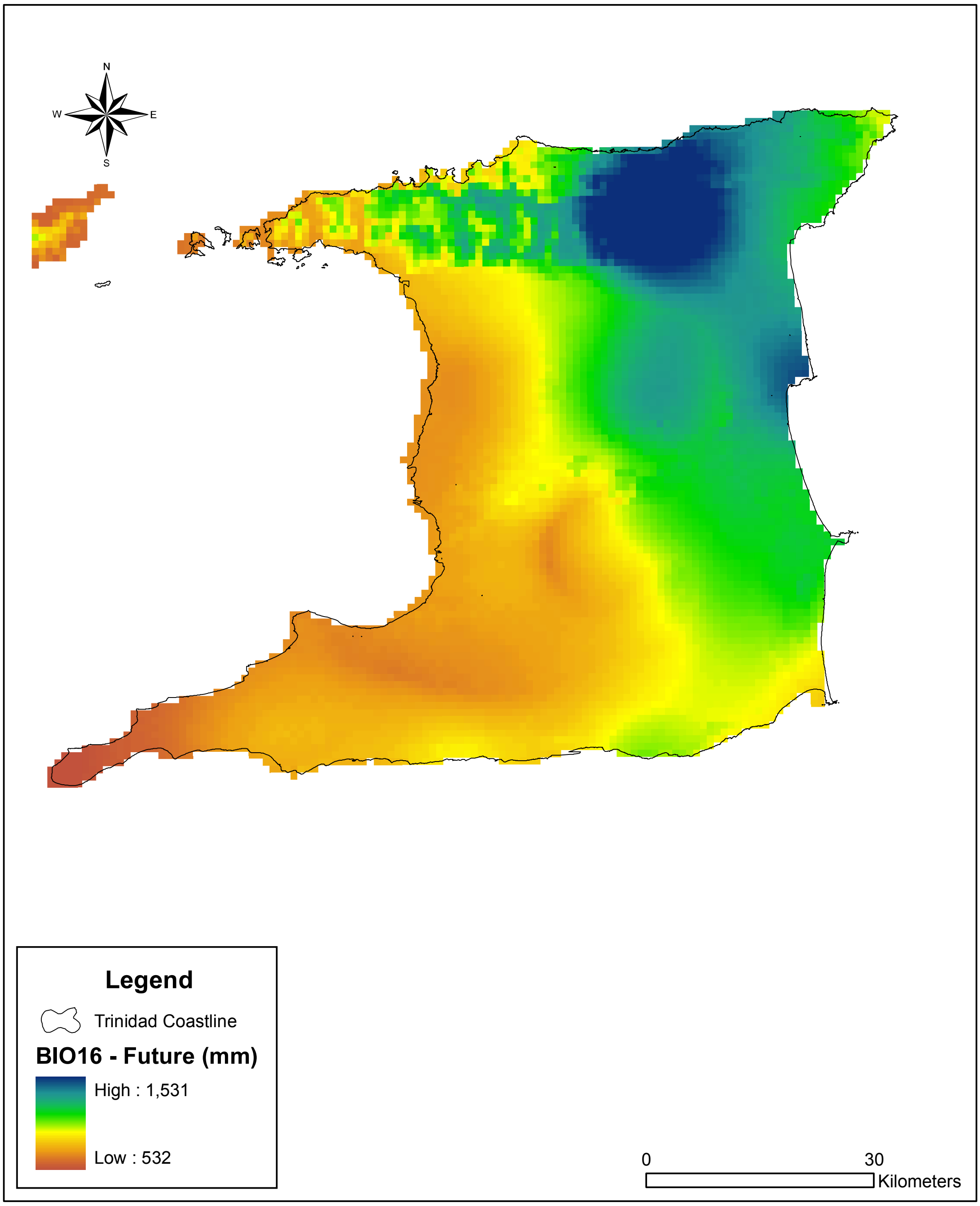


Figure C.20: BIO16 (Precipitation of wettest quarter) across Trinidad for the future (SRES A2 scenario) climate.

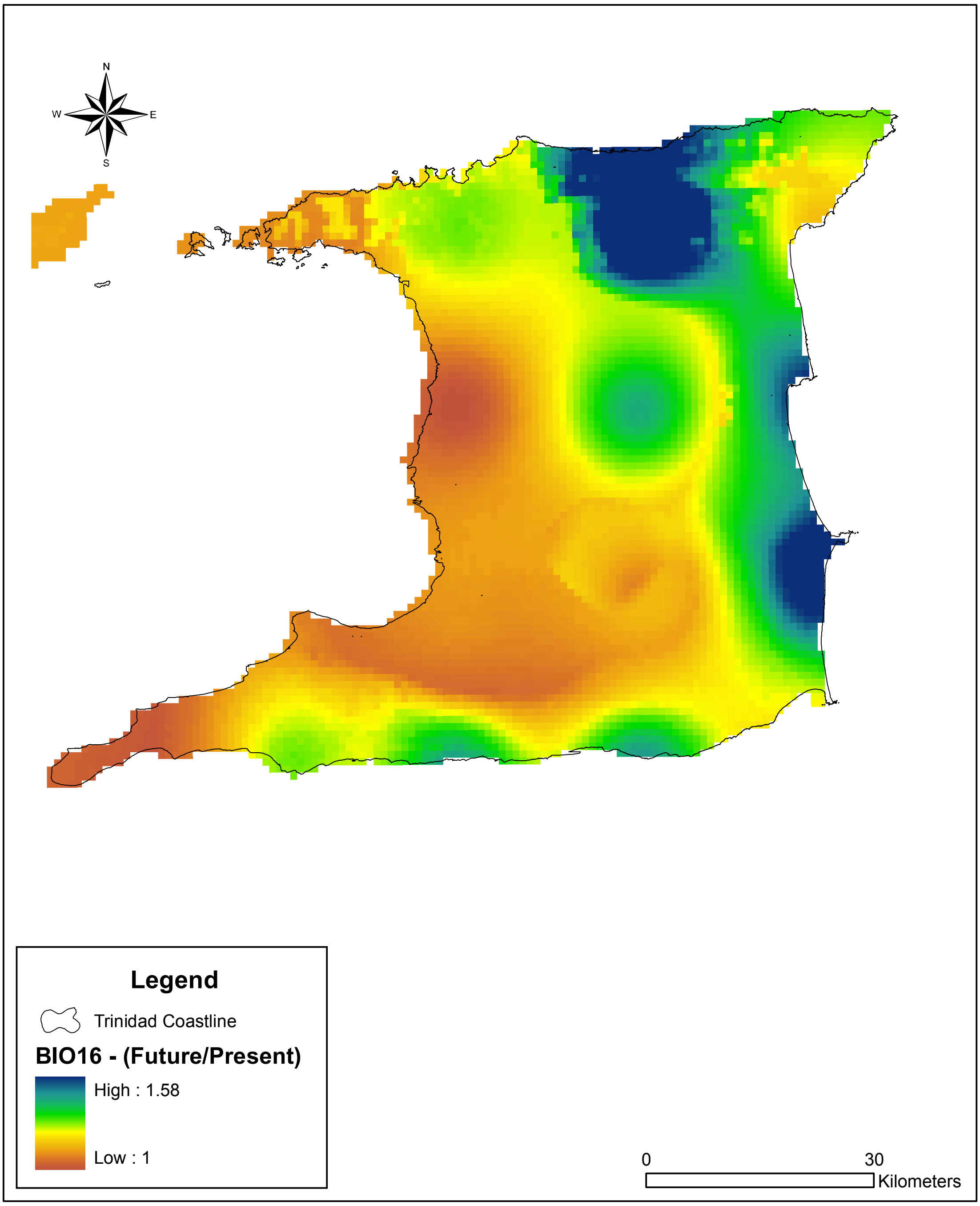


Figure C.21: Change in BIO16 (Precipitation of wettest quarter) across Trinidad between the present and future (SRES A2 scenario) climates.

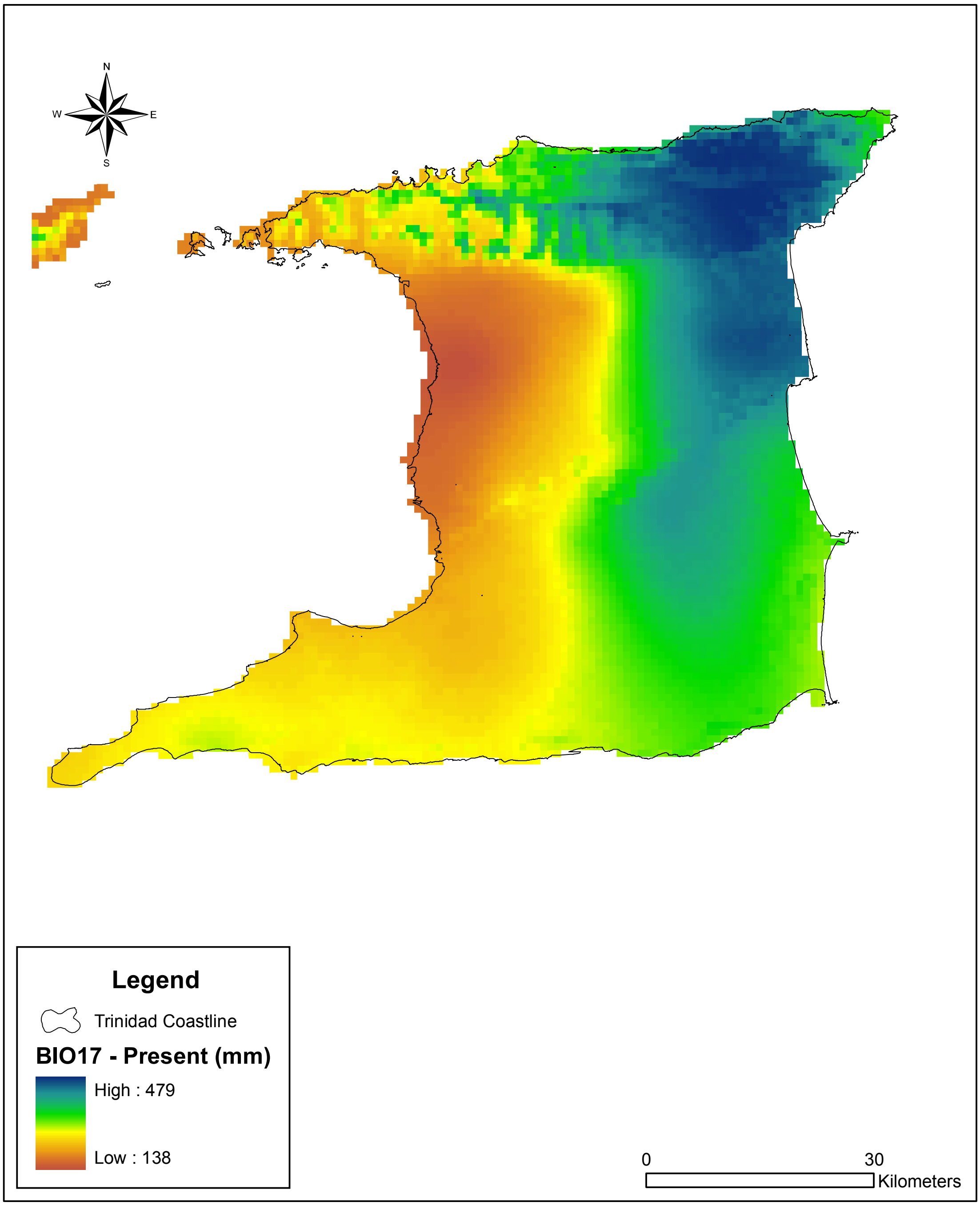


Figure C.22: BIO17 (Precipitation of driest quarter) across Trinidad for present climate.

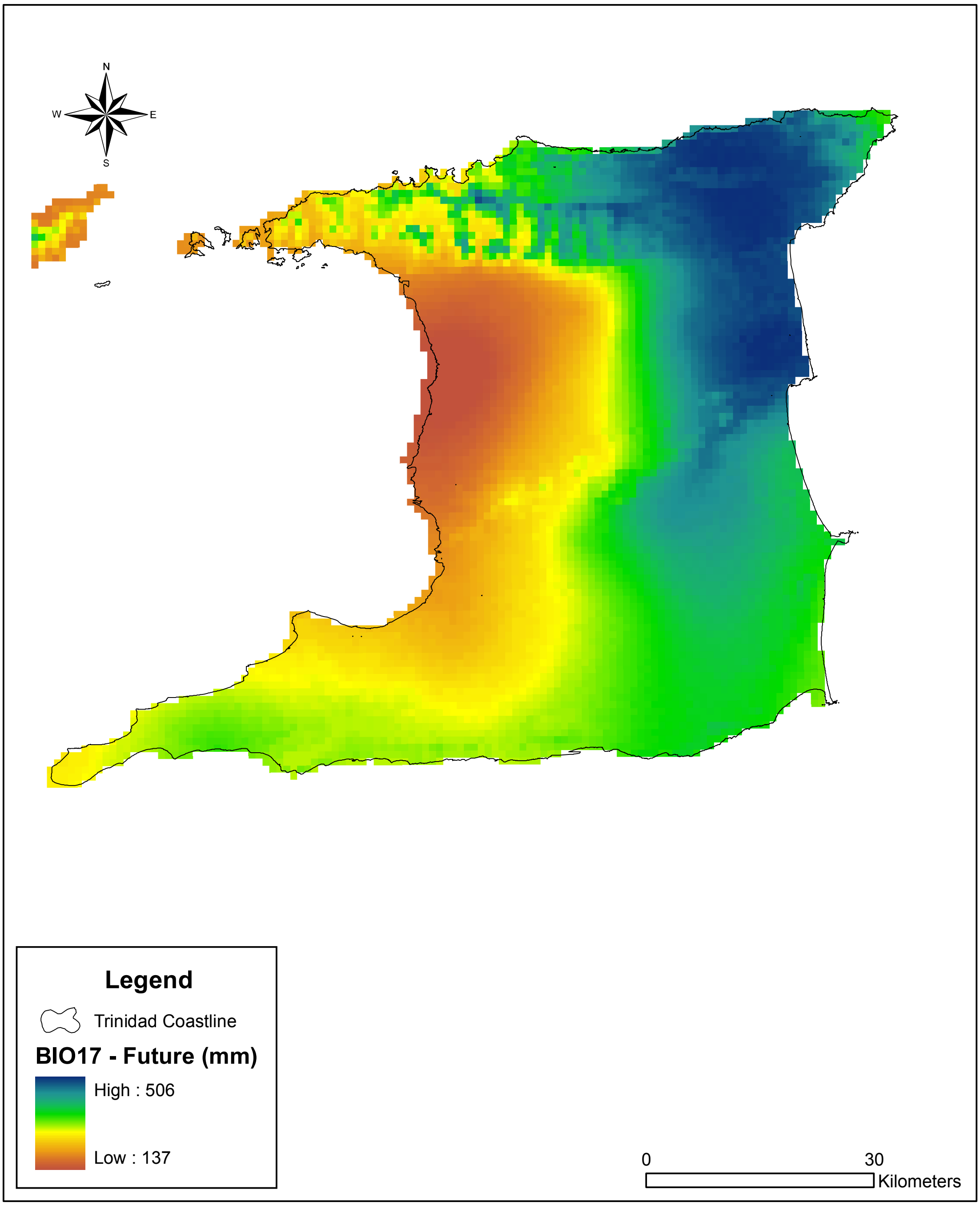


Figure C.23: BIO17 (Precipitation of driest quarter) across Trinidad for the future (SRES A2 scenario) climate.

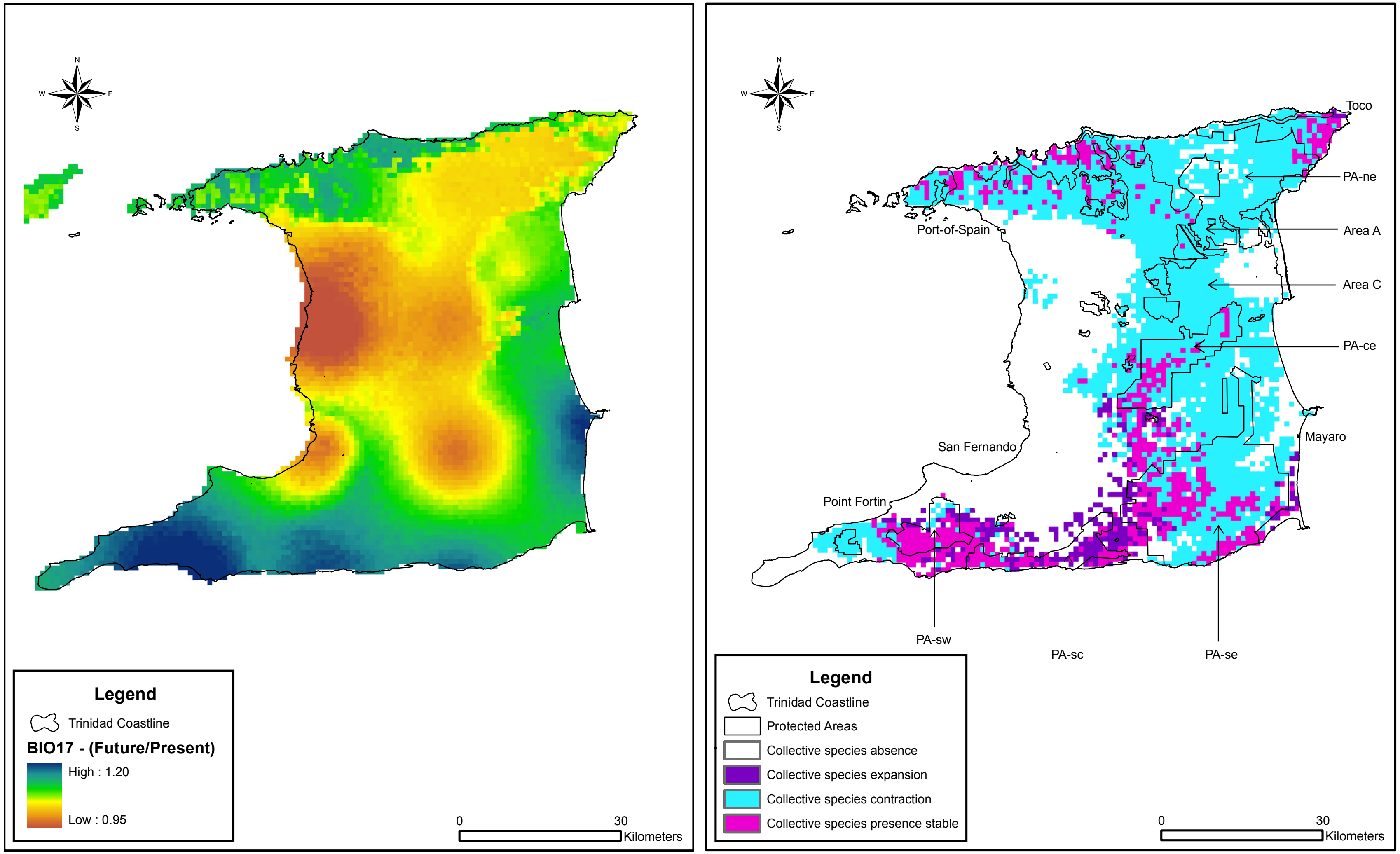


Figure C.24: Change in BIO17 (Precipitation of driest quarter) across Trinidad between the present and future (SRES A2 scenario) climates compared to Collective Species Change Map.

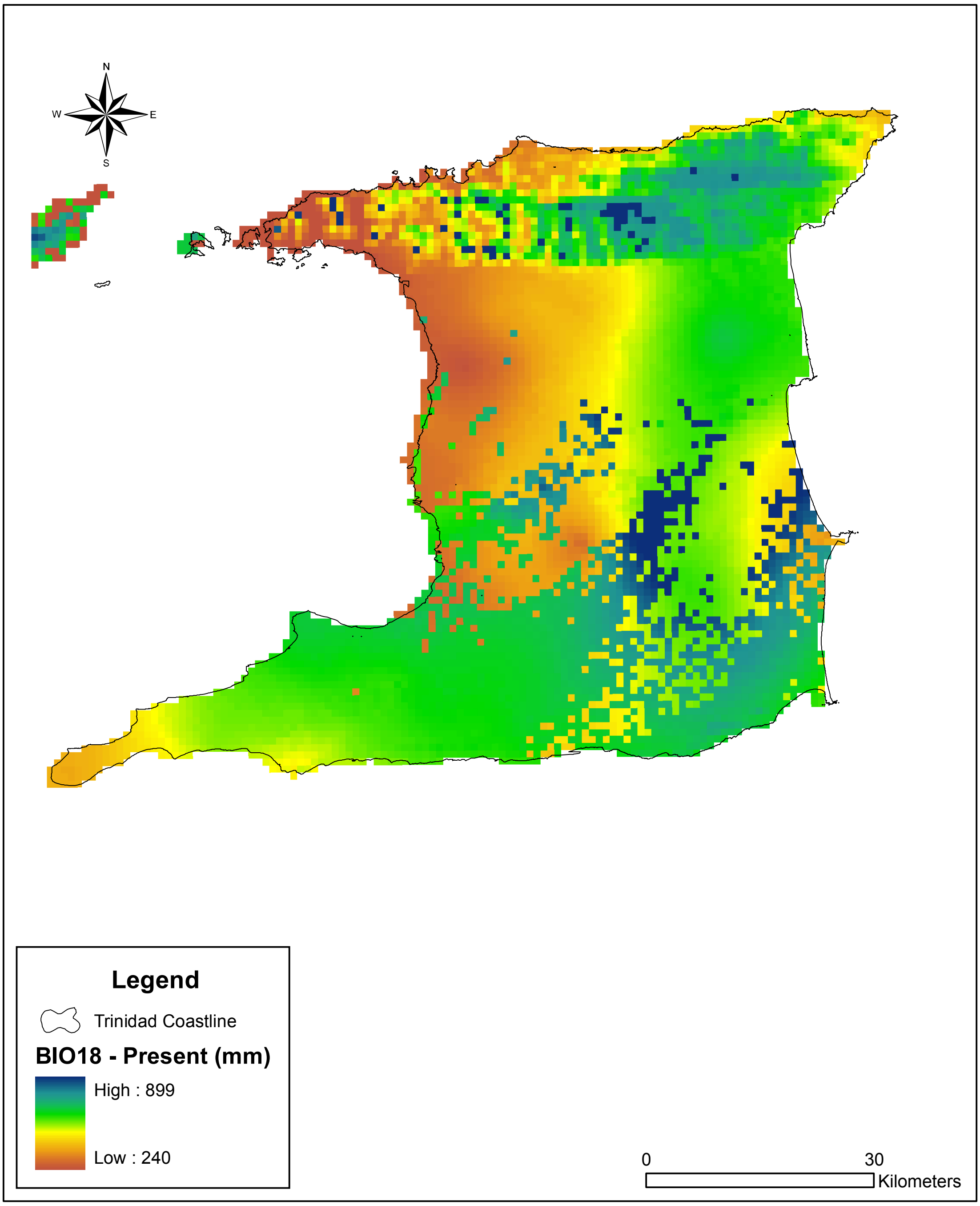


Figure C.25: BIO18 (Precipitation of warmest quarter) across Trinidad for present climate.

