

The Ecology of Vascular Epiphytes in the Peruvian Andes



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ACRONYMS AND ABBREVIATIONS

ABERG = Andes biodiversity and ecosystems research group

ACCA = Asociación para la Conservación de la Cuenca Amazónica

AET = Actual evapotranspiration

AP = Annual precipitation

AUC = Area under curve

CAM = Crassulacean acid metabolism

CCM = Carbon concentrating mechanism

CIR = Carbon isotope ratio

DBH = Diameter at breast height

GLM = General linear model

INRENA = Ministry for the Environment (Peru)

LAI = Leaf area index

LFI = Leaf form index

LRF = Lowland tropical rainforest

MAT = Mean annual temperature

MCWD = Maximum climatological water deficit

MDE = Mid-domain effect

MLC = Manu Learning Centre

mol. = moles (unit)

NERC = Natural Environment Research Council

NMDS = Non-metric multi-dimensional scaling

PET = Potential evapotranspiration

PFI = Plant form index

PSP = Permanent sample plot

REDD = Reduced emissions from deforestation and forest degradation

RH = Relative humidity

ROC = Receiver operating characteristic

SSAI = Stem surface area index

TCF = Tropical montane cloud forest

TMF = Tropical montane forest

VPD = Vapour pressure deficit

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DECLARATION

I composed this thesis; the work is my own, except where otherwise acknowledged. No part of this thesis has been submitted for any other degree or qualification.

Steven John Heathcote

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THESIS ABSTRACT

Little is known about the composition of tropical epiphytic communities and the influence of environmental variables on community composition. In this thesis I quantify the diversity and biomass of bromeliads, and other vascular epiphytes along an altitudinal transect on the eastern slope of the southeast Peruvian Andes and then look for species' adaptations related to patterns of diversity and biomass. I compare patterns with those of woody species. Bromeliad species, like tree species, were found to form ecological zones related to climate. The lowest altitude ecological zone (below 1250 m) is the lowland rainforest (LRF), which has the warmest climate and highest evapotranspiration. In LRF vascular epiphytes are less prominent than other ecological zones, with the lowest bromeliad species richness and lowest vascular epiphyte biomass. However, low water-availability gives rise to most variable shoot morphology of bromeliads. The tropical montane forest (TMF), between 1250 m and 2250 m, is intermediate in climate between the LRF and the tropical montane cloud forest (TCF). The TMF has the highest α -diversity, but species richness is lower than the TCF. The shoot morphology of bromeliads is intermediate between TCF and LRF. The highest altitude ecological zone with forest is the TCF (above 2250 m). The TCF has the highest bromeliad species richness, and lowest diversity of shoot forms. The low diversity of shoot forms represents the need for a large phytotelm (water-impounding shoot) to intercept and store precipitation. The TCF has the highest vascular epiphyte biomass, although the biomass is variable as a consequence of the natural disturbance caused by landslides. Along the transect bromeliad species with CAM photosynthesis are only present in the LRF. Terrestrial bromeliad distribution records covering the Neotropics show CAM photosynthesis is more prevalent in drier environments showing that CAM photosynthesis is primarily an adaptation to drought. Epiphytic bromeliads, pre-adapted to a water-stressed environment show no differences in presence along rainfall gradients, but species with CAM photosynthesis occupy warmer environments.

1. THESIS INTRODUCTION

The aim of this thesis is to understand the vascular epiphyte ecology, with particular focus on the family Bromeliaceae, along an elevation gradient, and to see if climate factors underlying their diversity, distribution and abundance are the same as those that have been proposed as controls over the wider forest community. When compared with the detailed synecological descriptions of terrestrial vegetation, little is known about the composition of epiphytic communities and the influence of environmental variables on community composition. Altitudinal patterns of woody plant ecology in the Andes are well-established and show distinct ecological zones based on climate (Grubb *et al.* 1963; Grubb & Whitmore 1966) and many life-forms mirror the diversity and biomass patterns of the tree flora on the landscape scale (e.g. termites (Palin *et al.* 2011), arthropods (Basset *et al.* 2012) and other plant groups (Wang *et al.* 2011)). Ecological zones of epiphytes are likely to be similarly defined by climate, but within the zones patterns of diversity and biomass in these zones are likely to vary significantly from those of woody species (Gentry & Dodson 1987b; Kessler 2000). Vascular epiphytes are critical species in montane forests (Gentry & Dodson 1987a), but their diversity and biomass vary across multiple scales (Krömer *et al.* 2005). Both diversity and biomass reflect the success of different taxa in an environment, and these community-level properties result from the interaction between individual plant traits and the environment (Soberón & Nakamura 2009). The altitudinal transect used in this study presents the opportunity to study the relationship between epiphytes and trees on the eastern slope of the Andes in Southern Peru, and to establish the importance of climate in similarities and differences between the ecology of epiphytes and the ecology of terrestrially-rooted woody species.