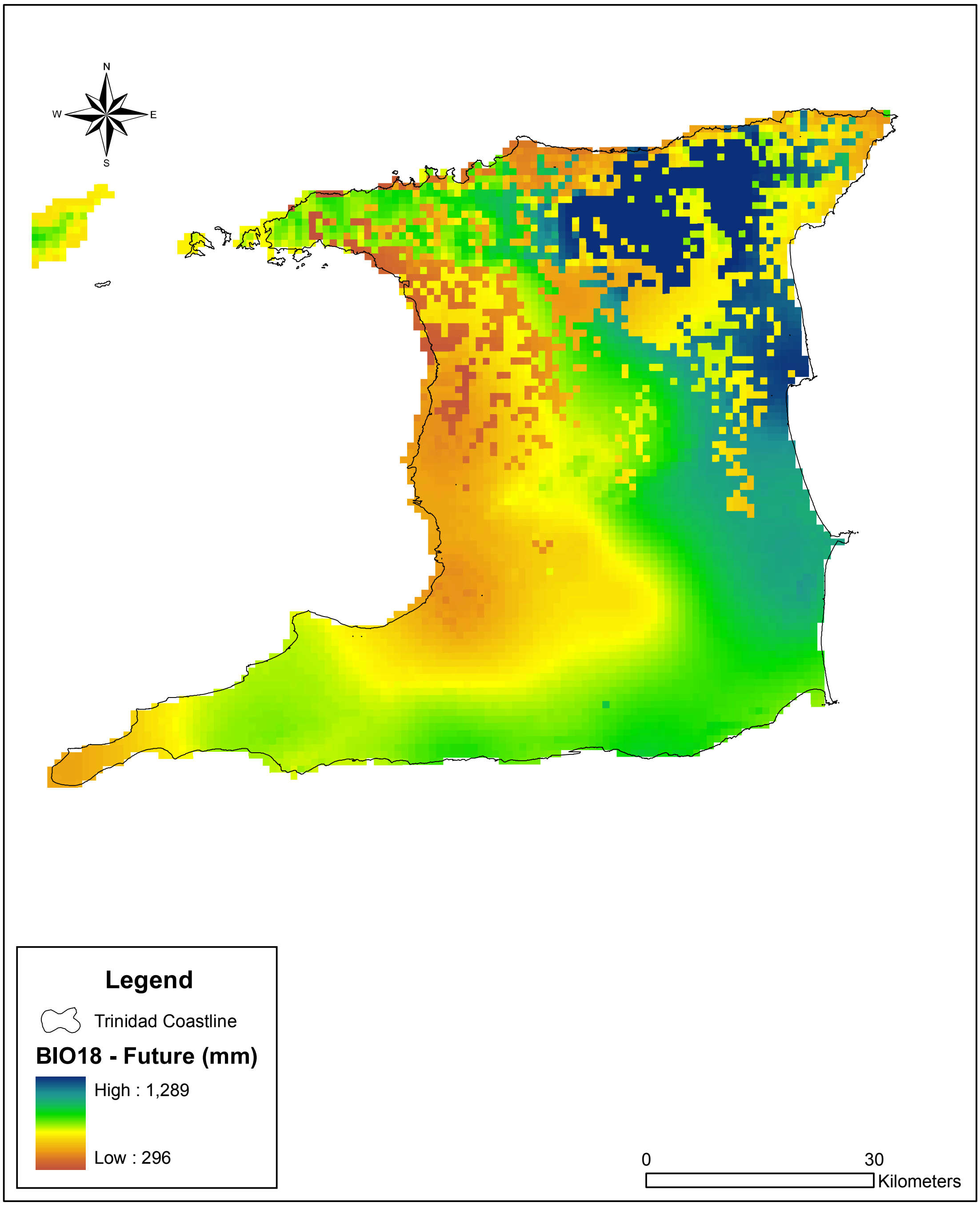


Figure C.26: BIO18 (Precipitation of warmest quarter) across Trinidad for the future (SRES A2 scenario) climate.

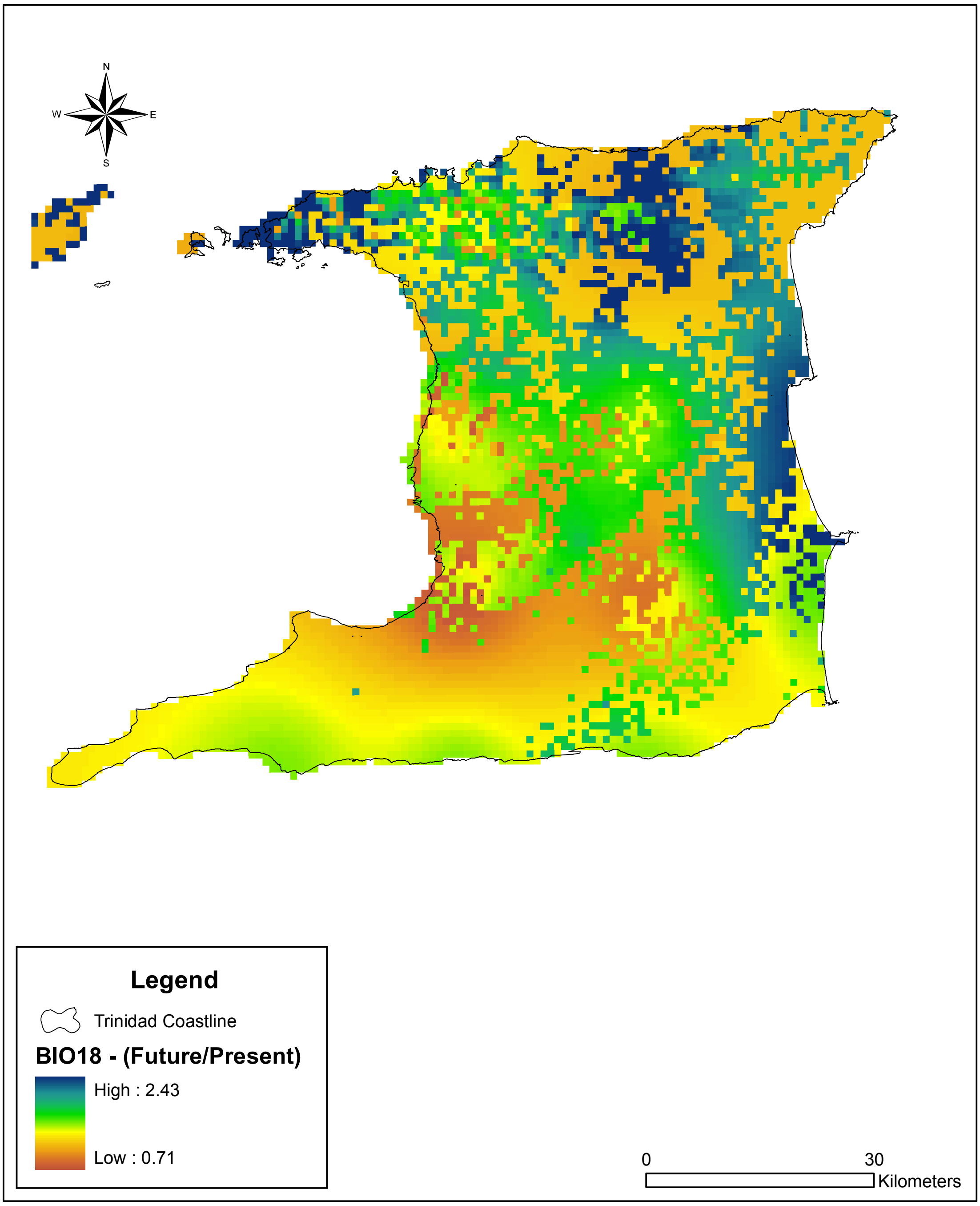


Figure C.27: Change in BIO18 (Precipitation of warmest quarter) across Trinidad between the present and future (SRES A2 scenario) climates.

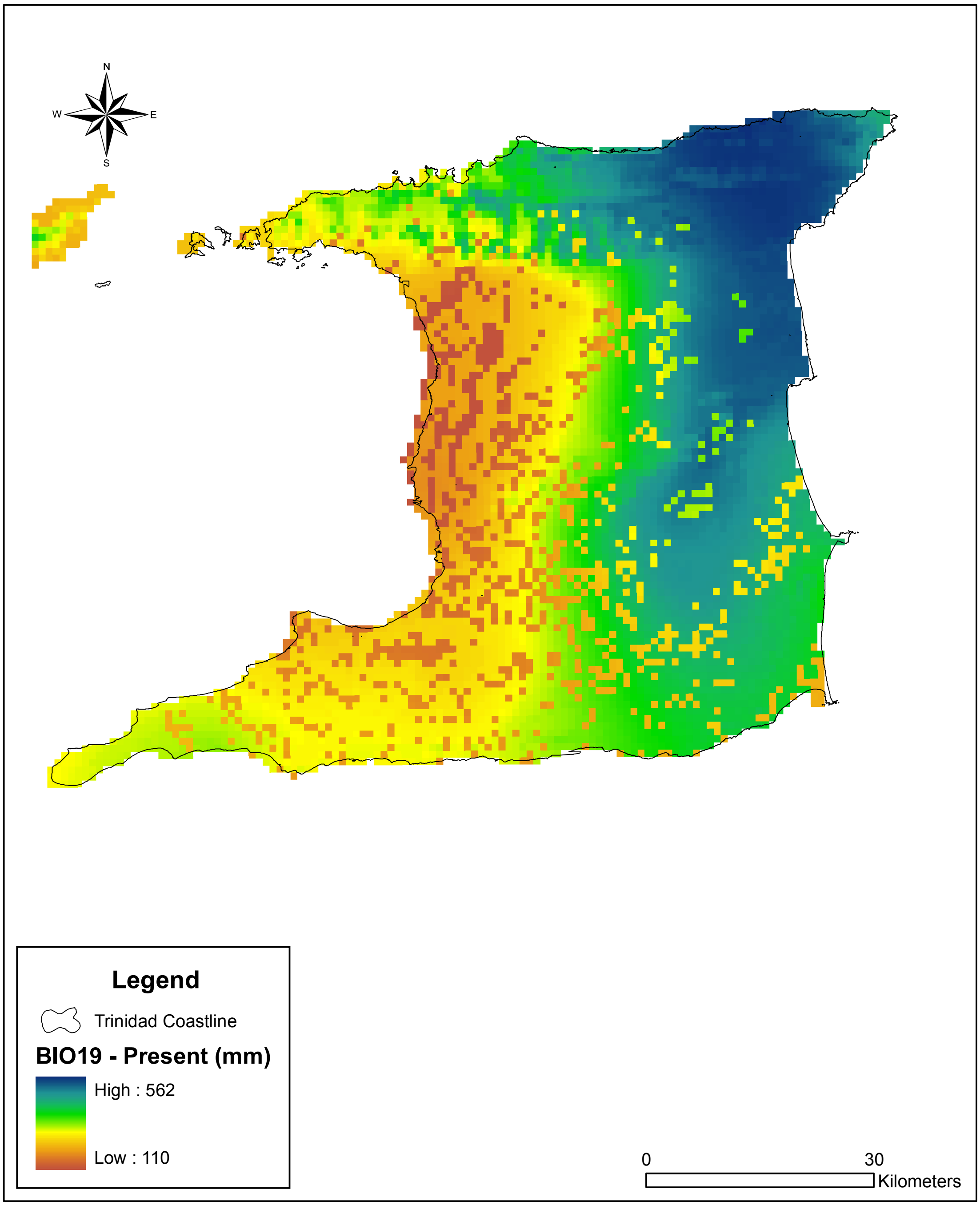


Figure C.28: BIO19 (Precipitation of coolest quarter) across Trinidad for present climate.

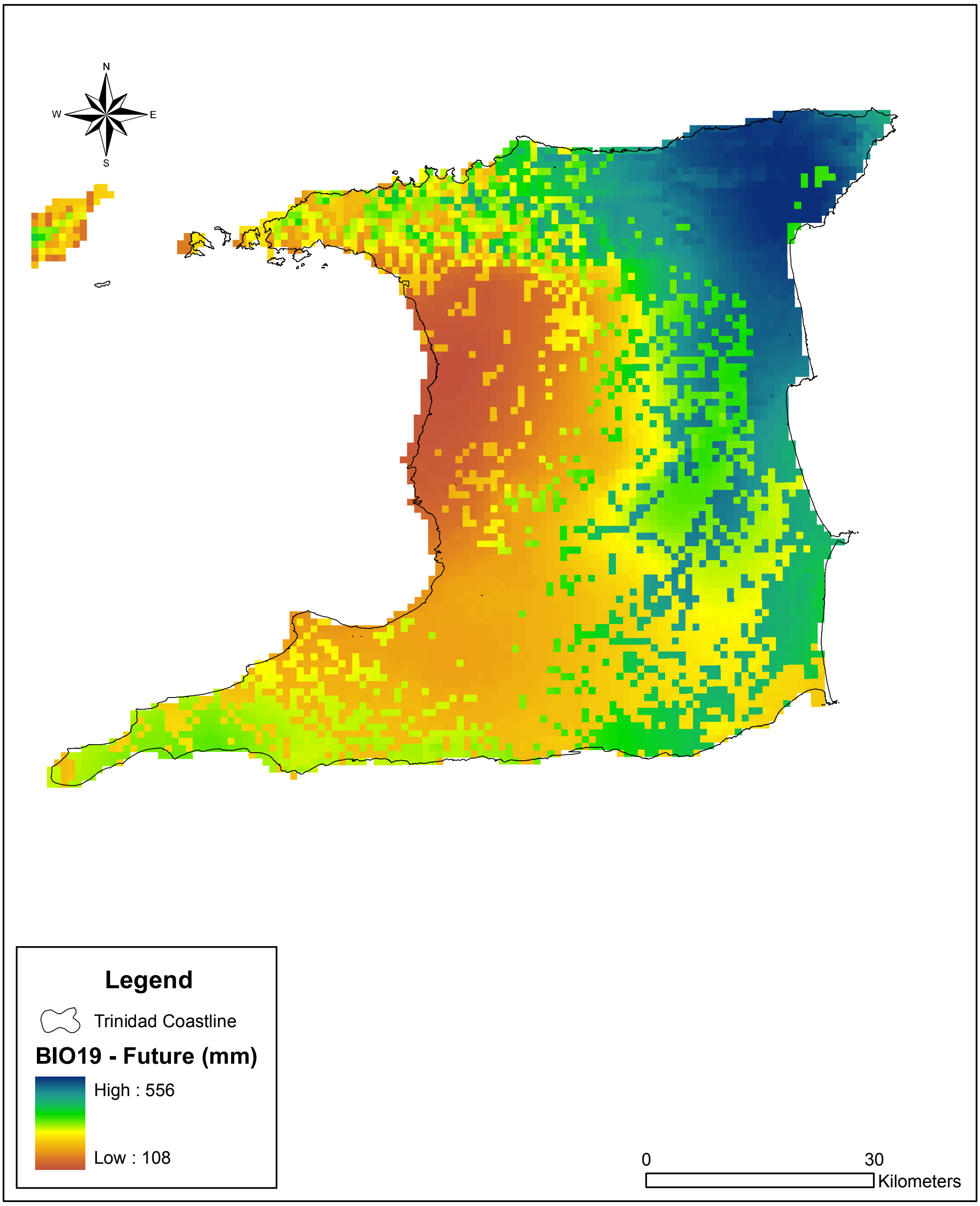


Figure C.29: BIO19 (Precipitation of coolest quarter) across Trinidad for the future (SRES A2 scenario) climate.

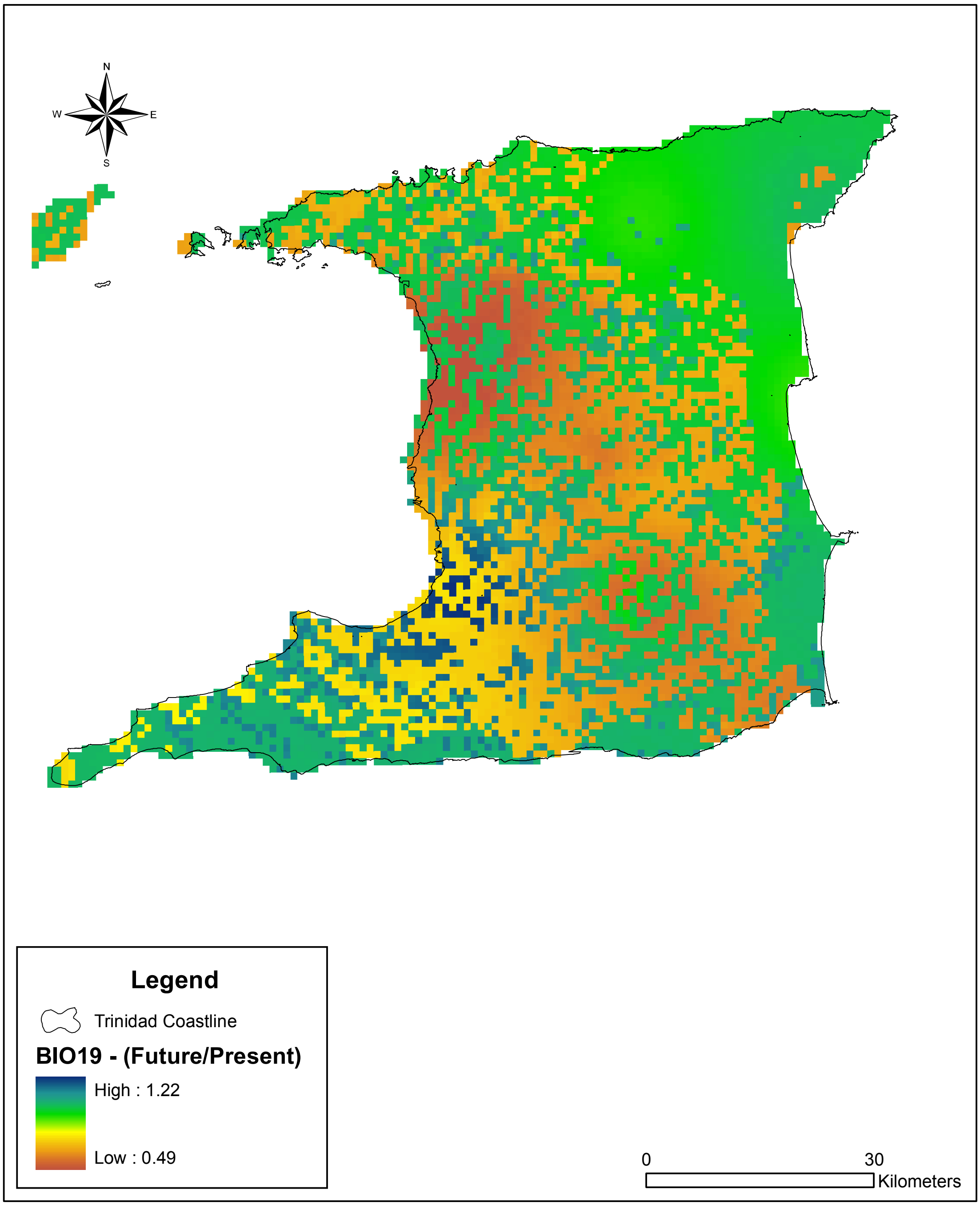


Figure C.30: Change in BIO19 (Precipitation of coolest quarter) across Trinidad between the present and future (SRES A2 scenario) climates.

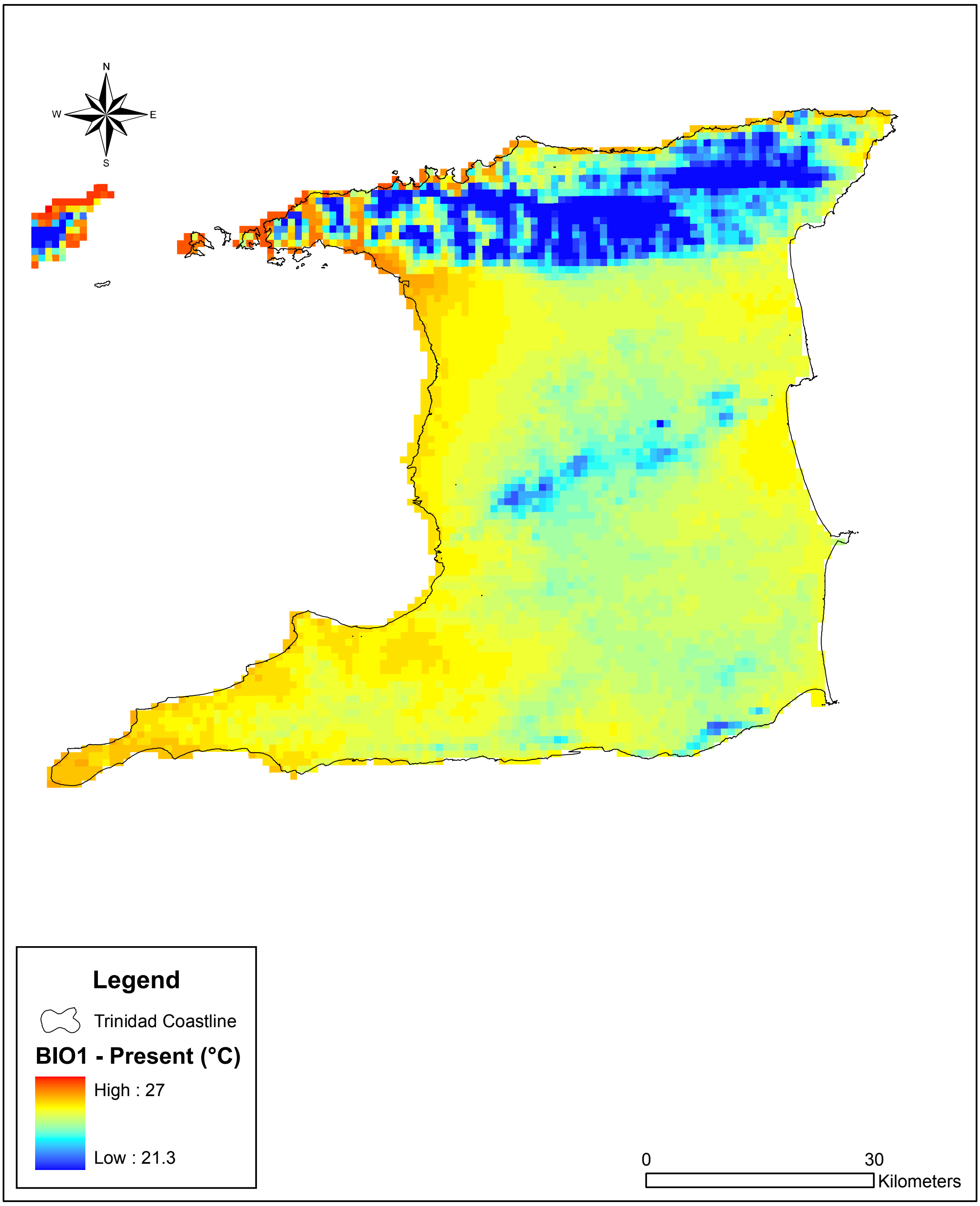


Figure C.31: BIO1 (Annual mean temperature) across Trinidad for present climate.

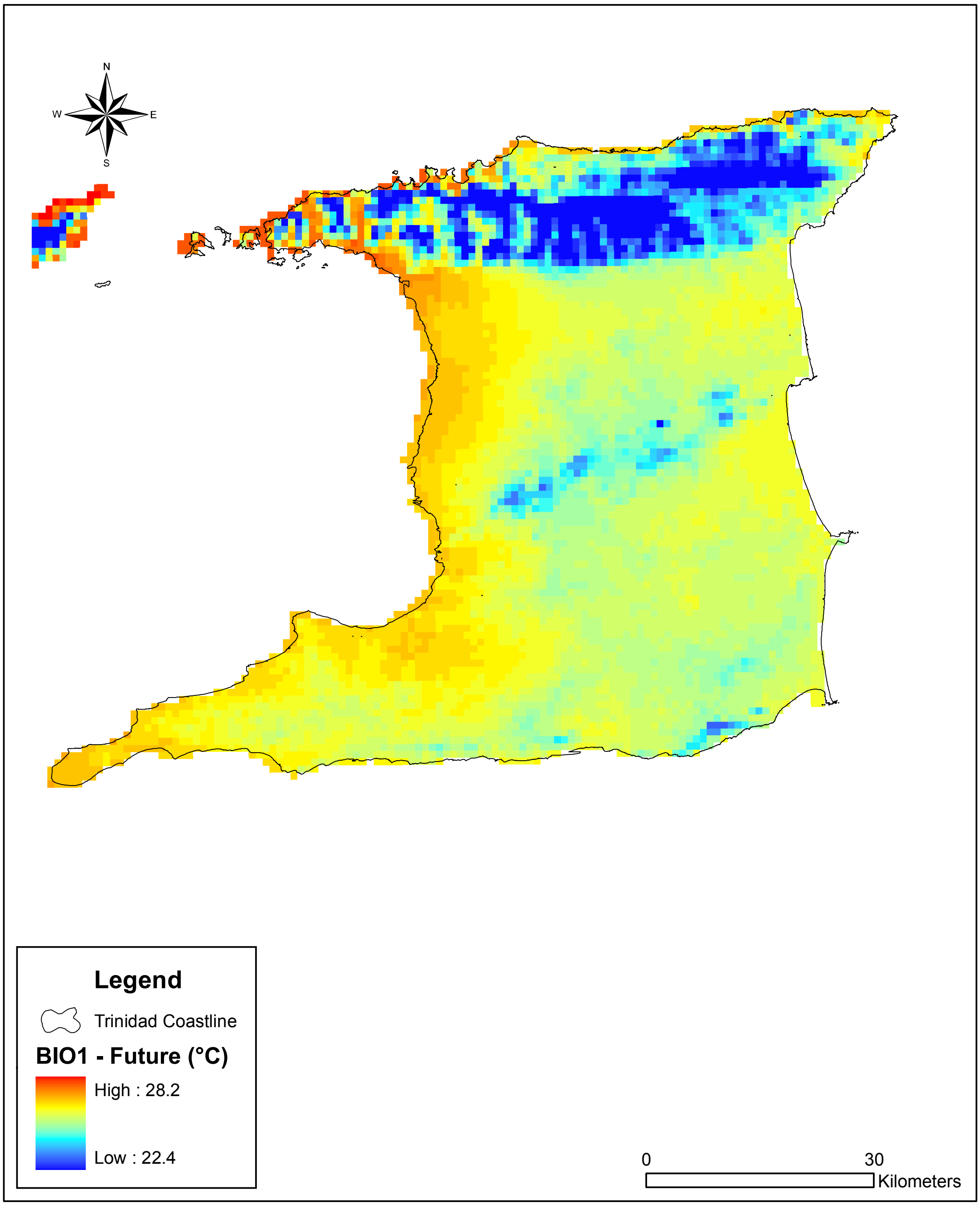


Figure C.32: BIO1 (Annual mean temperature) across Trinidad for the future (SRES A2 scenario) climate.

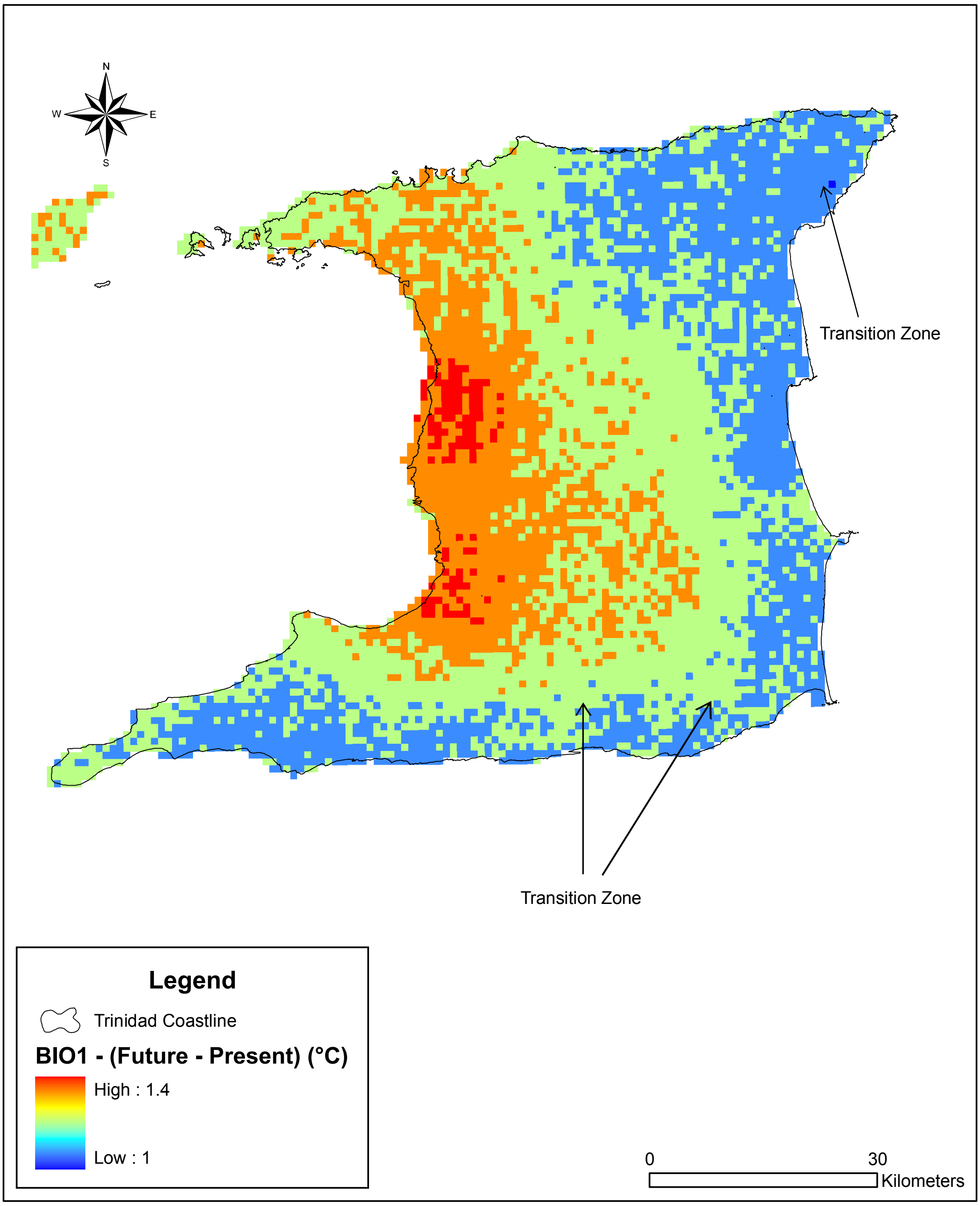


Figure C.33: Change in BIO1 (Annual mean temperature) across Trinidad between the present and future (SRES A2 scenario) climates.

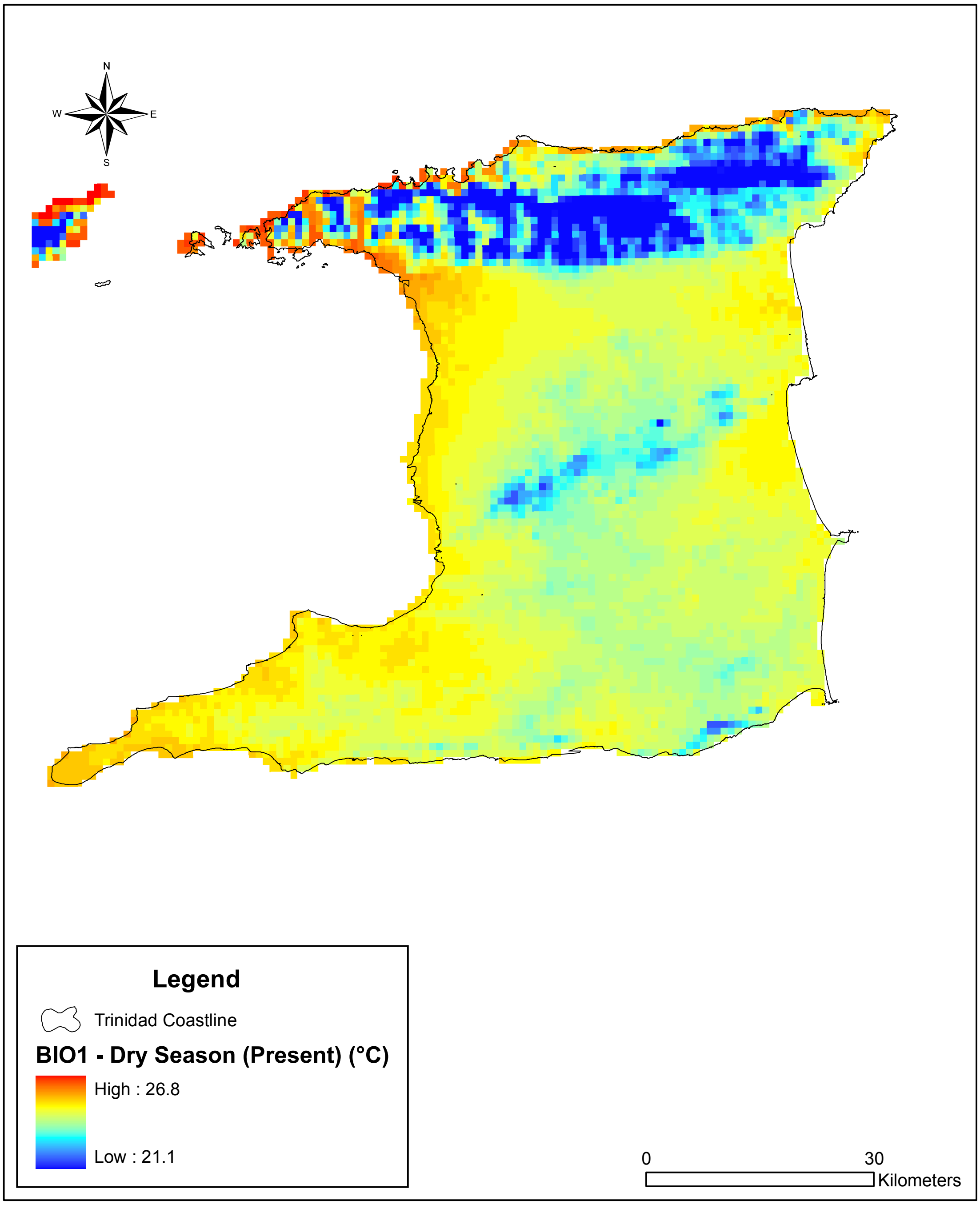


Figure C.34: BIO1 (Annual mean temperature) across Trinidad (Dry Season) for the present climate.

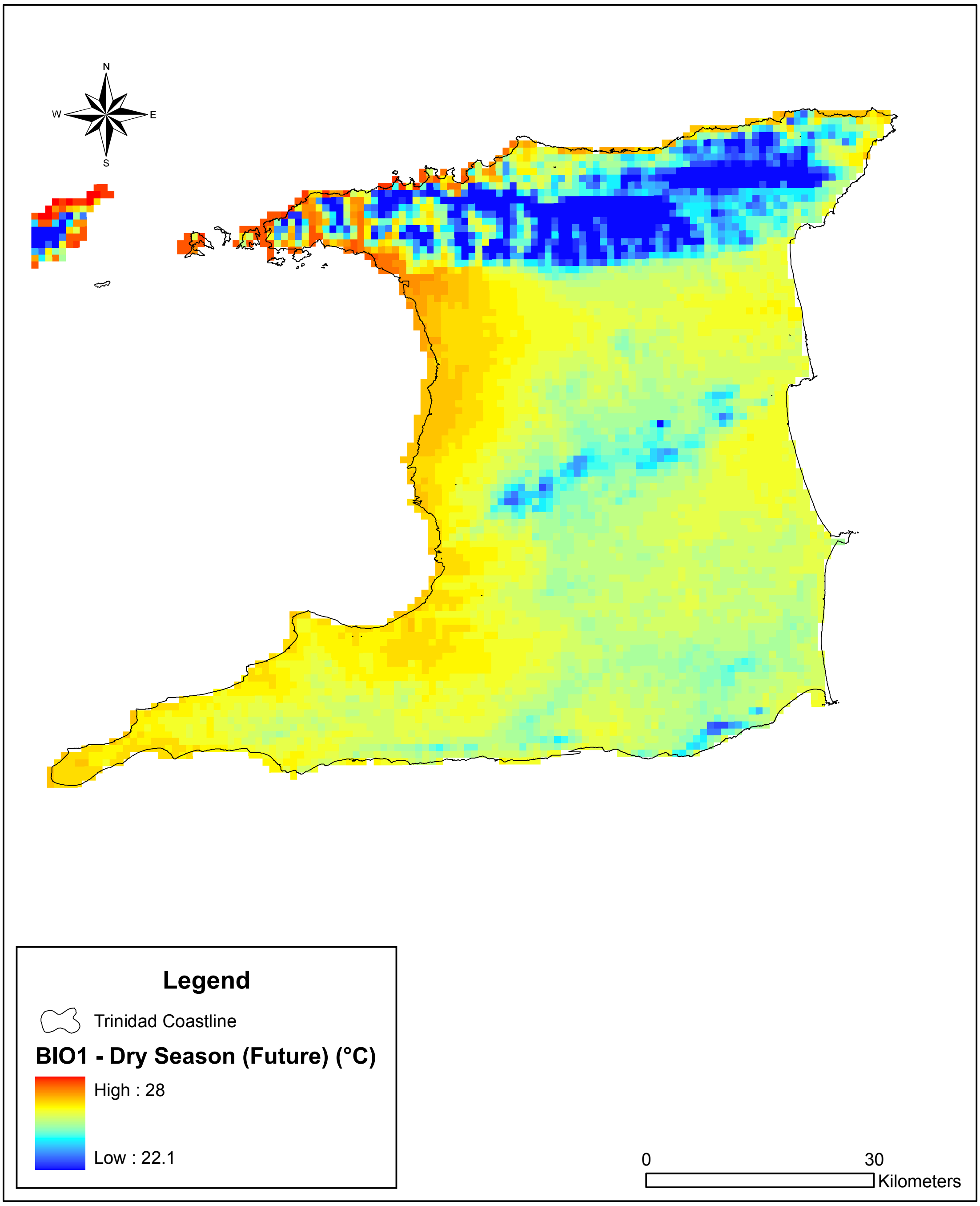


Figure C.35: BIO1 (Annual mean temperature) across Trinidad (Dry Season) for the future (SRES A2 scenario) climate.

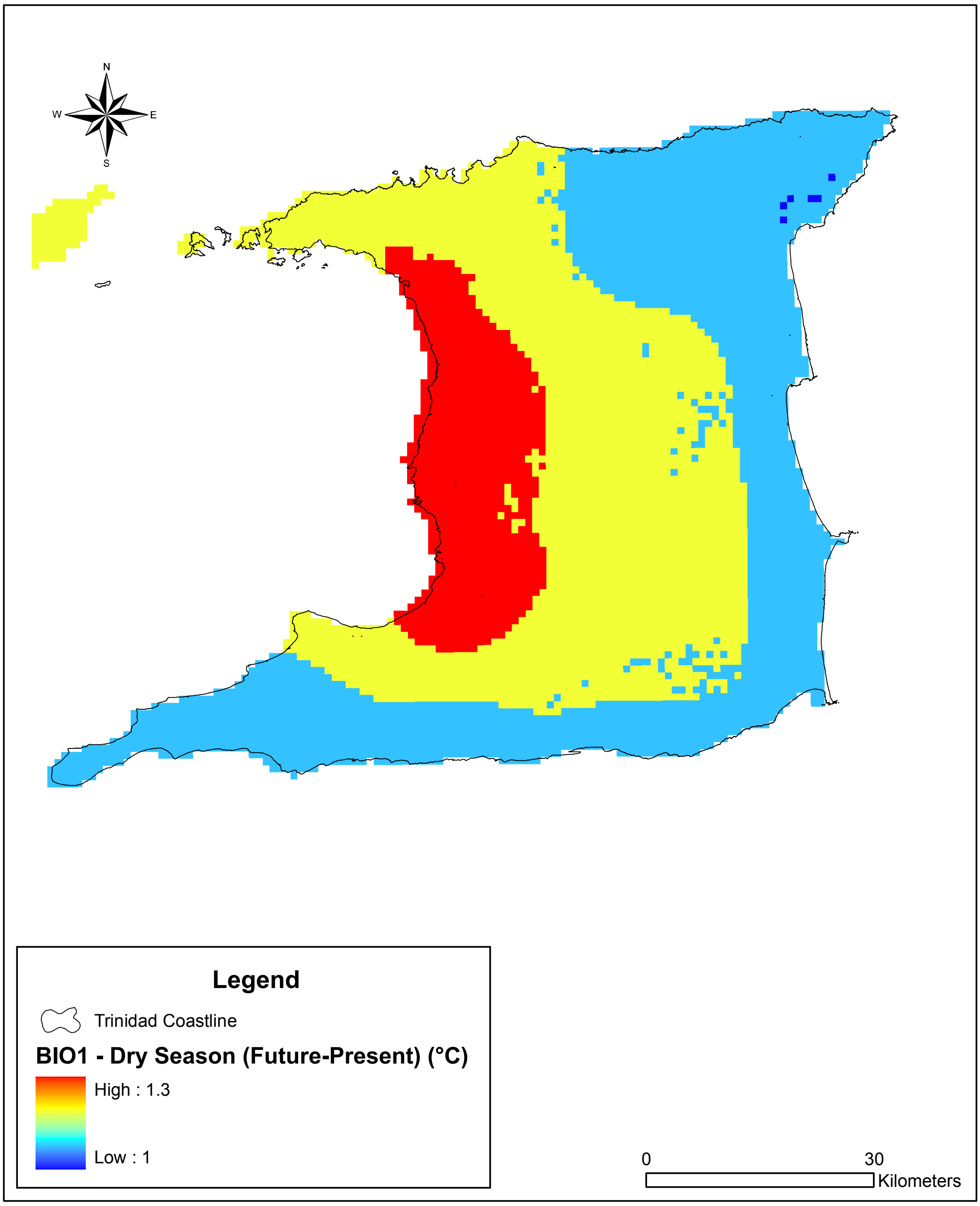


Figure C.36: Change in BIO1 (Annual mean temperature) across Trinidad during the Dry Season: between the present and future (SRES A2 scenario) climates.

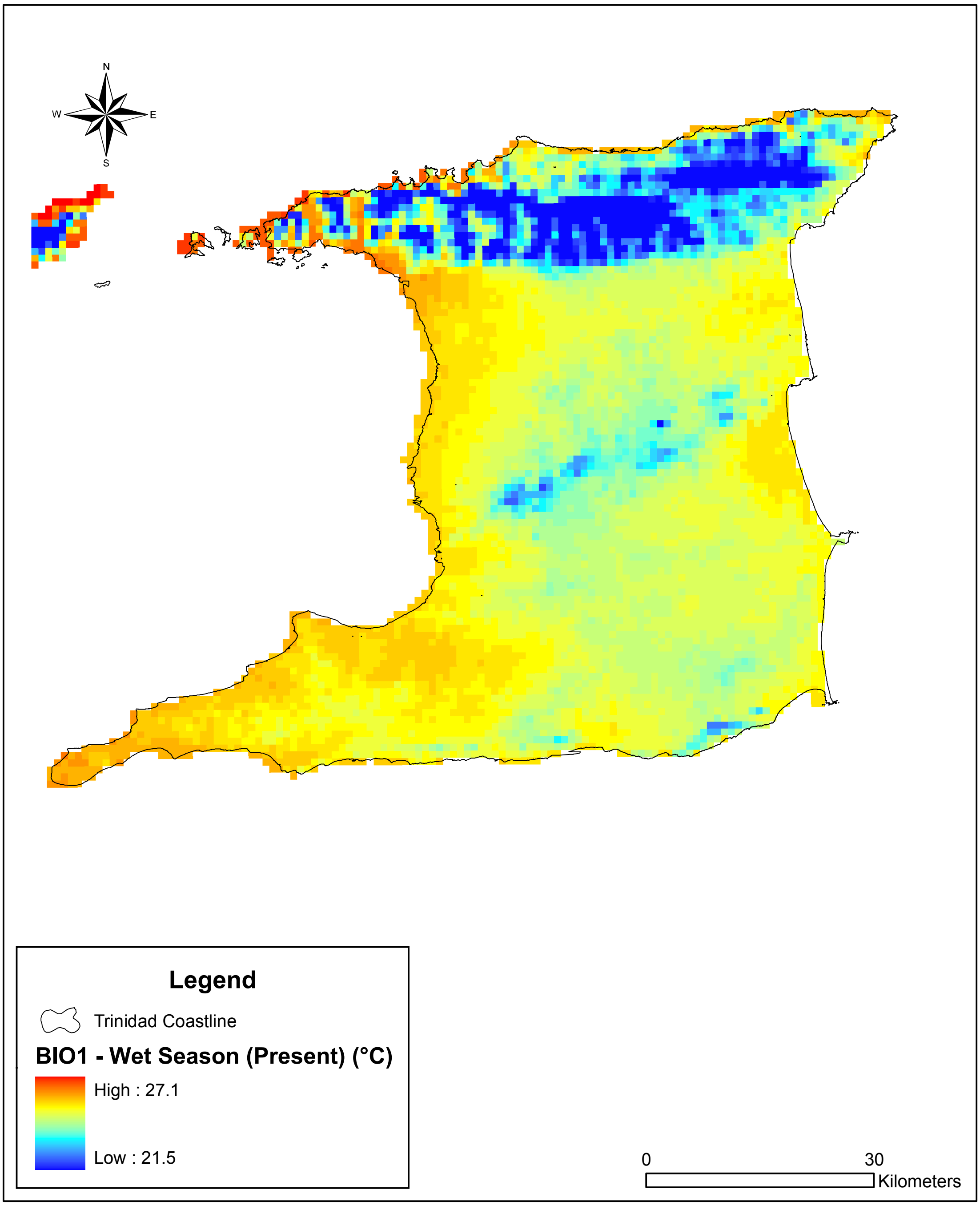


Figure C.37: BIO1 (Annual mean temperature) across Trinidad (Wet Season) for the present climate.