1.1 EPIPHYTES IN ECOLOGY

One of the most stressful niches exploited by higher plants is that of the epiphyte. In this introduction I will argue why epiphytes, and in particular members of the family Bromeliaceae, are such useful study organisms. I will also explain why tropical mountains provide the best location to study epiphytes, and then proceed to outline the research objectives of this thesis.

Epiphytes use another plant as their substrate for growth, but are not parasitic on the host vascular systems, using the host trees only for support (Lüttge 1989). The epiphytic niche is stressful (*sensu* Grime (1977)), lacking the buffering properties that the soil provides for many environmental resources. Epiphytes are exposed to low water availability and low and variable nutrient supplies. They also often inhabit exposed, canopy-top positions where they lack the buffering properties of a sub-canopy microclimate and are subjected to high evaporative potentials and variable but often excessive light levels. The physiological and morphological responses to these stresses, which ultimately have allowed epiphytes to occupy most tropical ecosystems and significant areas of temperate ecosystems, make epiphytes fascinating subjects for ecological research (Gentry & Dodson 1987b; Lüttge 1989; Zotz 2005). In this thesis I aim to examine the composition of epiphyte communities along a steep environmental gradient. I will investigate whether the abundance and diversity of epiphytes co-vary with that of the wider forest ecosystem at a variety of scales. I will test the competing hypotheses that in the tropics both diversity and biomass of epiphytes is strongly linked to that of tree species, or that epiphytes represent a unique way of living that results in patterns of diversity and biomass that contrast with the tree flora.

The tight linkage of epiphytes to climate is well established (Benzing 1998). This relationship with climate means epiphytes will be closer to equilibrium with the abiotic environment than terrestrial species where biotic factors are typically overwhelmingly

important (Bampfylde *et al.* 2005; Levine & HilleRisLambers 2009; Mangan *et al.* 2010). It has been well demonstrated that many tree species are not growing in optimal conditions, but lag behind climate changes due to slow migration rates and the sheltered conditions of the forest understory (Leathwick 1998; Feeley & Silman 2010). The tight link between epiphytes and climate means they will be useful indicators of climate change (Benzing 1998). They are likely to respond much quicker than terrestrially rooted species to climate change, and therefore are useful as indicator species.

The ecology and distribution of epiphytes, like that of all plants, is affected by different factors on different scales. From the very local microclimate to the continental climatic gradients, the factors involved operate at multiple scales. Historic studies have focused on scales easily measurable in field studies, or else concentrating on one or a few species at a wider scale (Benzing 2000). The increasing availability of distribution data, through high-precision digitized records, and continental-scale, high-resolution data sets for environmental variables, make analysis on larger scales easier to perform and more reliable (Yesson *et al.* 2007). However, with all these factors operating at different scales, it is important to define the scale and concepts under investigation with clarity. In this thesis I will test the importance of physiological adaptation on different scales, from looking within an ecosystem in Chapter 6, to looking across ecosystems in Chapter 7, to determine if there is evidence for the water-stressed nature of the epiphytic niche (Zotz & Hietz 2001).

As well as being intrinsically interesting, epiphytes are also keystone species in forests, and especially in the diverse tropical forests. They are important in nutrient cycling, water cycling and other forest processes (P'ocs 1980; Benzing 1998). Through provisions of habitat and food, epiphytes form an essential component of canopy life, supporting microbes, insects and higher animals (Benzing 2000).