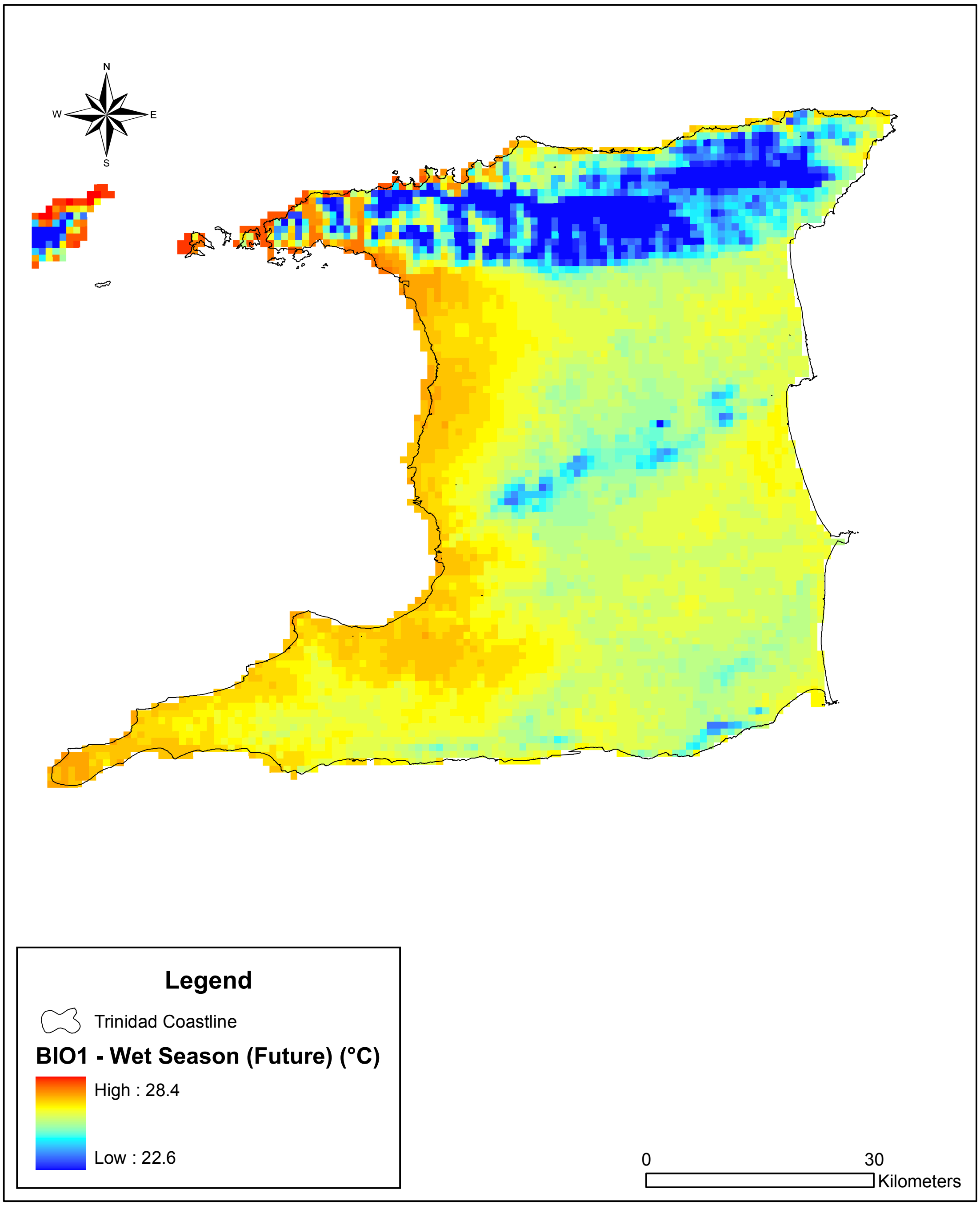


Figure C.38: BIO1 (Annual mean temperature) across Trinidad (Wet Season) for the future (SRES A2 scenario) climate.

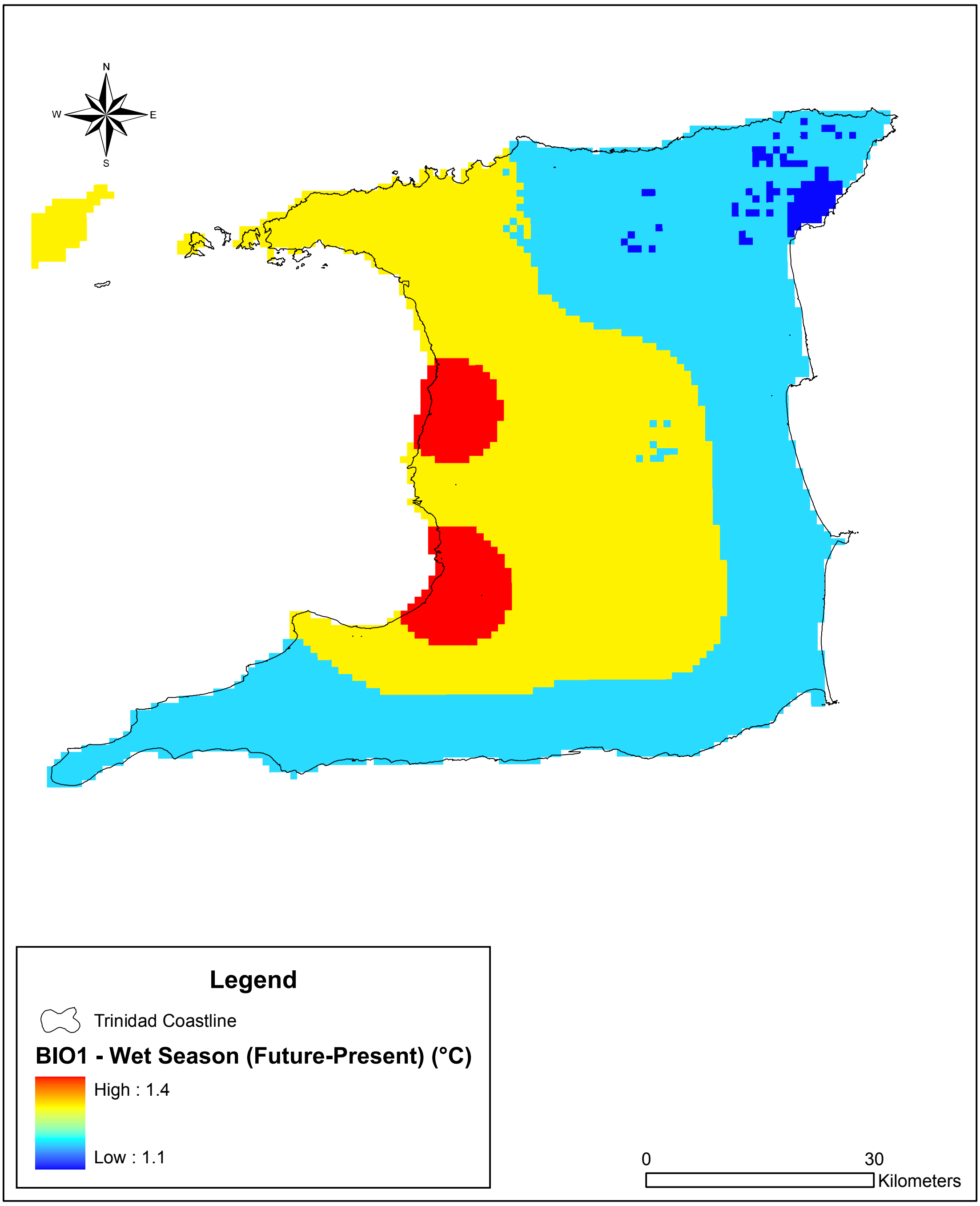


Figure C.39: Change in BIO1 (Annual mean temperature) across Trinidad during the Wet Season: between the present and future (SRES A2 scenario) climates.

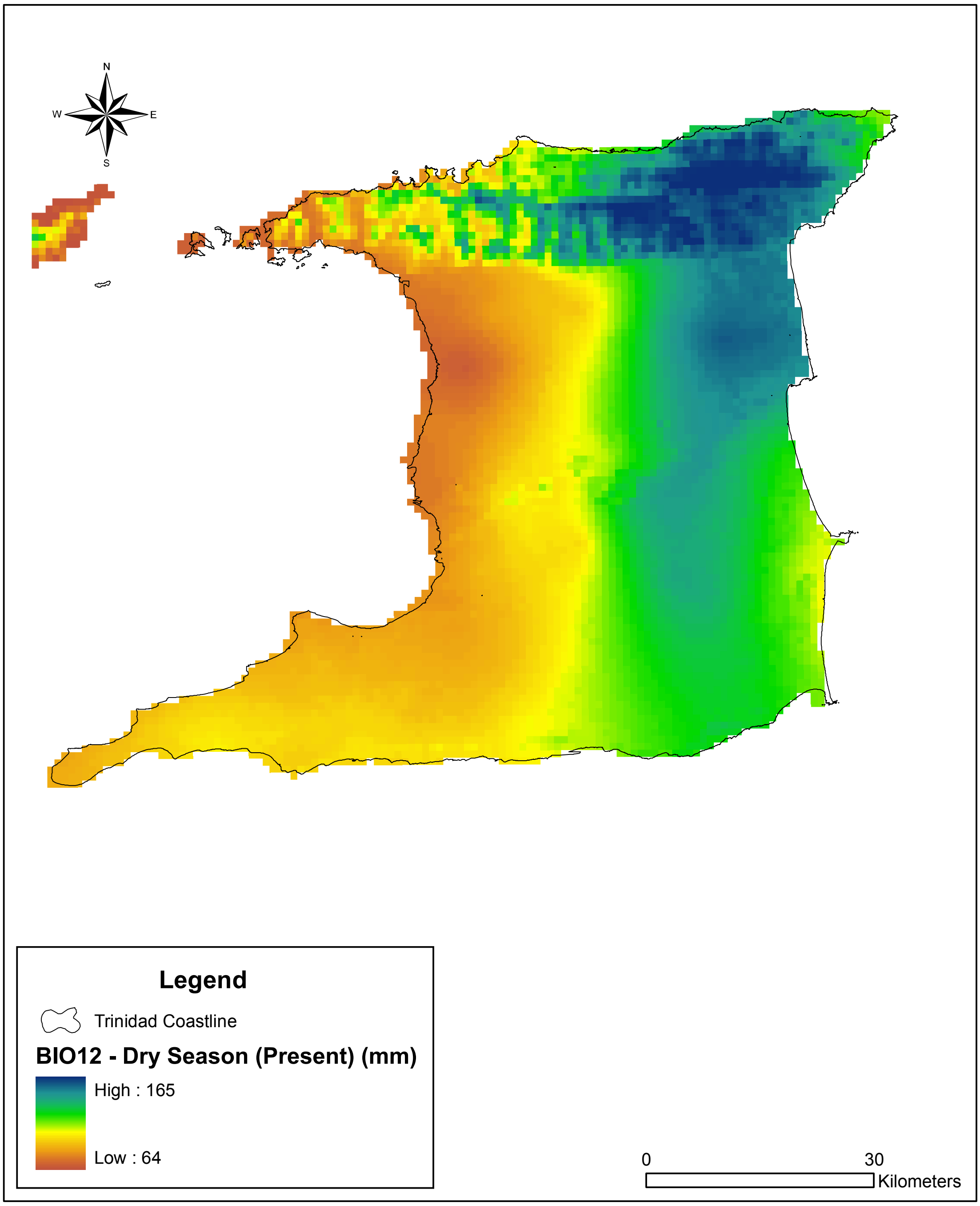


Figure C.40: BIO12 (Annual precipitation) across Trinidad (Dry Season) for the present climate.

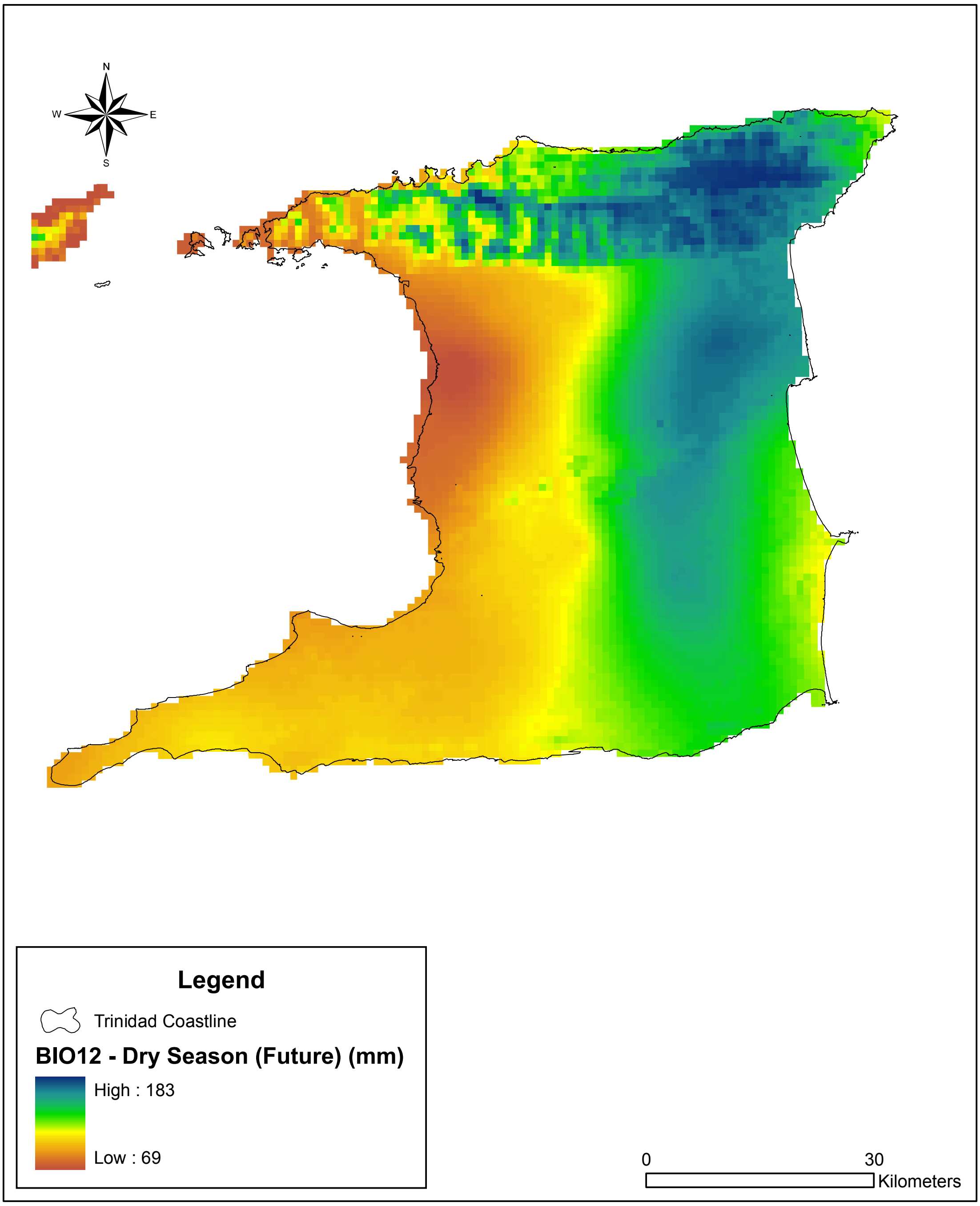


Figure C.41: BIO12 (Annual precipitation) across Trinidad (Dry Season) for the future (SRES A2 scenario) climate.

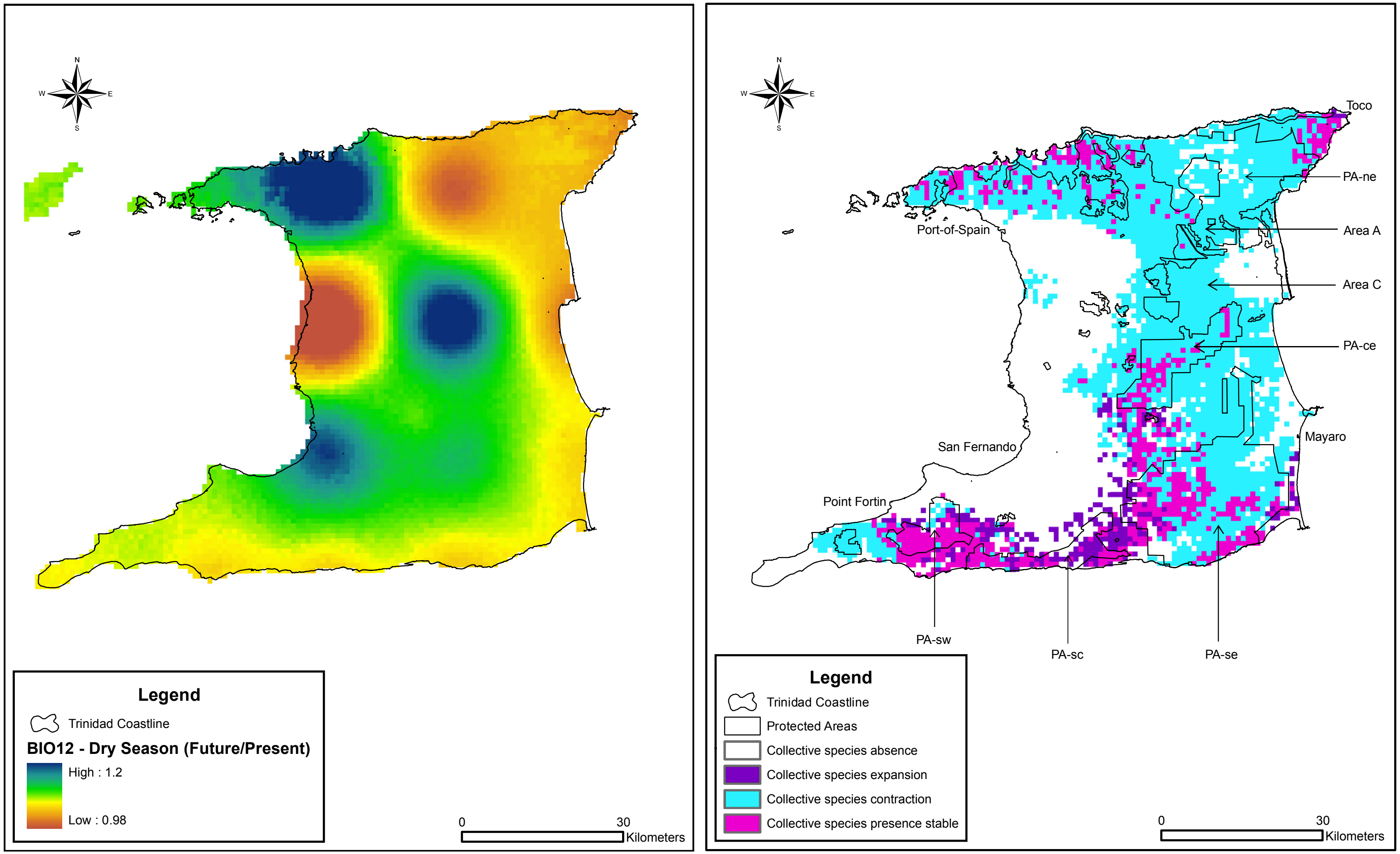


Figure C.42: Change in BIO12 (Annual precipitation) across Trinidad during the Dry season: between the present and future (SRES A2 scenario) climates compared to Collective Species Change Map.

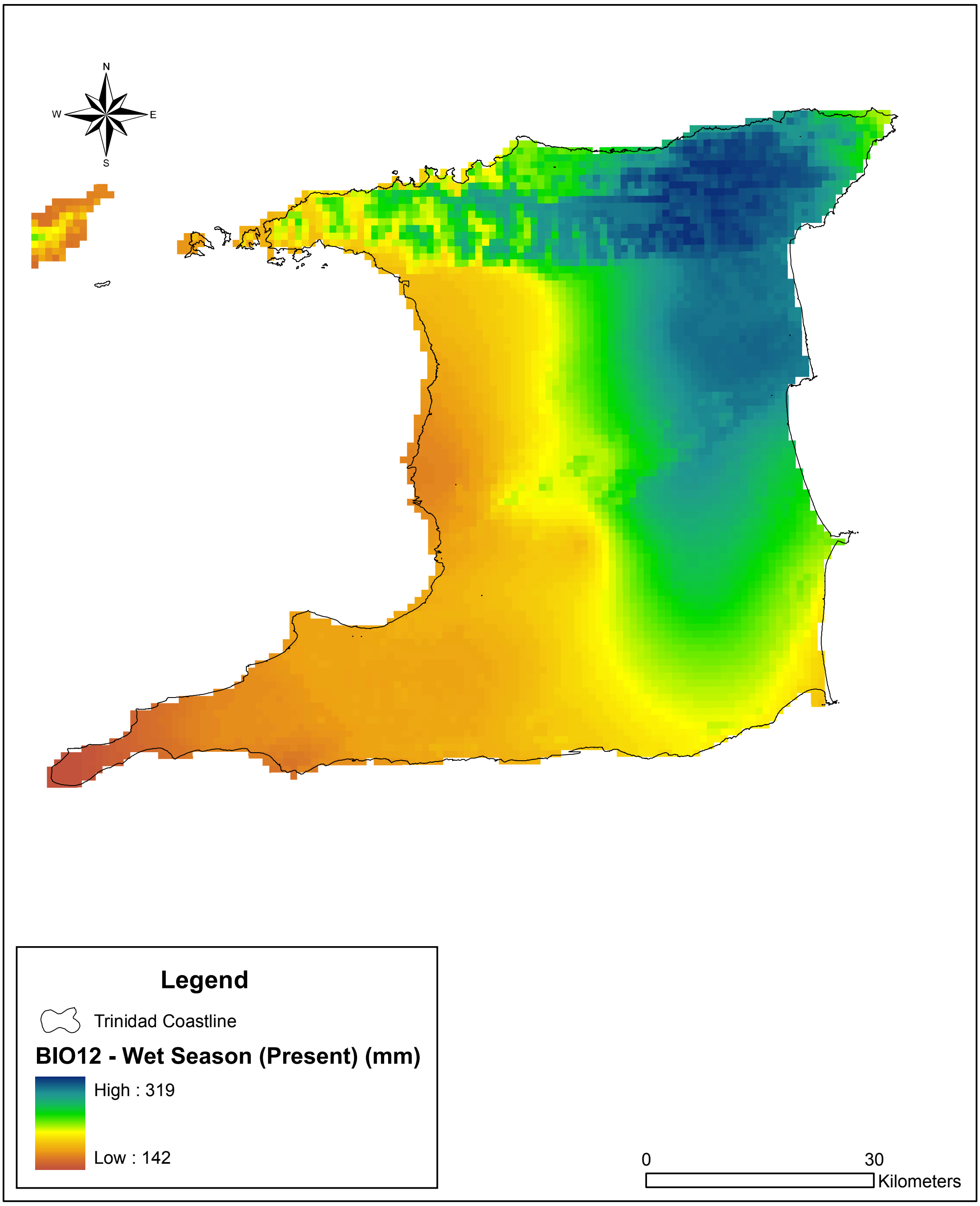


Figure C.43: BIO12 (Annual precipitation) across Trinidad (Wet Season) for the present climate.

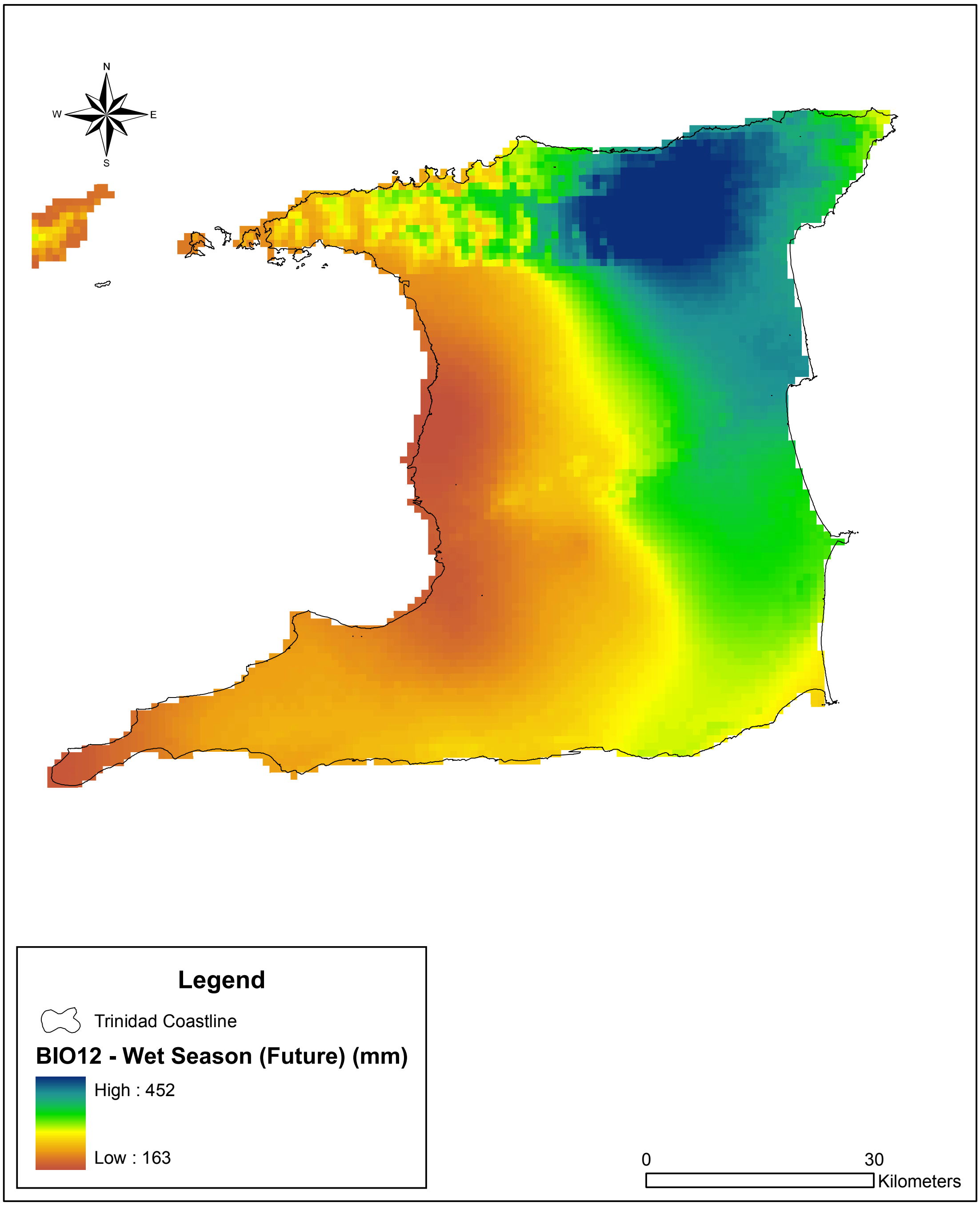


Figure C.44: BIO12 (Annual precipitation) across Trinidad (Wet Season) for the future (SRES A2 scenario) climate.

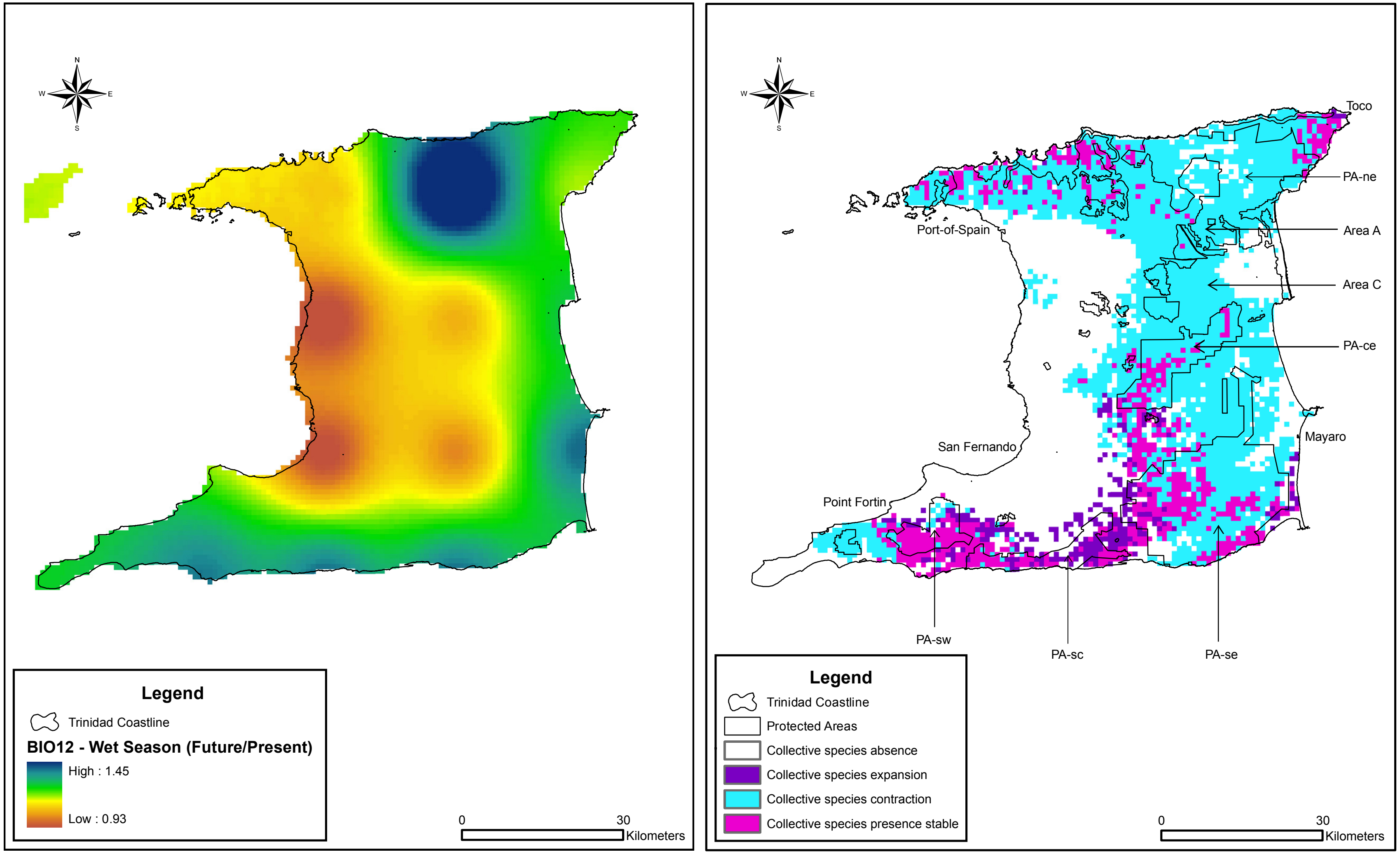


Figure C.45: Change in BIO12 (Annual precipitation) across Trinidad during the Wet season: between the present and future (SRES A2 scenario) climates compared to Collective Species Change Map.

Bibliography

Akçakaya, H. R., S. H. M. Butchart, G. M. Mace, S. N. Stuart and C. Hilton-Taylor. 2006. Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. *Global Change Biology* 12 (11): 2037–2043. doi:`10.1111/j.1365-2486.2006.01253.x`.

Alagador, D., M. J. Martins, J. O. Cerdeira, M. Cabeza and M. B. Araújo. 2011. A probability-based approach to match species with reserves when data are at different resolutions. *Biological Conservation* 144 (2): 811–820. doi:`10.1016/j.biocon.2010.11.011`.

Algar, S. T., and J. L. Pindell. 1993. Structure and deformation history of the Northern range of Trinidad and adjacent areas. *Tectonics* 12 (4): 814–829. doi:`10.1029/93TC00673`.

Ali, S. 2010. *Interview by author.* National Forestry Division of Trinidad and Tobago, July 27.

———. 2012. *Interview by author.* National Forestry Division of Trinidad and Tobago, Jan. 20.

Anderson, J. R., E. E. Hardy, J. T. Roach and R. E. Witmer. 1976. *A land use and land cover classification system for use with remote sensor data.* Geological Survey Professional Paper 964. United States Department of the Interior. `http://landcover.usgs.gov/pdf/anderson.pdf`.

Anderson, R. P., and E. Martínez-Meyer. 2004. Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. *Biological Conservation* 116 (2): 167–179. doi:`10.1016/S0006-3207(03)00187-3`.

Anderson, R. P., D. Lew and A. T. Peterson. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling* 162 (3): 211–232. doi:`10.1016/s0304-3800(02)00349-6`.

Araújo, M. B., R. G. Pearson, W. Thuiller and M. Erhard. 2005. Validation of species-climate impact models under climate change. *Global Change Biology* 11 (9): 1504–1513. doi:`10.1111/j.1365-2486.2005.01000.x`.

Araújo, M. B., W. Thuiller and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33 (10): 1712–1728. doi:`10.1111/j.1365-2699.2006.01482.x`.

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33 (10): 1677–1688. doi:`10.1111/j.1365-2699.2006.01584.x`.

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16 (6): 743–753. doi:`10.1111/j.1466-8238.2007.00359.x`.

Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* 22 (1): 42–47. doi:`10.1016/j.tree.2006.09.010`.

Araújo, M. B., M. Cabeza, W. Thuiller, L. Hannah and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* 10 (9): 1618–1626. doi:`10.1111/j.1365-2486.2004.00828.x`.

Araújo, M. B., D. Alagador, M. Cabeza, D. Nogués-Bravo and W. Thuiller. 2011. Climate change threatens European conservation areas. *Ecology Letters* 14 (5): 484–492. doi:`10.1111/j.1461-0248.2011.01610.x`.

Armesto, J. J., D. Manuschevich, A. Mora, C. Smith-Ramirez, R. Rozzi, A. M. Abarzúa and P. A. Marquet. 2010. From the Holocene to the Anthropocene: a historical framework for land cover change in southwestern South America in the past 15,000 years. *Land Use Policy* 27 (2): 148–160. doi:`10.1016/j.landusepol.2009.07.006`.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157 (2-3): 101–118. doi:`10.1016/S0304-3800(02)00205-3`.

Austin, M. P., L. Belbin, J. A. Meyers, M. D. Doherty and M. Luoto. 2006. Evaluation of statistical models used for predicting plant species distributions: role of artificial data and theory. *Ecological Modelling* 199 (2): 197–216. doi:`10.1016/j.ecolmodel.2006.05.023`.

Baksh-Comeau, Y. S. 2010. *Interview by author.* Curator, National Herbarium of Trinidad and Tobago.

Baksh-Comeau, Y. S., W. D. Hawthorne, S. A. Harris, S. S. Maharaj and D. L. Filer. 2011. The vascular flora of Trinidad and Tobago: a checklist with conservation status. (in preparation).

Baldwin, R. A. 2009. Use of maximum entropy modeling in wildlife research. *Entropy* 11 (4): 854–866. doi:`10.3390/e11040854`.

Barlow, J., T. A. Gardner, I. S. Araujo, T. C. Ávila Pires, A. B. Bonaldo, J. E. Costa, M. C. Esposito, L. V. Ferreira, J. Hawes, M. I. M. Hernandez, M. S. Hoogmoed, R. N. Leite, N. F. Lo-Man-Hung, J. R. Malcolm, M. B. Martins, L. A. M. Mestre, R. Miranda-Santos, A. L. Nunes-Gutjahr, W. L. Overal, L. Parry, S. L. Peters, M. A. Ribeiro-Junior, M. N. F. da Silva, C. da Silva Motta and C. A. Peres. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America* 104 (47): 18555–18560. doi:`10.1073/pnas.0703333104`.

Barrett, N. E., and J. P. Barrett. 1997. Reserve design and the new conservation theory. Chap. 19 in *The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity,* ed. S. Pickett, R. S. Ostfeld, M. Shachak and G. E. Likens. New York: Chapman & Hall. ISBN:0412098512.

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology* 43 (3): 413–423. doi:`10.1111/j.1365-2664.2006.01136.x`.

Beard, J. S. 1944a. Provisional list of trees and shrubs of the Lesser Antilles. *Caribbean Forester* 5 (2): 48–67.

———. 1944b. The natural vegetation of the island of Tobago, British West Indies. *Ecological Monographs* 14 (2): 135–163. doi:`10.2307/1943531`.

———. 1946a. The mora forests of Trinidad, British West Indies. *Journal of Ecology* 33 (2): 173–192. `http://www.jstor.org/stable/2256464`.

———. 1946b. *The natural vegetation of Trinidad.* Vol. 20. Oxford Forestry Memoirs. Oxford: Clarendon Press.

———. 1949. *The natural vegetation of the Windward and Leeward Islands.* Vol. 21. Oxford Forestry Memoirs. Oxford: Clarendon Press.

Beaumont, L. J., L. Hughes and A. J. Pitman. 2008. Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters* 11 (11): 1135–1146. doi:`10.1111/j.1461-0248.2008.01231.x`.

Bekele, F. L. 2003. The History of Cocoa Production in Trinidad and Tobago. Presented at the Seminar/exhibition on revitalization of the Trinidad and Tobago cocoa industry: targets, problems and options, the Association of Professional Agricultural Scientists of Trinidad and Tobago. `http://sta.uwi.edu/cru/fb-hocp-ncnp.pdf`.

Benestad, R. 2004. Empirical-statistical downscaling in climate modeling. *Eos, Transactions, American Geophysical Union* 85 (42): 417–422. doi:`10.1029/2004EO420002`.

Benning, T. L., D. LaPointe, C. T. Atkinson and P. M. Vitousek. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proceedings of the National Academy of Sciences of the United States of America* 99 (22): 14246–14249. doi:`10.1073/pnas.162372399`.

Bergstrom, D. M., and S. L. Chown. 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology & Evolution* 14 (12): 472–477. doi:`10.1016/S0169-5347(99)01688-2`.

Berry, P. M., T. P. Dawson, P. A. Harrison and R. G. Pearson. 2002. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography* 11 (6): 453–462. doi:`10.1111/j.1466-8238.2002.00304.x`.

Berry, P. M., P. A. Harrison, T. P. Dawson and C. A. Walmsley, eds. 2005. *Modelling Natural Resource Responses to Climate Change (MONARCH): a local approach.* UKCIP Technical Report. Oxford: United Kingdom Climate Impacts Programme (UKCIP).

Berry, P. M., J. R. O'Hanley, C. L. Thomson, P. A. Harrison, G. J. Masters and T. P. Dawson, eds. 2007. *Modelling Natural Resource Responses to Climate Change (MONARCH): MONARCH 3 contract report.* UKCIP Technical Report. Oxford: United Kingdom Climate Impacts Programme (UKCIP).

Bloem, S. J. van, P. G. Murphy, A. E. Lugo, R. Ostertag, M. R. Costa, I. R. Bernard, S. M. Colón and M. C. Mora. 2005. The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. *Biotropica* 37 (4): 571–583. doi:`10.1111/j.1744-7429.2005.00074.x`.

Botkin, D. B., H. Saxe, M. B. Araújo, R. Betts, R. H. W. Bradshaw, T. Cedhagen, P. Chesson, T. P. Dawson, J. R. Etterson, D. P. Faith, S. Ferrier, A. Guisan, A. S. Hansen, D. W. Hilbert, C. Loehle, C. Margules, M. New, M. J. Sobel and D. R. B. Stockwell. 2007. Forecasting the effects of global warming on biodiversity. *BioScience* 57 (3): 227–236. doi:`10.1641/B570306`.

Bowles, M., and J. McBride. 1996. Pitcher's thistle (*Cirsium pitcheri*) reintroduction. In *Restoring diversity: strategies for reintroduction of endangered plants,* ed. D. A. Falk, C. I. Millar and M. Olwell, 423–432. Washington, DC: Island Press. ISBN:1559632976.

Box, E. O. 1981. Predicting physiognomic vegetation types with climate variables. *Plant Ecology* 45 (2): 127–139. doi:`10.1007/bf00119222`.

Bray, J. R., and J. T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27 (4): 325–349. doi:`10.2307/1942268`.

Brook, B. W., H. R. Akçakaya, D. A. Keith, G. M. Mace, R. G. Pearson and M. B. Araújo. 2009. Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters* 5 (6): 723–725. doi:`10.1098/rsbl.2009.0480`.

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. *Science* 313 (5783): 58–61. doi:`10.1126/science.1127609`.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin and C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16 (4): 909–923. doi:`10.1046/j.1523-1739.2002.00530.x`.

Brothers, T. S. 1997. Deforestation in the Dominican Republic: a village-level view. *Environmental Conservation* 24 (03): 213–223. doi:`10.1017/S0376892997000301`.

Brown, N., T. Geoghegan and Y. Renard. 2007. *A situation analysis for the wider Caribbean.* Gland, Switzerland: International Union for Conservation of Nature (IUCN). `http://data.iucn.org/dbtw-wpd/edocs/2007-035.pdf`.

Burgman, M. A., D. B. Lindenmayer and J. Elith. 2005. Managing landscapes for conservation under uncertainty. *Ecology* 86 (8): 2007–2017. doi:`10.1890/04-0906`.

Busby, J. R. 1991. Bioclim – a bioclimate analysis and prediction system. *Plant Protection Quarterly* 6 (1): 8–9.

Callaway, R. M., and J. L. Maron. 2006. What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology & Evolution* 21 (7): 369–374. doi:`10.1016/j.tree.2006.04.008`.

Cambers, C., R. Claro, R. Juman and S. Scott. 2008. *Climate change impacts on coastal and marine biodiversity in the insular Caribbean: Report of Working Group II, Climate Change and Biodiversity in the Insular Caribbean.* 382. Technical Report. Port of Spain, Trinidad: Caribbean Natural Resources Institute (CANARI). `http://www.canari.org/CCBIC%20WG%20II%20-%20final.pdf`.

Campbell, J. D., M. A. Taylor, T. S. Stephenson, R. A. Watson and F. S. Whyte. 2011. Future climate of the Caribbean from a regional climate model. *International Journal of Climatology* 31 (12): 1866–1878. doi:`10.1002/joc.2200`.

Canadell, J. G., C. L. Quéré, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton and G. Marland. 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America* 104 (47): 18866–18870. doi:`10.1073/pnas.0702737104`.

Carlquist, S. J. 1965. *Island life: a natural history of the islands of the world.* Garden City, NY: Published for the American Museum of Natural History [by] the Natural History Press.

———. 1980. *Hawaii: a natural history.* 2nd ed. Hawaii: Pacific Tropical Botanical Gardens. ISBN:0915809192.

Carlquist, S. 1966a. The biota of long-distance dispersal. I. Principles of dispersal and evolution. *The Quarterly Review of Biology* 41 (3): 247–270. `http://www.jstor.org/stable/2819932`.

———. 1966b. The biota of long-distance dispersal. II. Loss of dispersibility in Pacific Compositae. *Evolution* 20 (1): 30–48. `http://www.jstor.org/stable/2406147`.

Carvalho, S. B., J. C. Brito, E. G. Crespo, M. E. Watts and H. P. Possingham. 2011. Conservation planning under climate change: toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. *Biological Conservation* 144 (7): 2020–2030. doi:`10.1016/j.biocon.2011.04.024`.

Castillo, A., and V. M. Toledo. 2000. Applying ecology in the third world: the case of Mexico. *BioScience* 50 (1): 66–76. doi:`10.1641/0006-3568(2000)050[0066:AEITTW]2.3.CO;2`.

Chalmers, W. S. 1981. Forests. Chap. 8 in *The natural resources of Trinidad and Tobago,* ed. S. G. C. Cooper and P. R. Bacon. London: Edward Arnold. ISBN:0713180129.

Chape, S., M. D. Spalding and M. D. Jenkins. 2008. The Caribbean. Chap. Regional analysis 2 in *The world's protected areas: status, values, and prospects in the twenty-first century: status, values and prospects in the 21*st *century,* 190–198. Prepared by the UNEP World Conservation Monitoring Centre. Berkeley: University of California Press. ISBN:9780520246607.

Chapuis, J.-L., Y. Frenot and M. Lebouvier. 2004. Recovery of native plant communities after eradication of rabbits from the subantarctic Kerguelen Islands, and influence of climate changes. *Biological Conservation* 117 (2): 167–179. doi:`10.1016/S0006-3207(03)00290-8`.

Charlery, J., and L. Nurse. 2010. Areal downscaling of global climate models: an approach that avoids data remodeling. *Climate Research* 43 (3): 241–249. doi:`10.3354/cr00875`.

Chefaoui, R. M., and J. M. Lobo. 2008. Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling* 210 (4): 478–486. doi:`10.1016/j.ecolmodel.2007.08.010`.

Chen, A., M. Taylor, A. Centella and D. Farrell. 2008. *Climate trends and scenarios for climate change in the insular Caribbean: Report of Working Group I, Climate Change and Biodiversity in the Insular Caribbean.* 381. Technical Report. Port of Spain, Trinidad: Caribbean Natural Resources Institute (CANARI). `http://www.canari.org/docs/CCBIC%20WG%20I%20final.pdf`.

Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *The American Naturalist* 152 (2): 204–224. doi:`10.1086/286162`.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18 (1): 117–143. doi:`10.1111/j.1442-9993.1993.tb00438.x`.

Clarke, K. R., and R. N. Gorley. 2006. *PRIMER v6: user manual/tutorial.* Plymouth, UK: PRIMER-E.

Clarke, K. R., and R. M. Warwick. 2001. *Change in marine communities: an approach to statistical analysis and interpretation.* 2nd ed. Plymouth, UK: PRIMER-E.

Clements, F. E. 1928. *Plant succession and indicators: a definitive edition of plant succession and plant indicators.* New York: H. W. Wilson Company. `http://www.jstor.org/stable/2256278`.

———. 1936. Nature and structure of the climax. *Journal of Ecology* 24 (1): 252–284. `http://www.jstor.org/stable/2256278`.

Cody, M. L., and J. M. Overton. 1996. Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* 84 (1): 53–61. `http://www.jstor.org/stable/2261699`.

Coetzee, B. W. T., M. P. Robertson, B. F. N. Erasmus, B. J. van Rensburg and W. Thuiller. 2009. Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography* 18 (6): 701–710. doi:`10.1111/j.1466-8238.2009.00485.x`.

Collingham, Y. C., and B. Huntley. 2000. Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications* 10 (1): 131–144. doi:`10.1890/1051-0761(2000)010[0131:IOHFAP]2.0.CO;2`.