There are approximately 24 000 species of flowering plants and 2 800 species of fern classified as epiphytes (Kress 1989). While epiphytes are distributed globally, the diversity of epiphytic vascular plants is highest in the Neotropics, and especially in Neotropical montane forests (Gentry & Dodson 1987a). The high water availability, topped up by frequent cloud immersion, combined with year-round equatorial warmth has resulted in ecosystems where, in the most suitable locations, over 30% of the above ground biomass is found in canopy epiphytes (Nadkarni 1984; Nadkarni & Matelson 1992; Hofstede, Wolf & Benzing 1993; Freiberg & Freiberg 2000; Kohler *et al.* 2007).

Epiphytes, then, are a component of tropical montane ecosystems which are very important for the forest ecology. Combined with their tight linkage to climate and myriad of adaptations they are a perfect study group for research on ecology, physiology and plant distribution. This thesis focuses predominantly on one group of Neotropical vascular epiphytes, the Bromeliaceae. This family, which contains both epiphytic and terrestrial species, is common in most habitats throughout the Neotropics, and is well represented in botanical studies, providing valuable background data (Benzing 2000).

1.2 THE BROMELIACEAE

The Bromeliaceae are ideal for studies on the role of plant physiology in relation to distribution. They have many traits that are important for the epiphytic lifestyle, but which are present only in certain clades. This means it is possible to make comparisons of the different traits within and between different taxonomic levels within the family. Epiphytism itself is present only in about 45% of the species, providing a useful contrast between the two habits within the family (Crayn, Winter & Smith 2004). The Bromeliaceae are also relatively simple to identify to species from floral characters, and separable into morphospecies on foliar characteristics. This means

that it is possible to work with the plants in the natural environment without detailed taxonomic knowledge, or in the absence of flowering specimens.

1.2.1 PHYLOGENY AND EVOLUTION

The Bromeliaceae is a monocot family of over 3 100 species (Luther 2008), with new species being described regularly, and taxonomic revisions based on molecular data now providing a well-supported picture of evolutionary history and ancestral states (Givnish *et al.* 2011), as well as the relationships between subfamilies and genera. The family is almost exclusively Neotropical, except for one species from West Africa (Smith & Downs 1974). The Bromeliaceae originated in the Guiana Shield area around 80 million years ago (Givnish *et al.* 2004). Bromeliaceae are one of the earliest diverging clades in the Poales, with their sister taxon, the Typhaceae (Smith & Donoghue 2008; APG III 2009; Givnish *et al.* 2011). The family was traditionally split into three subfamilies based on morphology, Pitcairnioideae, Tillandsioideae and Bromelioideae, and many classic texts refer to this sub-familial division. Recent molecular work supports the monophyly of the Tillandsioideae and Bromelioideae, but suggests Pitcairnioideae is polyphyletic (Crayn, Winter & Smith 2004; Givnish *et al.* 2004; Givnish *et al.* 2007; Givnish *et al.* 2011). Givnish *et al.* (2011) proposes dividing the family into 8 subfamilies, and throughout this thesis I will use this new classification. For this thesis the most important change is the removal of the genus *Puya* from the old subfamily Pitcairnioideae and into a separate subfamily, Puyoideae, based on its sister group relationship with the Bromelioideae. The subfamilies all differ in their evolutionary history and their biology, but most contain species with CAM photosynthesis, species with a pronounced phytotelm (water-impounding shoot) and epiphytic species.

1.2.2 PHYSIOLOGICAL ADAPTATION TO WATER AVAILABILITY

In Benzing (2000) the physiological and metabolic adaptations of the Bromeliaceae are comprehensively discussed, and their importance to the adaptive radiation of the Bromeliaceae

are discussed in great detail. Benzing's discussion illustrates the numerous studies that have investigated the role of adaptations to plant performance, primarily through carbon assimilation parameters. Less obvious are the importance of these adaptations in the ecology of the species at different scales. The adaptations relevant to environmental water availability discussed in great detail in Benzing's book are summarised here.