Consiglio, T., G. E. Schatz, G. McPherson, P. P. Lowry, J. Rabenantoandro, Z. S. Rogers, R. Rabevohitra and D. Rabehevitra. 2006. Deforestation and plant diversity of Madagascar's littoral forests. *Conservation Biology* 20 (6): 1799–1803. doi:`10.1111/j.1523-1739.2006.00562.x`.

Coppin, A., and R. N. Olsen. 2007. Public vs. private sector earnings differentials in the Caribbean Region: evidence from the economy of Trinidad & Tobago. *The Journal of developing areas* 40 (2): 51–74. doi:`10.1353/jda.2007.0017`.

Coulston, J. W., and K. H. Riitters. 2005. Preserving biodiversity under current and future climates: a case study. *Global Ecology and Biogeography* 14 (1): 31–38. doi:`10.1111/j.1466-822X.2004.00135.x`.

Cronk, Q. C. B. 1997. Islands: stability, diversity, conservation. *Biodiversity and Conservation* 6 (3): 477–493. doi:`10.1023/A:1018372910025`.

Cropper, M., J. Puri and C. Griffiths. 2001. Predicting the location of deforestation: the role of roads and protected areas in North Thailand. *Land Economics* 77 (2): 172–186. `http://www.jstor.org/stable/3147088`.

Crossman, N. D., and D. A. Bass. 2008. Application of common predictive habitat techniques for post-border weed risk management. *Diversity and Distributions* 14 (2): 213–224. doi:`10.1111/j.1472-4642.2007.00436.x`.

Daehler, C. C., J. S. Denslow, S. Ansari and H.-C. Kuo. 2004. A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Conservation Biology* 18 (2): 360–368. doi:`10.1111/j.1523-1739.2004.00066.x`.

Daly, C., J. W. Smith, J. I. Smith and R. B. McKane. 2007. High-resolution spatial modeling of daily weather elements for a catchment in the Oregon Cascade Mountains, United States. *Journal of Applied Meteorology and Climatology* 46 (10): 1565–1586. doi:`10.1175/jam2548.1`.

Day, O. 2009. *The impacts of climate change on biodiversity in Caribbean islands: what we know, what we need to know, and building capacity for effective adaptation.* 386. Technical Report. Port of Spain, Trinidad: Caribbean Natural Resources Institute (CANARI). `http://www.canari.org/CANARI%20Tech%20Report%20386.pdf`.

De Marco, P., J. A. F. Diniz-Filho and L. M. Bini. 2008. Spatial analysis improves species distribution modelling during range expansion. *Biology Letters* 4 (5): 577–580. doi:`10.1098/rsbl.2008.0210`.

DeFries, R., A. Hansen, A. C. Newton and M. C. Hansen. 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecological Applications* 15 (1): 19–26. doi:`10.1890/03-5258`.

Department of Plant Sciences, University of Oxford. 2004. *BRAHMS - Botanical Research and Herbarium Management System. Version 5.54.* `http://dps.plants.ox.ac.uk/bol/`.

Diffenbaugh, N. S., F. Giorgi and J. S. Pal. 2008. Climate change hotspots in the United States. *Geophysical Research Letters* 35:L16709. doi:`10.1029/2008gl035075`.

Dillon Consulting. 2004. *Long-term development planning study – towards vision 2020: environment and natural resources management for Trinidad and Tobago.* Inter-American Development Bank (IADB).

Dobrowski, S. Z., J. H. Thorne, J. A. Greenberg, H. D. Safford, A. R. Mynsberge, S. M. Crimmins and A. K. Swanson. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. *Ecological Monographs* 81 (2): 241–257. doi:`10.1890/10-1325.1`.

Dormann, C. 2007. Promising the future? Global change projections of species distributions. *Basic and Applied Ecology* 8 (5): 387–397. doi:`10.1016/j.baae.2006.11.001`.

DPSOX. *See* Department of Plant Sciences, University of Oxford.

Driver, T. 2001. *Comparative study of land administration systems: Trinidad & Tobago case study.* Trinidad & Tobago: Ministry of Agriculture, Land and Marine Resources. `http://www.landcoalition.org/pdf/wbtcstnt.pdf`.

Dunn, R. R. 2004. Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18 (2): 302–309. doi:`10.1111/j.1523-1739.2004.00151.x`.

Ebdon, D. 1985. *Statistics in geography.* 2nd ed. Oxford: Blackwell Publishing. ISBN:0631136886.

Echarri, F., C. Tambussi and C. Acosta Hospitaleche. 2009. Predicting the distribution of the crested tinamous, *Eudromia* spp. (Aves, Tinamiformes). *Journal of Ornithology* 150 (1): 75–84. doi:`10.1007/s10336-008-0319-5`.

ECLAC. *See* Economic Commission for Latin America and the Caribbean.

Economic Commission for Latin America and the Caribbean. 2009. *Economic survey of Latin America and the Caribbean 2008–2009.* Santiago, Chile. `http://www.eclac.org/publicaciones/xml/5/36465/2009-484-EEI-BOOK_WEB.pdf`.

Elith, J., and C. H. Graham. 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. *Ecography* 32 (1): 66–77. doi:`10.1111/j.1600-0587.2008.05505.x`.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697. doi:`10.1146/annurev.ecolsys.110308.120159`.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17 (1): 43–57. doi:`10.1111/j.1472-4642.2010.00725.x`.

Ellis, E. A., and L. Porter-Bolland. 2008. Is community-based forest management more effective than protected areas? A comparison of land use/land cover change in two neighboring study areas of the Central Yucatan Peninsula, Mexico. *Forest Ecology and Management* 256 (11): 1971–1983. doi:`10.1016/j.foreco.2008.07.036`.

EMA. *See* Environmental Management Authority.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* 436:686–688. doi:`10.1038/nature03906`.

Environmental Management Authority. 1999. *The legislative and institutional landscape for protection of the environment in Trinidad & Tobago.* State of the Environment Report 1999. `http://www.ema.co.tt/docs/techServ/SOE/1999_SOE.pdf`.

———. 2005. *Report of an assessment of the Northern Range, Trinidad and Tobago: people and the Northern Range.* State of the Environment Report 2004. `http://www.ema.co.tt/docs/techServ/SOE/EMA%20SOE%20Report%202004.pdf`.

Environmental Systems Research Institute. 2009. *ArcGIS. Version 9.3.* Redlands, CA. `http://www.arcgis.com/`.

ESRI. *See* Environmental Systems Research Institute.

Etterson, J. R., and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294 (5540): 151–154. doi:`10.1126/science.1063656`.

Evelyn, O. B., and R. Camirand. 2003. Forest cover and deforestation in Jamaica: an analysis of forest cover estimates over time. *International Forestry Review* 5 (4): 354–363. doi:`10.1505/IFOR.5.4.354.22659`.

Eyre, L. A. 1987. Jamaica: test case for tropical deforestation? *Ambio* 16 (6): 338–343. `http://www.jstor.org/stable/4313397`.

Fairhead, J., and M. Leach. 2003. *Science, society and power: environmental knowledge and policy in West Africa and the Caribbean.* Cambridge: Cambridge University Press. ISBN:0521535663.

Fairhead, J., and M. Leach. 2002. ‘Sustainable’ timber production and science/policy processes in Trinidad. *IDS Bulletin* 33 (1): 75–83. doi:`10.1111/j.1759-5436.2002.tb00009.x`.

FAO. *See* Food and Agriculture Organization of the United Nations.

Feeley, K. J., and M. R. Silman. 2011. Keep collecting: accurate species distribution modelling requires more collections than previously thought. *Diversity and Distributions* 17 (6): 1132—1140. doi:`10.1111/j.1472-4642.2011.00813.x`.

Ferraro, P. J., and S. K. Pattanayak. 2006. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. *PLoS Biology* 4, no. 4 (Apr.): e105. doi:`10.1371/journal.pbio.0040105`.

Ferrier, S., G. Watson, J. Pearce and M. Drielsma. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. *Biodiversity and Conservation* 11 (12): 2275–2307. doi:`10.1023/a:1021302930424`.

Fiedler, P. L., P. S. White and R. A. Leidy. 1997. The paradigm shift in ecology and its implications for conservation. Chap. 6 in *The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity,* ed. S. Pickett, R. S. Ostfeld, M. Shachak and G. E. Likens. New York: Chapman & Hall. ISBN:0412098512.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24 (01): 38–49. doi:`10.1017/S0376892997000088`.

Fischer, J., D. B. Lindenmayer and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment* 4 (2): 80–86. doi:`10.1890/1540-9295(2006)004[0080:BEFART]2.0.CO;2`.

Fitzpatrick, M. C., A. D. Gove, N. J. Sanders and R. R. Dunn. 2008. Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. *Global Change Biology* 14 (6): 1337–1352. doi:`10.1111/j.1365-2486.2008.01559.x`.

Food and Agriculture Organization of the United Nations. 2010. *Global Forest Resources Assessment 2010: Country Report – Trinidad and Tobago.* `http://www.fao.org/docrep/013/al647E/al647e.pdf`.

Fowler, H. J., S. Blenkinsop and C. Tebaldi. 2007. Linking climate change modelling to impacts studies: recent advances in downscaling techniques for hydrological modelling. *International Journal of Climatology* 27 (12): 1547–1578. doi:`10.1002/joc.1556`.

Franklin, J. F. 2009. *Mapping species distributions: spatial inference and prediction.* Cambridge, UK: Cambridge University Press.

Franklin, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* 19 (4): 474–499. doi:`10.1177/030913339501900403`.

Franklin, J., K. E. Wejnert, S. A. Hathaway, C. J. Rochester and R. N. Fisher. 2009. Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. *Diversity and Distributions* 15 (1): 167–177. doi:`10.1111/j.1472-4642.2008.00536.x`.

Franks, S. J., S. Sim and A. E. Weis. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences of the United States of America* 104 (4): 1278–1282. doi:`10.1073/pnas.0608379104`.

Freed, L. A., R. L. Cann, M. L. Goff, W. A. Kuntz and G. R. Bodner. 2005. Increase in avian malaria at upper elevations in Hawaii. *The Condor* 107 (4): 753–764. doi:`10.1650/7820.1`.

Frenot, Y., S. L. Chown, J. Whinam, P. M. Selkirk, P. Convey, M. Skotnicki and D. M. Bergstrom. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* 80 (1): 45–72. doi:`10.1017/S1464793104006542`.

Fuller, D. O. 2006. Tropical forest monitoring and remote sensing: a new era of transparency in forest governance? *Singapore Journal of Tropical Geography* 27 (1): 15–29. doi:`10.1111/j.1467-9493.2006.00237.x`.

Gaveau, D. L. A., H. Wandono and F. Setiabudi. 2007. Three decades of deforestation in southwest Sumatra: have protected areas halted forest loss and logging, and promoted re-growth? *Biological Conservation* 134 (4): 495–504. doi:`10.1016/j.biocon.2006.08.035`.

Gaveau, D. L. A., M. Linkie, Suyadi, P. Levang and N. Leader-Williams. 2009. Three decades of deforestation in southwest Sumatra: effects of coffee prices, law enforcement and rural poverty. *Biological Conservation* 142 (3): 597–605. doi:`10.1016/j.biocon.2008.11.024`.

Gitay, H., A. Suárez, R. T. Watson and D. J. Dokken. 2002. *Climate change and biodiversity.* IPCC Technical Paper V. Geneva, Switzerland: Intergovernmental Panel on Climate Change (IPCC). `http://www.ipcc.ch/pdf/technical-papers/climate-changes-biodiversity-en.pdf`.

Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53 (1): 7–26. `http://www.jstor.org/stable/2479933`.

GOTT. *See* Government of Trinidad and Tobago.

Government of Trinidad and Tobago. 1972a. 1:25,000 Soil Map Series. Ministry of Agriculture, Land and Marine Resources. Lands and Surveys Division.

———. 1972b. 1:25,000 Topographic Map Series, Sheet Numbers 3–76. Ministry of Agriculture, Land and Marine Resources. Lands and Surveys Division.

———. 1972c. *Land capability survey of Trinidad and Tobago.* Ministry of Agriculture, Land and Marine Resources.

———. 2009a. *National forestry policy draft.* Ministry of Agriculture, Land and Marine Resources.

———. 2009b. *National protected areas policy draft.* Ministry of Planning, Housing and the Environment.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz and A. T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution* 19 (9): 497–503. doi:`10.1016/j.tree.2004.07.006`.

Graham, C. H., B. A. Loiselle, J. Velásquez-Tibatá and F. Cuesta-Camacho. 2009. Species distribution modeling and the challenge of predicting future distributions. Chap. 21 in *Climate change and biodiversity in the tropical Andes,* ed. S. K. Herzog, R. Martínez, P. M. Jørgensen and H. Tiessen, 295–310. Inter-American Institute for Global Change Research (IAI) / Scientific Committee on Problems of the Environment (SCOPE). ISBN:9788599875056, `http://www.iai.int/files/communications/publications/scientific/Climate_Change_and_Biodiversity_in_the_Tropical_Andes/chapter21.pdf`.

Graham, R. W., and E. C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology & Evolution* 5 (9): 289–292. doi:`10.1016/0169-5347(90)90083-p`.

Grau, H. R., T. M. Aide, J. K. Zimmerman, J. R. Thomlinson, E. Helmer and X. Zou. 2003. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *BioScience* 53 (12): 1159–1168. doi:`10.1641/0006-3568(2003)053[1159:TECOSA]2.0.CO;2`.

Griffith, R. 1987. *A programme for the rehabilitation of cocoa and coffee in Trinidad and Tobago.* St. Augustine, Trinidad and Tobago: Cocoa Research Unit, University of the West Indies.

Grist, E. P. M., A. O'Hagan, M. Crane, N. Sorokin, I. Sims and P. Whitehouse. 2005. Bayesian and time-independent species sensitivity distributions for risk assessment of chemicals. *Environmental Science & Technology* 40 (1): 395–401. doi:`10.1021/es050871e`.

Groombridge, B., ed. 1992. *Global biodiversity: status of the earth's living resources.* London: Chapman & Hall. ISBN:0412472406.

Grumbine, R. E. 1997. Reflections on "What is ecosystem management?" *Conservation Biology* 11 (1): 41–47. doi:`10.1046/j.1523-1739.1997.95479.x`.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8 (9): 993–1009. doi:`10.1111/j.1461-0248.2005.00792.x`.

Guisan, A., A. Lehmann, S. Ferrier, M. Austin, J. M. C. Overton, R. Aspinall and T. Hastie. 2006. Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology* 43 (3): 386–392. doi:`10.1111/j.1365-2664.2006.01164.x`.

Gunderson, L. H., and C. S. Holling, eds. 2001. *Panarchy: understanding transformations in human and natural systems.* Washington, DC: Island Press. ISBN:1559638579.

Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* 19 (9): 470–474. doi:`10.1016/j.tree.2004.07.005`.

Gutiérrez, D., P. Fernández, A. S. Seymour and D. Jordano. 2005. Habitat distribution models: are mutualist distributions good predictors of their associates? *Ecological Applications* 15 (1): 3–18. doi:`10.1890/03-5344`.

Halley, J. M., S. Hartley, A. S. Kallimanis, W. E. Kunin, J. J. Lennon and S. P. Sgardelis. 2004. Uses and abuses of fractal methodology in ecology. *Ecology Letters* 7 (3): 254–271. doi:`10.1111/j.1461-0248.2004.00568.x`.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography* 13 (5): 469–471. doi:`10.1111/j.1466-822X.2004.00090.x`.

Hannah, L., G. F. Midgley, T. Lovejoy, W. J. Bond, M. Bush, J. C. Lovett, D. Scott and F. I. Woodward. 2002. Conservation of biodiversity in a changing climate. *Conservation Biology* 16 (1): 264–268. doi:`10.1046/j.1523-1739.2002.00465.x`.

Hannah, L., G. Midgley, G. Hughes and B. Bomhard. 2005. The view from the cape: extinction risk, protected areas, and climate change. *BioScience* 55 (3): 231–242. doi:`10.1641/0006-3568(2005)055[0231:TVFTCE]2.0.CO;2`.

Hannah, L. 2008. Protected areas and climate change. *Annals of the New York Academy of Sciences* 1134 (1): 201. doi:`10.1196/annals.1439.009`.

———. 2010. A global conservation system for climate-change adaptation. *Conservation Biology* 24 (1): 70–77. doi:`10.1111/j.1523-1739.2009.01405.x`.

Hannah, L., G. Midgley, S. Andelman, M. Araújo, G. Hughes, E. Martinez-Meyer, R. Pearson and P. Williams. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* 5 (3): 131–138. doi:`10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2`.

Hannah, L., R. Dave, P. P. Lowry, S. Andelman, M. Andrianarisata, L. Andriamaro, A. Cameron, R. Hijmans, C. Kremen, J. MacKinnon, H. H. Randrianasolo, S. Andriambololonera, A. Razafimpahanana, H. Randriamahazo, J. Randrianarisoa, P. Razafinjatovo, C. Raxworthy, G. E. Schatz, M. Tadross and L. Wilmé. 2008. Climate change adaptation for conservation in Madagascar. *Biology Letters* 4 (5): 590–594. doi:`10.1098/rsbl.2008.0270`.

Hansen, D. M., C. N. Kaiser and C. B. Müller. 2008. Seed dispersal and establishment of endangered plants on oceanic islands: the Janzen-Connell model, and the use of ecological analogues. *PLoS ONE* 3 (5): e2111. doi:`10.1371/journal.pone.0002111`.

Hansen, L. J., J. L. Biringer and J. R. Hoffmann, eds. 2003. *Buying time: a user's manual for building resistance and resilience to climate change in natural systems.* Berlin: WWF Climate Change Program. `http://assets.panda.org/downloads/buyingtime_unfe.pdf`.

Hawkins, E., and R. Sutton. 2009. The potential to narrow uncertainty in regional climate predictions. *Bulletin of the American Meteorological Society* 90 (8): 1095–1107. doi:`10.1175/2009BAMS2607.1`.

———. 2011. The potential to narrow uncertainty in projections of regional precipitation change. *Climate Dynamics* 37 (1): 407–418. doi:`10.1007/s00382-010-0810-6`.

Hawthorne, W. D., and M. Abu-Juam. 1995. *Forest protection in Ghana: with particular reference to vegetation and plant species.* Gland, Switzerland and Cambridge, UK: IUCN in collaboration with ODA and the Forest Department Republic of Ghana. ISBN:2831702615.

Heikkinen, R. K., M. Luoto, M. B. Araújo, R. Virkkala, W. Thuiller and M. T. Sykes. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* 30 (6): 751–777. doi:`10.1177/0309133306071957`.

Helmer, E. H. 2004. Forest conservation and land development in Puerto Rico. *Landscape Ecology* 19 (1): 29–40. doi:`10.1023/B:LAND.0000018364.68514.fb`.

Helmer, E. H., O. Ramos, T. D. M. López, M. Quiñonez and W. Díaz. 2002. Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. *Caribbean Journal of Science* 38 (3-4): 165–183. `http://academic.uprm.edu/publications/cjs/Vol38b/38_165-183.pdf`.

Helmer, E. H., T. A. Kennaway, D. H. Pedreros, M. L. Clark, H. Marcano-Vega, L. L. Tieszen, T. R. Ruzycki, S. R. Schill and C. M. S. Carrington. 2008. Land cover and forest formation distributions for St. Kitts, Nevis, St. Eustatius, Grenada and Barbados from decision tree classification of cloud-cleared satellite imagery. *Caribbean Journal of Science* 44, no. 2 (July): 175–198. `http://caribjsci.org/July08/44_175-198.pdf`.

Hernandez, P. A., C. H. Graham, L. L. Master and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29 (5): 773–785. doi:`10.1111/j.0906-7590.2006.04700.x`.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12 (3): 450–455. doi:`10.1111/j.1365-2486.2006.01116.x`.

Hijmans, R. J., and C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* 12 (12): 2272–2281. doi:`10.1111/j.1365-2486.2006.01256.x`.

Hijmans, R. J., L. Guarino, A. Jarvis, R. O'Brien, P. Mathur, C. Bussink, M. Cruz, I. Barrantes and E. Rojas. 2005a. *DIVA-GIS. Version 5.2: manual.* `http://www.diva-gis.org/`.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones and A. Jarvis. 2005b. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25 (15): 1965–1978. doi:`10.1002/joc.1276`.

Hirzel, A. H., and G. Le Lay. 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45 (5): 1372–1381. doi:`10.1111/j.1365-2664.2008.01524.x`.

Hodder, K. H., and J. M. Bullock. 1997. Translocations of native species in the UK: implications for biodiversity. *Journal of Applied Ecology* 34 (3): 547–565. doi:`10.2307/2404906`.

Hodgson, J. A., C. D. Thomas, B. A. Wintle and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology* 46 (5): 964–969. doi:`10.1111/j.1365-2664.2009.01695.x`.

Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi and M. E. Hatziolos. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318 (5857): 1737–1742. doi:`10.1126/science.1152509`.

Hof, C., I. Levinsky, M. B. Araújo and C. Rahbek. 2011. Rethinking species' ability to cope with rapid climate change. *Global Change Biology* 17 (9): 2987–2990. doi:`10.1111/j.1365-2486.2011.02418.x`.

Holdridge, L. R. 1964. *Life zone ecology.* San Jose, Costa Rica: Tropical Science Centre.

Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters* 12 (5): 420–431. doi:`10.1111/j.1461-0248.2009.01297.x`.

Holt, R. D. 1990. The microevolutionary consequences of climate change. *Trends in Ecology & Evolution* 5 (9): 311–315. doi:`10.1016/0169-5347(90)90088-u`.

Honychurch, L. 1997. Crossroads in the Caribbean: a site of encounter and exchange on Dominica. *World Archaeology* 28 (3): 291–304. doi:`10.1080/00438243.1997.9980349`.

Hosein, R. 2007. Booming hydrocarbon exports, deagriculturalization and food security in Trinidad and Tobago. *Farm & Business: The Journal of the Caribbean Agro-Economic Society* 7 (1): 51–79. `http://purl.umn.edu/36801`.

Hossell, J. E., N. E. Ellis, M. J. Harley and I. R. Hepburn. 2003. Climate change and nature conservation: implications for policy and practice in Britain and Ireland. *Journal for Nature Conservation* 11 (1): 67–73. doi:`10.1078/1617-1381-00034`.

Hunter, M. L. 2007. Climate change and moving species: furthering the debate on assisted colonization. *Conservation Biology* 21 (5): 1356–1358. doi:`10.1111/j.1523-1739.2007.00780.x`.

Huntley, B., Y. C. Collingham, R. E. Green, G. M. Hilton, C. Rahbek and S. G. Willis. 2006. Potential impacts of climatic change upon geographical distributions of birds. *IBIS* 148:8–28. doi:`10.1111/j.1474-919X.2006.00523.x`.

Huston, M. A. 1994. *Biological diversity: the co-existence of species.* Cambridge, UK: Cambridge University Press. ISBN:0521369304.

ICL. *See* Institutional Consultants (International) Ltd.

Imbert, D., and J. Portecop. 2008. Hurricane disturbance and forest resilience: assessing structural vs. functional changes in a Caribbean dry forest. *Forest Ecology and Management* 255 (8–9): 3494–3501. doi:`10.1016/j.foreco.2008.02.030`.

Institutional Consultants (International) Ltd. 1980. *Inventory of the indigenous forests of Trinidad and Tobago. Vol. X.* Government of Trinidad and Tobago.

Intergovernmental Panel on Climate Change. 2007. *Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Ed. Core Writing Team, R. K. Pachauri and A. Reisinger. Geneva, Switzerland. `http://www.ipcc.ch/publications_and_data/ar4/syr/en/contents.html`.

IPCC. *See* Intergovernmental Panel on Climate Change.

Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs* 68 (4): 465–485. doi:`10.1890/0012-9615(1998)068[0465:PAOTSF]2.0.CO;2`.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical rainforests. *American Naturalist* 104:501–527. doi:`10.1086/282687`.

Jehu, A. 2011. Use of principal component analysis and geostatistics for the derivation of a forest fragmentation model. MSc. diss. Department of Geomatics Engineering and Land Management, University of the West Indies.

Jeschke, J. M., and D. L. Strayer. 2008. Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences* 1134 (1): 1–24. doi:`10.1196/annals.1439.002`.

Jetz, W., D. S. Wilcove and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5 (6): 1211–1219. doi:`10.1371/journal.pbio.0050157`.

Jetz, W., H. Kreft, G. Ceballos and J. Mutke. 2009. Global associations between terrestrial producer and vertebrate consumer diversity. *Proceedings of the Royal Society B: Biological Sciences* 276 (1655): 269–278. doi:`10.1098/rspb.2008.1005`.

Jiménez-Valverde, A., J. M. Lobo and J. Hortal. 2008. Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions* 14 (6): 885–890. doi:`10.1111/j.1472-4642.2008.00496.x`.

Jones, R. G., M. Noguer, D. C. Hassell, D. Hudson, J. Wilson S. S., G. Jenkins and J. F. B. Mitchell. 2004. *Generating high resolution climate change scenarios using PRECIS.* Exeter, UK: Met Office Hadley Centre. `http://precis.metoffice.com/docs/PRECIS_Handbook.pdf`.

Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, M. Stervander, A. Andersson, J. Waldenström, A. Lehikoinen, E. Edvardsen, R. Solvang and N. C. Stenseth. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312 (5782): 1959–1961. doi:`10.1126/science.1126119`.

Joppa, L. N., S. R. Loarie and S. L. Pimm. 2008. On the protection of “protected areas”. *Proceedings of the National Academy of Sciences of the United States of America* 105 (18): 6673–6678. doi:`10.1073/pnas.0802471105`.

Joseph, E. L. 1970. Geology. Chap. 2 in *History of Trinidad.* The West Indies 13. London: Frank Cass & Co. (Orig. pub. 1838.) ISBN:0714619396.

Kark, S., N. Levin, H. S. Grantham and H. P. Possingham. 2009. Between-country collaboration and consideration of costs increase conservation planning efficiency in the Mediterranean Basin. *Proceedings of the National Academy of Sciences of the United States of America* 106 (36): 15368–15373. doi:`10.1073/pnas.0901001106`.

Kearney, M. R., B. A. Wintle and W. P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters* 3 (3): 203–213. doi:`10.1111/j.1755-263X.2010.00097.x`.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12 (4): 334–350. doi:`10.1111/j.1461-0248.2008.01277.x`.

Keith, D. A., H. R. Akçakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araújo and T. G. Rebelo. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* 4 (5): 560–563. doi:`10.1098/rsbl.2008.0049`.

Kennaway, T., and E. H. Helmer. 2007. The forest types and ages cleared for land development in Puerto Rico. *GIScience & Remote Sensing* 44 (4): 356–382. doi:`10.2747/1548-1603.44.4.356`.

Kennedy, H. 2004. *Data in three dimensions: a guide to ArcGIS 3D analyst.* New York: OnWord Press. ISBN:1401848869.

Kenny, J. S. 2000. *Views from the ridge: exploring the natural history of Trinidad and Tobago.* Port-of-Spain, Trinidad and Tobago: Prespect Press. ISBN:9769505706.

Kremen, C., A. Cameron, A. Moilanen, S. J. Phillips, C. D. Thomas, H. Beentje, J. Dransfield, B. L. Fisher, F. Glaw, T. C. Good, G. J. Harper, R. J. Hijmans, D. C. Lees, E. Louis, R. A. Nussbaum, C. J. Raxworthy, A. Razafimpahanana, G. E. Schatz, M. Vences, D. R. Vieites, P. C. Wright and M. L. Zjhra. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* 320 (5873): 222–226. doi:`10.1126/science.1155193`.

Kudo, G., Y. Nishikawa, T. Kasagi and S. Kosuge. 2004. Does seed production of spring ephemerals decrease when spring comes early? *Ecological Research* 19 (2): 255–259. doi:`10.1111/j.1440-1703.2003.00630.x`.

Lackhan, N. 1980. *The Northern Range Reafforestation Project.* Trinidad and Tobago: Government Printery.

———. 1984. Watershed management in Trinidad and Tobago. *Commonwealth Forestry Review* 63 (2): 107–114. `http://pdf.usaid.gov/pdf_docs/PNAAR903.pdf`.

Lamb, D., P. D. Erskine and J. A. Parrotta. 2005. Restoration of degraded tropical forest landscapes. *Science* 310 (5754): 1628–1632. doi:`10.1126/science.1111773`.

Lambin, E. F., and H. J. Geist. 2003. Regional differences in tropical deforestation. *Environment* 45 (6): 22–36.

Laurance, W. F. 2007. Have we overstated the tropical biodiversity crisis? *Trends in Ecology & Evolution* 22 (2): 65–70. doi:`10.1016/j.tree.2006.09.014`.

Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. P. Maurer, A. R. Blaustein and P. J. Bartlein. 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90 (3): 588–597. doi:`10.1890/08-0823.1`.

Le Maitre, D. C., W. Thuiller and L. Schonegevel. 2008. Developing an approach to defining the potential distributions of invasive plant species: a case study of *Hakea* species in South Africa. *Global Ecology and Biogeography* 17 (5): 569–584. doi:`10.1111/j.1466-8238.2008.00407.x`.

Leach, M. 2008. Pathways to sustainability in the forest? Misunderstood dynamics and the negotiation of knowledge, power, and policy. *Environment and Planning A* 40 (8): 1783–1795. doi:`10.1068/a40215`.

Lee, T. M., and W. Jetz. 2008. Future battlegrounds for conservation under global change. *Proceedings of the Royal Society B: Biological Sciences* 275 (1640): 1261–1270. doi:`10.1098/rspb.2007.1732`.

Lenoir, J., J. C. Gégout, P. A. Marquet, P. de Ruffray and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320 (5884): 1768–1771. doi:`10.1126/science.1156831`.

Levine, J. M., M. Vilà, C. M. D. Antonio, J. S. Dukes, K. Grigulis and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences* 270 (1517): 775–781. doi:`10.1098/rspb.2003.2327`.

Lillesand, T. M., R. W. Kiefer and J. W. Chipman. 2008. *Remote sensing and image interpretation.* 6th ed. Hoboken, NJ: John Wiley & Sons. ISBN:9780470052457.

Liu, C., P. M. Berry, T. P. Dawson and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28 (3): 385–393. doi:`10.1111/j.0906-7590.2005.03957.x`.

Liu, J., M. Linderman, Z. Ouyang, L. An, J. Yang and H. Zhang. 2001. Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. *Science* 292 (5514): 98–101. doi:`10.1126/science.1058104`.

Lobo, J. M., P. Jay-Robert and J.-P. Lumaret. 2004. Modelling the species richness distribution for French Aphodiidae (Coleoptera, Scarabaeoidea). *Ecography* 27 (2): 145–156. doi:`10.1111/j.0906-7590.2004.03609.x`.

Lugo, A. E. 2000. Effects and outcomes of Caribbean hurricanes in a climate change scenarios. *Science of The Total Environment* 262 (3): 243–251. doi:`10.1016/S0048-9697(00)00526-X`.

———. 2002. Can we manage tropical landscapes? An answer from the Caribbean perspective. *Landscape Ecology* 17 (7): 601–615. doi:`10.1023/A:1021419815480`.

Lugo, A. E., R. Schmidt and S. Brown. 1981. Tropical forests in the Caribbean. *Ambio* 10 (6): 318–324. `http://www.jstor.org/stable/4312728`.

Luoto, M., R. K. Heikkinen, J. Pöyry and K. Saarinen. 2006. Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography* 33 (10): 1764–1778. doi:`10.1111/j.1365-2699.2005.01395.x`.

MA. *See* Millennium Ecosystem Assessment.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39 (4): 599–619. doi:`10.2307/1931600`.

MacArthur, R. H., and E. O. Wilson. 2001. *The theory of island biogeography.* Princeton, NJ: Princeton University Press. (Orig. pub. 1967.) ISBN:9780691088365.

MacArthur, R. H., J. M. Diamond and J. R. Karr. 1972. Density compensation in island faunas. *Ecology* 53 (2): 330–342. doi:`10.2307/1934090`.

MacArthur, R., J. MacArthur, D. MacArthur and A. MacArthur. 1973. The effect of island area on population densities. *Ecology* 54 (3): 657–658. doi:`10.2307/1935357`.

Maharaj, K. 2010. *Interview by author.* Ministry of Food Production, Land and Marine Affairs of Trinidad and Tobago.

Mar López, T. del, T. M. Aide and J. R. Thomlinson. 2001. Urban expansion and the loss of prime agricultural lands in Puerto Rico. *Ambio* 30 (1): 49–54. doi:`10.1579/0044-7447-30.1.49`.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405 (6783): 243–253. doi:`10.1038/35012251`.

Marini, M. A., M. Barbet-Massin, L. E. Lopes and F. Jiguet. 2009. Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. *Biological Conservation* 142 (12): 3039–3050. doi:`10.1016/j.biocon.2009.08.002`.

Marini, M. A., M. Barbet-Massin, J. Martinez, N. P. Prestes and F. Jiguet. 2010. Applying ecological niche modelling to plan conservation actions for the Red-spectacled Amazon (Amazona pretrei). *Biological Conservation* 143 (1): 102–112. doi:`10.1016/j.biocon.2009.09.009`.

Marshall, R. C. 1925. *Report on forestry in Trinidad and Tobago.* Port-of-Spain, Trinidad.

———. 1926. *Conservator of forests administration report for the year 1925.* Port-of-Spain, Trinidad.

———. 1928. *Conservator of forests administration report for the year 1927.* Port-of-Spain, Trinidad.

———. 1934. *Trees of Trinidad and Tobago.* Port-of-Spain, Trinidad: Government Printing Office.

Martinuzzi, S., W. A. Gould and O. M. Ramos González. 2007. Land development, land use, and urban sprawl in Puerto Rico integrating remote sensing and population census data. *Landscape and Urban Planning* 79 (3-4): 288–297. doi:`10.1016/j.landurbplan.2006.02.014`.

Mas, J.-F. 2005. Assessing protected area effectiveness using surrounding (buffer) areas environmentally similar to the target area. *Environmental Monitoring and Assessment* 105 (1-3): 69–80. doi:`10.1007/s10661-005-3156-5`.

Maunder, M., A. Leiva, E. Santiago-Valentín, D. Stevenson, P. Acevedo-Rodríguez, A. Meerow, M. Mejía, C. Clubbe and J. Francisco-Ortega. 2008. Plant conservation in the Caribbean island biodiversity hotspot. *The Botanical Review* 74 (1): 197–207. doi:`10.1007/s12229-008-9007-7`.

McDonald-Madden, E., A. Gordon, B. A. Wintle, S. Walker, H. Grantham, S. Carvalho, M. Bottrill, L. Joseph, R. Ponce, R. Stewart and H. P. Possingham. 2009. Environment: “true” conservation progress. *Science* 323 (5910): 43–44. doi:`10.1126/science.1164342`.

McDonald, I. 2004. The sugar industry of the Caribbean Community (CARICOM): an overview. *International Sugar Journal* 106 (1266): 324–328.

McDonald, R. I. 2009. The promise and pitfalls of systematic conservation planning. *Proceedings of the National Academy of Sciences of the United States of America* 106 (36): 15101–15102. doi:`10.1073/pnas.0908125106`.

McLachlan, J. S., J. J. Hellmann and M. W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* 21 (2): 297–302. doi:`10.1111/j.1523-1739.2007.00676.x`.

McNeely, J. A., and G. Ness. 1995. People, parks and biodiversity: issues in population-environment dynamics. In *Human population, biodiversity and protected areas: science and policy issues,* ed. V. Dompka. Washington, DC: American Association for the Advancement of Science's Program on Population and Sustainable Development (PSD). ISBN:9996108392, `http://www.aaas.org/international/ehn/biod/contents.htm`.

Menke, S. B., D. A. Holway, R. N. Fisher and W. Jetz. 2009. Characterizing and predicting species distributions across environments and scales: Argentine ant occurrences in the eye of the beholder. *Global Ecology and Biogeography* 18 (1): 50–63. doi:`10.1111/j.1466-8238.2008.00420.x`.

Meyer, C. B., and W. Thuiller. 2006. Accuracy of resource selection functions across spatial scales. *Diversity and Distributions* 12 (3): 288–297. doi:`10.1111/j.1366-9516.2006.00241.x`.

Midgley, G. F., G. O. Hughes, W. Thuiller and A. G. Rebelo. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Diversity and Distributions* 12 (5): 555–562. doi:`10.1111/j.1366-9516.2006.00273.x`.

Millennium Ecosystem Assessment. 2003. *Ecosystems and human well-being: a framework for assessment.* Washington, DC: Island Press. ISBN:1559634030.

Milly, P. C. D., J. Betancourt, M. Falkenmark, R. M. Hirsch, Z. W. Kundzewicz, D. P. Lettenmaier and R. J. Stouffer. 2008. Stationarity is dead: whither water management? *Science* 319 (5863): 573–574. doi:`10.1126/science.1151915`.

Mimura, N., L. Nurse, R. F. McLean, J. Agard, L. Briguglio, P. Lefale, R. Payet and G. Sem. 2007. Small islands. Chap. 16 in *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change,* ed. M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden and C. E. Hanson, 687–716. Cambridge, UK: Cambridge University Press. ISBN:9780521880107, `http://www.ipcc.ch/pdf/assessment-report/ar4/wg2/ar4-wg2-chapter16.pdf`.

Mitchell, A. 2005. *The ESRI guide to GIS analysis, volume 2: spatial measurements and statistics.* Redlands, CA: ESRI Press. ISBN:9781589481169.

Mittermeier, R. A., P. R. Gil, M. Hoffman, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux and G. A. B. da Fonseca. 2005. *Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions.* Conservation International. ISBN:9686397779.

Moguel, P., and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology* 13 (1): 11–21. doi:`10.1046/j.1523-1739.1999.97153.x`.

Mohammed, I. 2010. *Interview by author.* National Forestry Division of Trinidad and Tobago.

Montagnini, F. 2001. Strategies for the recovery of degraded ecosystems: experiences from Latin America. *Interciencia* 26 (10): 498–503.

Moss, R. H., J. A. Edmonds, K. A. Hibbard, M. R. Manning, S. K. Rose, D. P. van Vuuren, T. R. Carter, S. Emori, M. Kainuma, T. Kram, G. A. Meehl, J. F. B. Mitchell, N. Nakicenovic, K. Riahi, S. J. Smith, R. J. Stouffer, A. M. Thomson, J. P. Weyant and T. J. Wilbanks. 2010. The next generation of scenarios for climate change research and assessment. *Nature* 463 (7282): 747–756. doi:`10.1038/nature08823`.

Mueller, J. M., and J. J. Hellmann. 2008. An assessment of invasion risk from assisted migration. *Conservation Biology* 22 (3): 562–567. doi:`10.1111/j.1523-1739.2008.00952.x`.

Munroe, D., J. Clark and E. Irwin. 2005. Regional determinants of exurban land use in the U.S. Midwest, Nov. 12. Paper prepared for the 52nd Annual North American Meetings of the Regional Science Association. Las Vegas, NV. `http://exurban.osu.edu/papers/RSAI_munroe_et_al_2005.pdf`.

Murray-Smith, C., N. A. Brummitt, A. T. Oliveira-Filho, S. Bachman, J. Moat, E. M. N. Lughadha and E. J. Lucas. 2009. Plant diversity hotspots in the atlantic coastal forests of Brazil. *Conservation Biology* 23 (1): 151–163. doi:`10.1111/j.1523-1739.2008.01075.x`.

Myers, N. 1997. The world's forests and their ecosystem services. Chap. 12 in *Nature's services: societal dependence on natural ecosystems,* ed. G. C. Daily, 215–237. Washington, DC: Island Press. ISBN:1559634766.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403 (6772): 853–858. doi:`10.1038/35002501`.

Myers, N. 1988. Threatened biotas: “hot spots” in tropical forests. *The Environmentalist* 8 (3): 187–208. doi:`10.1007/BF02240252`.

———. 1990. The biodiversity challenge: expanded hot-spots analysis. *The Environmentalist* 10 (4): 243–256. doi:`10.1007/BF02239720`.

Myers, R. L. 2006. *Living with fire: sustaining ecosystems and livelihoods through integrated fire management.* Arlington, VA: The Nature Conservancy.

Nakićenović, N., J. Alcamo, G. Davis, B. J. M. de Vries, J. Fenhann, S. Gaffin, K. Gregory, A. Grübler, T. Y. Jung, T. Kram, E. Lèbre La Rovere, L. Michaelis, S. Mori, T. Morita, W. Pepper, H. Pitcher, L. Price, K. Riahi, A. R. Röhrl, H.-H. Rogner, A. Sankovski, M. Schlesinger, P. Shukla, S. Smith, R. Swart, S. van Rooijen, N. Victor and Z. Dadi. 2000. *Special report on emissions scenarios. A special report of Working Group III of the Intergovernmental Panel on Climate Change.* Cambridge, UK: Cambridge University Press. `http://www.ipcc.ch/ipccreports/sres/emission/index.php?idp=0`.

Naughton-Treves, L., M. B. Holland and K. Brandon. 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annual Review of Environment and Resources* 30:219–252. doi:`10.1146/annurev.energy.30.050504.164507`.

Nelson, H. P. 2004. Forest ecosystems of trinidad: ecological patterns and public perceptions. PhD thesis, University of Wisconsin-Madison.

Nurse, L. A., G. Sem, J. E. Hay, A. G. Suarez, P. P. Wong, L. Briguglio and S. Ragoonaden. 2001. Small island states. Chap. 17 in *Climate change 2001: impacts, adaptation and vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change,* ed. J. J. McCarthy, O. F. Canziani, N. A. Leary, D. J. Dokken and K. S. White, 842–975. Cambridge, UK: Cambridge University Press. ISBN:0521015009, `http://www.grida.no/climate/ipcc_tar/wg2/pdf/wg2TARchap17.pdf`.

Oliveira, P. J. C., G. P. Asner, D. E. Knapp, A. Almeyda, R. Galván-Gildemeister, S. Keene, R. F. Raybin and R. C. Smith. 2007. Land-use allocation protects the Peruvian Amazon. *Science* 317 (5842): 1233–1236. doi:`10.1126/science.1146324`.

Ostertag, R., W. L. Silver and A. E. Lugo. 2005. Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica* 37 (1): 16–24. doi:`10.1111/j.1744-7429.2005.04052.x`.

Pagiola, S., P. Agostini, J. Gobbi, C. de Haan, M. Ibrahim, E. Murgueitio, E. Ramírez, M. Rosales and J. P. Ruíz. 2005. Paying for biodiversity conservation services: experience in Colombia, Costa Rica, and Nicaragua. *Mountain Research and Development* 25 (3): 206–211. doi:`10.1659/0276-4741(2005)025[0206:PFBCS]2.0.CO;2`.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421 (6918): 37–42. doi:`10.1038/nature01286`.

Parsram, K. 2007. *Capacity building for protected areas planning and management and associated livelihoods. Protected areas training needs assessment. St. Kitts and Nevis country report.* OECS Protected Areas and Associated Livelihoods Project. `http://archive.oceanfdn.org/index.php?tg=fileman&idx=get&id=7&gr=Y&path=&file=TNA+Country+Report+-+St+Kitts+and+Nevis.pdf`.

Parés-Ramos, I. K., W. A. Gould and T. M. Aide. 2008. Agricultural abandonment, suburban growth, and forest expansion in Puerto Rico between 1991 and 2000. *Ecology and Society* 13 (2): 1. `http://www.ecologyandsociety.org/vol13/iss2/art1/`.

Pearce, J. L., and M. S. Boyce. 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology* 43 (3): 405–412. doi:`10.1111/j.1365-2664.2005.01112.x`.

Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133 (3): 225–245. doi:`10.1016/s0304-3800(00)00322-7`.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12 (5): 361–371. doi:`10.1046/j.1466-822X.2003.00042.x`.

Pearson, R. G., W. Thuiller, M. B. Araújo, E. Martinez-Meyer, L. Brotons, C. McClean, L. Miles, P. Segurado, T. P. Dawson and D. C. Lees. 2006. Model-based uncertainty in species' range prediction. *Journal of Biogeography* 33 (10): 1704–1711. doi:`10.1111/j.1365-2699.2006.01460.x`.

Pearson, R. G., C. J. Raxworthy, M. Nakamura and A. T Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34:102–117. doi:`10.1111/j.1365-2699.2006.01594.x`.

Pearson, R. G., and T. P. Dawson. 2004. Bioclimate envelope models: what they detect and what they hide — response to Hampe (2004). *Global Ecology and Biogeography* 13 (5): 471–473. doi:`10.1111/j.1466-822X.2004.00112.x`.

Pearson, R. G., T. P. Dawson and C. Liu. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27 (3): 285–298. doi:`10.1111/j.0906-7590.2004.03740.x`.

Pelling, M., and J. I. Uitto. 2001. Small island developing states: natural disaster vulnerability and global change. *Global Environmental Change Part B: Environmental Hazards* 3 (2): 49–62. doi:`10.1016/s1464-2867(01)00018-3`.

Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarrés, M. B. Araújo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guénette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila and M. Walpole. 2010. Scenarios for global biodiversity in the 21st century. *Science* 330 (6010): 1496–1501. doi:`10.1126/science.1196624`.

Perkins, S. E., A. J. Pitman, N. J. Holbrook and J. McAneney. 2007. Evaluation of the AR4 climate models' simulated daily maximum temperature, minimum temperature and precipitation over Australia using probability density functions. *Journal of Climate* 20 (17): 4356–4376. doi:`10.1175/JCLI4253.1`.

Petersen, F. T., R. Meier and M. Nykjær Larsen. 2003. Testing species richness estimation methods using museum label data on the danish asilidae. *Biodiversity and Conservation* 12 (4): 687–701. doi:`10.1023/a:1022464710930`.

Peterson, A. T., M. Papeş and J. Soberón. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213 (1): 63–72. doi:`10.1016/j.ecolmodel.2007.11.008`.

Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31 (2): 161–175. doi:`10.1111/j.0906-7590.2008.5203.x`.

Phillips, S. J., M. Dudík and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. In *Proceedings of the 21st International Conference on Machine Learning,* 83. ICML '04. New York: ACM. ISBN:1581138385, doi:`10.1145/1015330.1015412`.

Phillips, S. J., R. P. Anderson and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190 (3–4): 231–259. doi:`10.1016/j.ecolmodel.2005.03.026`.

Phillips, S. J., M. Dudík, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19 (1): 181–197. doi:`10.1890/07-2153.1`.