Whilst this thesis focuses on water-availability, many adaptations often have multiple uses. A typical example of this is the absorptive foliar trichome. These trichomes allow uptake of water and nutrients from the leaf surface. If they are large enough, they also provide a reflective cover, which reflects excess light and heat.

Overlapping leaf bases which form a phytotelm (a water-impounding 'tank') is also an adaptation which provides advantages for water balance, some species being able to maintain a year-round supply of water despite a pronounced dry season. The tanks also collect detritus, which provides the plants with a constant supply of nutrients.

Size is also an important response to environmental challenges. The effectiveness of a phytotelm is very size-dependent, with smaller size much less effective in storing water (Schmidt, Stuntz & Zotz 2001). This can present a big problem during the juvenile stage. To avoid this problem many phytotelm bromeliad species display heterophylly (Adams & Martin 1986), with very distinct juvenile and adult forms. Size can also be important in response to extreme temperatures. Several species of *Puya* growing at high altitude have a 'giant rosette' growth form. The large plant size traps a layer of air around the plant, which keeps the temperature of the plant above that of the atmosphere. Other species in the family use low-lying, prostrate forms (e.g. *Deuterocohnia* spp.) where keeping low to the ground allows the plants to remain in the warm layer of air close to the ground (Benzing 2000).

Along with size, shape also plays a key role in physiology. Narrow leaf syndrome is a common adaptation found in fog-intercepting plants (Martorell & Ezcurra 2007). The vertical and horizontal profiles will also affect the interception of rainwater and fog. However, changing architecture also influences light-interception (Sugden 1981). In Chapter 6 I will look at the role of morphology in influencing the distribution of species in the different water-regimes found along the altitudinal gradient on the eastern slope of the Andes.

Almost half of the species of bromeliads use CAM photosynthesis (Crayn, Winter & Smith 2004), an alternative photosynthetic pathway which is known to increase water-use efficiency (West-Eberhard, Smith & Winter 2011). Within ecosystems there is a strong negative relationship between mean annual rainfall and the proportion of species with CAM photosynthesis (Griffiths *et al.* 1986). As well as increasing water use efficiency, CAM photosynthesis has important photoprotective benefits, and many plants in exposed environments display CAM photosynthesis (Griffiths & Maxwell 1999). In Chapters 6 and 7 I will look at the importance of CAM photosynthesis on local and global scales respectively.

1.3 THE DISTRIBUTION OF BROMELIADS

1.3.1 DISTRIBUTION ECOLOGY

Like all plants, bromeliad distributions are controlled by a complex set of variables. From the environment all plants require optimal water, light, carbon dioxide and temperatures to achieve a positive carbon balance and hence sustain growth and reproduction. In terms of abiotic factors all plants require a substrate, as well as physical space for growth. Biotic interactions are another area of importance, with pollination, seed dispersal and predation all important. On a broader scale there is a large phylogeographic component to distributions, with many species ranges close to hypothesized ‘evolutionary centres’ for the taxon (e.g. many Bromelioideae concentrated in southeast Brazil), and radiations away from these centres may be slow, and

limited by 'phylogenetic niche conservatism' (Losos 2008). The importance of evolutionary history can be determined using detailed molecular phylogenies, however bromeliads have a low rate of accumulating mutations (Smith & Donoghue 2008), and detailed phylogenies at the species level are not available for most taxa.

1.3.2 THE ROLE OF WATER AVAILABILITY ON DIFFERENT ECOLOGICAL SCALES

Bromeliads occupy a wide range of environmental water availability, from the dry Atacama Desert, to periodically flooded restingas (Benzing 2000). The influence of water is important across all scales.

Total precipitation (both rainfall and fog) affects bromeliads on the local scale where it influences the occurrence of species within single trees, creating stratification. Stratification due to water availability, rather than light exposure, has been reported from Mexican forests where fog-intercepting species are located in more exposed sites within a tree to better access the fog (Reyes-Garcia *et al.* 2008), in Mexican cloud forests where drought tolerance determined canopy position (Graham & Andrade 2004), and in Bolivia where humidity gradients within the canopy are important for species occurrences (Krömer, Kessler & Gradstein 2007).