Ponder, W. F., G. A. Carter, P. Flemons and R. R. Chapman. 2001. Evaluation of museum collection data for use in biodiversity assessment. *Conservation Biology* 15 (3): 648–657. doi:`10.1046/j.1523-1739.2001.015003648.x`.

Porter-Bolland, L., E. A. Ellis, M. R. Guariguata, I. Ruiz-Mallén, S. Negrete-Yankelevich and V. Reyes-García. 2012. Community managed forests and forest protected areas: an assessment of their conservation effectiveness across the tropics. *Forest Ecology and Management* 268:6—17. doi:`10.1016/j.foreco.2011.05.034`.

Pounds, A. J., M. R. Bustamante, L. A. Coloma, J. A. Consuegra, M. P. L. Fogden, P. N. Foster, E. La Marca, K. L. Masters, A. Merino-Viteri, R. Puschendorf, S. R. Ron, G. A. Sánchez-Azofeifa, C. J. Still and B. E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439 (7073): 161–167. doi:`10.1038/nature04246`.

Pressey, R. L., and R. M. Cowling. 2001. Reserve selection algorithms and the real world. *Conservation Biology* 15 (1): 275–277. doi:`10.1111/j.1523-1739.2001.99541.x`.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling and K. A. Wilson. 2007. Conservation planning in a changing world. *Trends in Ecology & Evolution* 22 (11): 583–592. doi:`10.1016/j.tree.2007.10.001`.

Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3 (4): 349–361. doi:`10.1046/j.1461-0248.2000.00143.x`.

Pulwarty, R. S., and N. Hutchinson. 2009. *Vulnerability and capacity assessment: a guidance manual for the conduct and mainstreaming of climate change vulnerability and capacity assessments in the Caribbean region.* Technical Report. Belmopan, Belize: Caribbean Community Climate Change Centre (CCCCC). `http://200.32.211.67/M-Files/openfile.aspx?objtype=0&docid=2756`.

Pulwarty, R. S., L. A. Nurse and U. O. Trotz. 2010. Caribbean islands in a changing climate. *Environment: Science and Policy for Sustainable Development* 52 (6): 16–27. doi:`10.1080/00139157.2010.522460`.

Puyravaud, J.-P. 2003. Standardizing the calculation of the annual rate of deforestation. *Forest Ecology and Management* 177 (1): 593–596. doi:`10.1016/S0378-1127(02)00335-3`.

Pyke, C. R., and D. T. Fischer. 2005. Selection of bioclimatically representative biological reserve systems under climate change. *Biological Conservation* 121 (3): 429–441. doi:`10.1016/j.biocon.2004.05.019`.

Pyke, C. R., S. J. Andelman and G. Midgley. 2005. Identifying priority areas for bioclimatic representation under climate change: a case study for Proteaceae in the Cape Floristic Region, South Africa. *Biological Conservation* 125 (1): 1–9. doi:`10.1016/j.biocon.2004.08.004`.

Pyke, C. R. 2004. Habitat loss confounds climate change impacts. *Frontiers in Ecology and the Environment* 2 (4): 178–182. doi:`10.1890/1540-9295(2004)002[0178:HLCCCI]2.0.CO;2`.

Ragoonanan, L. 2012. *Interview by author.* National Forestry Division of Trinidad and Tobago, Jan. 19.

Rahmstorf, S. 2007. A semi-empirical approach to projecting future sea-level rise. *Science* 315 (5810): 368–370. doi:`10.1126/science.1135456`.

Ramdial, B. S. 1980. *Forestry in Trinidad and Tobago.* Trinidad and Tobago: Forestry Division, Ministry of Agriculture, Land and Fisheries.

Ramnath, S. 2012. *Interview by author.* National Forestry Division of Trinidad and Tobago, Jan. 19.

Randall, D. A., R. A. Wood, S. Bony, R. Colman, T. Fichefet, J. Fyfe, V. Kattsov, A. Pitman, J. Shukla, J. Srinivasan, R. J. Stouffer, A. Sumi and K. E. Taylor. 2007. Climate models and their evaluation. Chap. 8 in *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change,* ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller, 589–662. Cambridge, UK: Cambridge University Press. `http://www.ipcc.ch/pdf/assessment-report/ar4/wg1/ar4-wg1-chapter8.pdf`.

Raupach, M. R., G. Marland, P. Ciais, C. Le Quéré, J. G. Canadell, G. Klepper and C. B. Field. 2007. Global and regional drivers of accelerating CO_2 emissions. *Proceedings of the National Academy of Sciences of the United States of America* 104 (24): 10288–10293. doi:`10.1073/pnas.0700609104`.

Reddy, S., and L. M. Dávalos. 2003. Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography* 30 (11): 1719–1727. doi:`10.1046/j.1365-2699.2003.00946.x`.

Rice, R. A., and R. Greenberg. 2000. Cacao cultivation and the conservation of biological diversity. *AMBIO: A Journal of the Human Environment* 29 (3): 167–173. doi:`10.1579/0044-7447-29.3.167`.

Richards, P. W. 1936. Ecological observations on the rain forest of Mount Dulit, Sarawak. Part II. *Journal of Ecology* 24 (2): 340–360. `http://www.jstor.org/stable/2256430`.

Richards, P. W. 1996. *The tropical rainforest. an ecological study.* 2nd ed. Cambridge, UK: Cambridge University Press. ISBN:0521421942.

Richards, P. W., A. G. Tansley and A. S. Watt. 1940. The recording of structure, life form and flora of tropical forest communities as a basis for their classification. *Journal of Ecology* 28 (1): 224–239. `http://www.jstor.org/stable/2256171`.

Rissler, L. J., R. J. Hijmans, C. H. Graham, C. Moritz and D. B. Wake. 2006. Phylogeographic lineages and species comparisons in conservation analyses: a case study of California herpetofauna. *American Naturalist* 167 (5): 655–666. doi:`10.1086/503332`.

Rissler, L. J., and J. J. Apodaca. 2007. Adding more ecology into species delimitation: ecological niche models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). *Systematic Biology* 56 (6): 924–942. doi:`10.1080/10635150701703063`.

Rivera-Monroy, V. H., R. R. Twilley, D. Bone, D. L. Childers, C. Coronado-Molina, I. C. Feller, J. Herrera-Silveira, R. Jaffe, E. Mancera, E. Rejmankova, J. E. Salisbury and E. Weil. 2004. A conceptual framework to develop long-term ecological research and management objectives in the wider Caribbean region. *BioScience* 54 (9): 843–856. doi:`10.1641/0006-3568(2004)054[0843:acftdl]2.0.co;2`.

Rivera, L. W., and T. M. Aide. 1998. Forest recovery in the karst region of Puerto Rico. *Forest Ecology and Management* 108 (1-2): 63–75. doi:`10.1016/S0378-1127(97)00349-6`.

Robertson, M. P., N. Caithness and M. H. Villet. 2001. A PCA-based modelling technique for predicting environmental suitability for organisms from presence records. *Diversity and Distributions* 7 (1-2): 15–27. doi:`10.1046/j.1472-4642.2001.00094.x`.

Rodrigues, A. S. L., S. J. Andelman, M. I. Bakan, L. Boitani, T. M. Brooks, R. M. Cowling, L. D. C. Fishpool, G. A. B. Da Fonseca, K. J. Gaston, M. Hoffmann, J. S. Long, P. A. Marquet, J. D. Pilgrim, R. L. Pressey, J. Schipper, W. Sechrest, S. H. Stuart, L. G. Underhill, R. W. Waller, M. E. J. Watts and X. Yan. 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* 428 (6983): 640–643. doi:`10.1038/nature02422`.

Rodríguez-Sánchez, F., and J. Arroyo. 2008. Reconstructing the demise of Tethyan plants: climate-driven range dynamics of *Laurus* since the Pliocene. *Global Ecology and Biogeography* 17 (6): 685–695. doi:`10.1111/j.1466-8238.2008.00410.x`.

Rompré, G., W. D. Robinson and A. Desrochers. 2008. Causes of habitat loss in a Neotropical landscape: the Panama Canal corridor. *Landscape and Urban Planning* 87 (2): 129–139. doi:`10.1016/j.landurbplan.2008.05.006`.

Root, T. L., and S. H. Schneider. 1993. Can large-scale climatic models be linked with multiscale ecological studies? *Conservation Biology* 7 (2): 256–270. doi:`10.1046/j.1523-1739.1993.07020256.x`.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421 (6918): 57–60. doi:`10.1038/nature01333`.

Rudel, T. K. 2005. *Tropical forests: regional paths of destruction and regeneration in the late twentieth century.* New York: Columbia University Press. ISBN:023113195X.

———. 2006. Shrinking tropical forests, human agents of change, and conservation policy. *Conservation Biology* 20 (6): 1604–1609. doi:`10.1111/j.1523-1739.2006.00532.x`.

Rudel, T. K., M. Perez-Lugo and H. Zichal. 2000. When fields revert to forest: development and spontaneous reforestation in post-war Puerto Rico. *The Professional Geographer* 52 (3): 386–397. doi:`10.1111/0033-0124.00233`.

Sachs, J., and S. N. Ladd, eds. 2011. Climate and oceanography of the Galápagos in the 21st century: expected changes and research needs. Chap. 1 in *Climate change vulnerability assessment of the Galápagos Islands,* 17–28. USA: WWF and Conservation International. `http://awsassets.panda.org/downloads/integrated_report_final.pdf`.

Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287 (5459): 1770–1774. doi:`10.1126/science.287.5459.1770`.

Santiago-Valentin, E., and R. G. Olmstead. 2004. Historiacl biogeography of Caribbean plants: introduction to current known knowledge and possibilities from a phylogenetic perspective. *Taxon* 53 (2): 299–319. `http://www.jstor.org/stable/4135610`.

Schatz, G., A. Cameron and T. Raminosoa. 2008. Modeling of endemic plant species of Madagascar under climate changes. In *Assessing the impact of climate change on Madagascar's livelihoods and biodiversity.* Jan. 28.

Schulman, L., T. Toivonen and K. Ruokolainen. 2007. Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography* 34 (8): 1388–1399. doi:`10.1111/j.1365-2699.2007.01716.x`.

Scott, D., and C. Lemieux. 2005. Climate change and protected area policy and planning in Canada. *Forestry Chronicle* 81 (5): 696–703.

Scott, D., J. R. Malcolm and C. Lemieux. 2002. Climate change and modelled biome representation in Canada's national park system: implications for system planning and park mandates. *Global Ecology and Biogeography* 11 (6): 475–484. doi:`10.1046/j.1466-822X.2002.00308.x`.

Segurado, P., and M. B. Araújo. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31 (10): 1555–1568. doi:`10.1111/j.1365-2699.2004.01076.x`.

Seo, C., J. H. Thorne, L. Hannah and W. Thuiller. 2009. Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters* 5 (1): 39–43. doi:`10.1098/rsbl.2008.0476`.

Smithers, R. J., C. Cowan, M. Harley, J. J. Hopkins, H. Pontier and O. Watts. 2008. *England biodiversity strategy: climate change adaptation principles: conserving biodiversity in a changing climate.* Bristol: Department for Environment, Food and Rural Affairs (defra). `http://www.defra.gov.uk/publications/files/pb13168-ebs-ccap-081203.pdf`.

Snedecor, G. W., and W. G. Cochran. 1968. *Statistical methods.* 6th ed. The Iowa State University Press.

Soberón, J., and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2:1–10. `https://journals.ku.edu/index.php/jbi/article/download/4/2`.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10 (12): 1115–1123. doi:`10.1111/j.1461-0248.2007.01107.x`.

Sodhi, N. S., L. P. Koh, D. M. Prawiradilaga, Darjono, I. Tinulele, D. D. Putra and T. H. T. Tan. 2005. Land use and conservation value for forest birds in Central Sulawesi (Indonesia). *Biological Conservation* 122 (4): 547–558. doi:`10.1016/j.biocon.2004.07.023`.

Sokolov, A. P., P. H. Stone, C. E. Forest, R. Prinn, M. C. Sarofim, M. Webster, S. Paltsev, C. A. Schlosser, D. Kicklighter, S. Dutkiewicz, J. Reilly, C. Wang, B. Felzer, J. M. Melillo and H. D. Jacoby. 2009. Probabilistic forecast for twenty-first-century climate based on uncertainties in emissions (without policy) and climate parameters. *Journal of Climate* 22 (19): 5175–5204. doi:`10.1175/2009jcli2863.1`.

Southworth, J., H. Nagendra, L. A. Carlson and C. Tucker. 2004. Assessing the impact of Celaque National Park on forest fragmentation in western Honduras. *Applied Geography* 24 (4): 303–322. doi:`10.1016/j.apgeog.2004.07.003`.

Spak, S., T. Holloway, B. Lynn and R. Goldberg. 2007. A comparison of statistical and dynamical downscaling for surface temperature in North America. *Journal of Geophysical Research* 112:D08101. doi:`10.1029/2005jd006712`.

SPSS Inc. 2008. *SPSS Statistics 17.0 command syntax reference.* SPSS Inc., Chicago. `www.ibm.com/software/uk/analytics/spss/`.

Stouffer, P. C., R. O. Bierregaard, C. Strong and T. E. Lovejoy. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20 (4): 1212–1223. doi:`10.1111/j.1523-1739.2006.00427.x`.

Strömquist, L., and I. Backéus. 2009. Integrated landscape analyses of change of miombo woodland in Tanzania and its implication for environment and human livelihoods. *Geografiska Annaler, Series A: Physical Geography* 91 (1): 31–45. doi:`10.1111/j.1468-0459.2009.00351.x`.

Suárez, A., E. Garraway, D. Vilamajó, L. Mujica, J. Gerhartz, R. Capote and N. Blake. 2008. *Climate change impacts on terrestrial biodiversity in the insular Caribbean: Report of Working Group III, Climate Change and Biodiversity in the Insular Caribbean.* 383. Technical Report. Port of Spain, Trinidad: Caribbean Natural Resources Institute (CANARI). `http://www.canari.org/docs/CCBIC%20WG%20III%20-%20final..pdf`.

Sánchez-Azofeifa, G. A., G. C. Daily, A. S. P. Pfaff and C. Busch. 2003. Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover. *Biological Conservation* 109 (1): 123–135. doi:`10.1016/S0006-3207(02)00145-3`.

Tabor, K, and J. W. Williams. 2010. Globally downscaled climate projections for assessing the conservation impacts of climate change. *Ecological Applications* 20 (2): 554–565. doi:`10.1890/09-0173.1`.

The MathWorks Inc. 2009. *MATLAB. Version 7.9.* Natick, Massachusetts. `http://www.mathworks.co.uk/`.

Thelen, K. D., and S. Faizool. 1980. *Plan for a system of national parks and other protected areas in Trinidad and Tobago.* Trinidad and Tobago: Forestry Division, Ministry of Agriculture, Lands and Fisheries.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips and S. E. Williams. 2004. Extinction risk from climate change. *Nature* 427 (6970): 145–148. doi:`10.1038/nature02121`.

Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* 10 (12): 2020–2027. doi:`10.1111/j.1365-2486.2004.00859.x`.

Thuiller, W. 2007. Biodiversity: climate change and the ecologist. *Nature* 448:550–552. doi:`10.1038/448550a`.

Thuiller, W., L. Brotons, M. B. Araújo and S. Lavorel. 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27 (2): 165–172. doi:`10.1111/j.0906-7590.2004.03673.x`.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102 (23): 8245–8250. doi:`10.1073/pnas.0409902102`.

Thuiller, W., S. Lavorel, M. T. Sykes and M. B. Araújo. 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions* 12 (1): 49–60. doi:`10.1111/j.1366-9516.2006.00216.x`.

Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes and N. E. Zimmermann. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9 (3-4): 137–152. doi:`10.1016/j.ppees.2007.09.004`.

Thuiller, W., S. Lavergne, C. Roquet, I. Boulangeat, B. Lafourcade and M. B. Araujo. 2011. Consequences of climate change on the tree of life in Europe. *Nature* 470 (7335): 531–534. doi:`10.1038/nature09705`.

Tole, L. 2001. Jamaica's disappearing forests: physical and human aspects. *Environmental Management* 28 (4): 455–467. doi:`10.1007/s002670010236`.

———. 2002. An estimate of forest cover extent and change in Jamaica using Landsat MSS data. *International Journal of Remote Sensing* 23 (1): 91–106. doi:`10.1080/01431160010014837`.

Tompkins, E. L., and W. N. Adger. 2005. Defining response capacity to enhance climate change policy. *Environmental Science & Policy* 8 (6): 562–571. doi:`10.1016/j.envsci.2005.06.012`.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33 (2): 200–209. doi:`10.2307/2404743`.

Veken, S. van der, M. Hermy, M. Vellend, A. Knapen and K. Verheyen. 2008. Garden plants get a head start on climate change. *Frontiers in Ecology and the Environment* 6 (4): 212–216. doi:`10.1890/070063`.

Veldkamp, A., and E. F. Lambin. 2001. Editorial: predicting land-use change. *Agriculture, Ecosystems & Environment* 85 (1-3): 1–6. doi:`10.1016/S0167-8809(01)00199-2`.

Veregin, H. 1989. *A taxonomy of error in spatial databases.* Technical Papers Series, 89-12. Technical Report. National Center for Geographic Information and Analysis (NCGIA). `http://www.ncgia.ucsb.edu/technical-reports/PDF/89-12.pdf`.

Vitousek, P. M. 1994. Beyond global warming: ecology and global change. *Ecology* 75 (7): 1861–1876. doi:`10.2307/1941591`.

Wagner, W. L., and V. A. Funk, eds. 1995. *Hawaiian biogeography: evolution on a hot spot archipelago.* Washington, DC: Smithsonian Institution Press. ISBN:1560984627.

Wallace, G. N., J. Barborak and C. G. MacFarland. 2005. Land use planning and regulation in and around protected areas: a study of best practices and capacity building needs in Mexico and Central America. *Natureza & Conservação (Brazilian Journal of Nature Conservation)* 3 (2): 147–167.

Walling, L. J., C. Douglas, M. Mason and M. Chevannes-Creary. 2006. *Caribbean environment outlook.* Nairobi: United Nations Environment Programme (UNEP). `http://www.unep.org/PDF/SIDS/Caribbean_EO_final.pdf`.

Walmsley, C. A., R. J. Smithers, P. M. Berry, M. Harley, M. J. Stevenson and R. Catchpole, eds. 2007. *MONARCH – Modelling Natural Resource Responses to Climate Change: a synthesis for biodiversity conservation.* United Kingdom Climate Impacts Programme (UKCIP), Oxford.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416 (6879): 389–395. doi:`10.1038/416389a`.

Warwick, R. M., and K. R. Clarke. 1995. New ‘biodiversity’ measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* 129:301–305. doi:`10.3354/meps129301`.

WBG. *See* World Bank Group.

Weis, T. 2000. Beyond peasant deforestation: environment and development in rural Jamaica. *Global Environmental Change* 10 (4): 299–305. doi:`10.1016/S0959-3780(00)00036-4`.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26 (1): 1–80. doi:`10.2307/1943577`.

———. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30 (3): 279–338. doi:`10.2307/1943563`.

Whittaker, R. H., S. A. Levin and R. B. Root. 1973. Niche, habitat, and ecotope. *The American Naturalist* 107 (955): 321–338. `http://www.jstor.org/stable/2459534`.

Whittaker, R. J., and J. M. Fernández-Palacios. 2007. *Island biogeography: ecology, evolution, and conservation.* 2nd ed. Oxford: Oxford University Press. ISBN:0198566123.

Whittaker, R. J., and S. H. Jones. 1994. The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography* 21 (3): 245–258. `http://www.jstor.org/stable/2845528`.

Wiens, J. A., and D. Bachelet. 2010. Matching the multiple scales of conservation with the multiple scales of climate change. *Conservation Biology* 24 (1): 51–62. doi:`10.1111/j.1523-1739.2009.01409.x`.

Wiens, J. A., D. Stralberg, D. Jongsomjit, C. A. Howell and M. A. Snyder. 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences of the United States of America* 106 (Supplement 2): 19729–19736. doi:`10.1073/pnas.0901639106`.

Wilby, R. L., T. M. L. Wigley, D. Conway, P. D. Jones, B. C. Hewitson, J. Main and D. S. Wilks. 1998. Statistical downscaling of general circulation model output: a comparison of methods. *Water Resources Research* 34 (11): 2995–3008. doi:`10.1029/98wr02577`.

Wilby, R. L., S. P. Charles, E. Zorita, P. Whetton and L. O. Mearns. 2004. *Guidelines for use of climate scenarios developed from statistical downscaling methods.* Geneva, Switzerland: Intergovernmental Panel on Climate Change (IPCC). `www.ipcc-data.org/guidelines/dgm_no2_v1_09_2004.pdf`.

Wildi, O. 2010. Ordination. Chap. 5 in *Data analysis in vegetation ecology,* 35–58. John Wiley & Sons. ISBN:9780470661017, doi:`10.1002/9780470664971`.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5 (9): 475–482. doi:`10.1890/070037`.

Williams, P., L. E. E. Hannah, S. Andelman, G. U. Y. Midgley, M. Araújo, G. Hughes, L. Manne, E. Martinez-Meyer and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology* 19 (4): 1063–1074. doi:`10.1111/j.1523-1739.2005.00080.x`.

Williams, S. E., E. E. Bolitho and S. Fox. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society B: Biological Sciences* 270 (1527): 1887–1892. doi:`10.1098/rspb.2003.2464`.

Williamson, M. H., and A. Fitter. 1996. The characters of successful invaders. *Biological Conservation* 78 (1–2): 163–170. doi:`10.1016/0006-3207(96)00025-0`.

Willis, S. G., D. G. Hole and B. Huntley. 2010. Climate change and conservation. Chap. 18 in *Trade-offs in conservation: deciding what to save,* ed. N. Leader-Williams, W. M. Adams and R. J. Smith, 331–348. Oxford: Blackwell Publishing Ltd. ISBN:9781405193832.

Wollan, A. K., V. Bakkestuen, H. Kauserud, G. Gulden and R. Halvorsen. 2008. Modelling and predicting fungal distribution patterns using herbarium data. *Journal of Biogeography* 35 (12): 2298–2310. doi:`10.1111/j.1365-2699.2008.01965.x`.

Woodward, F. I. 1987. *Climate and plant distribution.* Cambridge Studies in Ecology. Cambridge, UK: Cambridge University Press. ISBN:9780521282147, doi:`10.2277/0521282144`.

World Bank Group. 2011. Population density (people per sq. km of land area). `http://data.worldbank.org/indicator/EN.POP.DNST` (accessed July 14, 2011).

Wright, J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130 (1): 1–14. doi:`10.1007/s004420100809`.

Wright, S. J., and H. C. Muller-Landau. 2006. The future of tropical forest species. *Biotropica* 38 (3): 287–301. doi:`10.1111/j.1744-7429.2006.00154.x`.

Yu, C. M. 2004. *Seqüestro florestal de carbono no Brasil: dimensões políticas, socioeconômicas e ecológicas.* São Paulo: Annablume. ISBN:8574194697.

Zadrozny, B. 2004. Learning and evaluating classifiers under sample selection bias. In *Proceedings of the 21st International Conference on Machine Learning,* 114. ICML '04. New York: ACM. ISBN:1581138385, doi:`10.1145/1015330.1015425`.