Within ecosystems, there is strong evidence that higher bromeliad abundance and/or diversity are found in wetter ecosystems, especially those with high levels of cloud immersion (Sugden & Robins 1979; Benzing 2000; Obregon *et al.* 2011). The presence of fog is critical in determining the occurrence of bromeliads in the Atacama desert (Rauh & Temple 1979; Rundel *et al.* 1997; Rundel & Dillon 1998; Pinto, Barria & Marquet 2006) and the lowland rainforest of French Guiana (Gehrig-Downie *et al.* 2011), however, high humidity inhibits the growth of the 'extreme atmospheric' bromeliads in Trinidad (Griffiths & Smith 1983). The effect of water availability influences distribution by influencing population dynamics. The effect is most pronounced where water is scarce. In wet Panamanian forests (annual precipitation = 2 300

mm) demographic parameters of populations of *Werauhia sanguinolenta*, were not affected by water-availability. In Mexican populations of *Tillandsia brachycaulos*, which receive annual precipitation of 880 mm, demographic population parameters were strongly influenced by rainfall (Mondragón *et al.* 2004).

Between ecosystems water availability is an important driver of bromeliad distributions, with species of bromeliads found on both sides of the Ecuadorian Andes found consistently lower (from 200 m to 2500 m) on the wetter eastern side than those on the dry western side (Gilmartin 1973). One of the most interesting quirks of the distribution of the Bromeliaceae is the apparent lack of diversity and abundance of bromeliads growing in most parts of the lowland Amazon. It is believed that this is a result of the high evapotranspiration combined with dense shade (Kessler 2002) although this hypothesis remains untested.

1.3.3 THE ASSOCIATIONS OF BROMELIADS (AND OTHER EPIPHYTES) INTO COMMUNITIES AND ECOLOGICAL ZONES

Just as individual species distributions are scale-dependent, so are the communities and ecological zones into which species can be classified.

At the scale of individual trees, phytosociological communities can be delimited using intensive, local sampling, and reveal that different communities form in different parts of the trees (Kelly *et al.* 2004). At this scale microclimate (especially water availability and light availability) is the main driving factor and the distinct communities and these are often referable to distinct strata within the canopy (Pittendrigh 1948; Johansson 1974; Bennett 1987; Kelly *et al.* 2004; Reyes-Garcia *et al.* 2008).

At a broader scale bromeliads may be found in ecological zones, areas delimited by a unique set of species, often corresponding to discrete sets of terrestrial vegetation. These ecological zones are often driven by the interaction of climate with species' adaptations to water and light availability (Burt-Utley & Utley 1980; Sugden 1981). For terrestrial species

ecological zones on the eastern slope of the Andes are defined by climate, and particularly water availability (Grubb & Whitmore 1966), and these ecological zones have different diversities of epiphytes (Ibisch *et al.* 1996), but a study of bryophyte communities revealed no specific ecological zones on the eastern slope of the Peruvian Andes (Kessler 2000). In this thesis I use species' distribution data to look for distinct ecological zones for the Bromeliaceae on the eastern slopes of the Andes (Chapter 4). Where zones have been reported studies in the literature have rarely investigated patterns underlying the ecological zones of epiphytes in terms of species' adaptations. Here we hypothesise that species in each zone will be adapted to the climate prevalent in that zone, and this is investigated in Chapter 6.

On the broadest scale, bromeliads are found in distinct ecoregions, driven by both climate and evolutionary history (Givnish *et al.* 2007; Givnish *et al.* 2011). While the ecoregions in Givnish *et al.* (2011) are delimited based expert knowledge, tools now exists to delimit these regions based on empirical data (Kreft & Jetz 2010). Provisional empirical biogeographic regions are delimited for the Bromeliaceae in Chapter 7 and compared to those of Givnish *et al.* (2011).

1.4 OBJECTIVES OF THIS THESIS

In order to address the aim stated at the beginning of this chapter, the following section sets out the objectives to be addressed in each chapter, and explains how they feed into the overall aim. Using field sites in the Peruvian Andes (Chapter 2) the distribution of bromeliads can be observed on a local scale, and it is possible to see the importance of adaptations to ecological zones within this ecosystems.

In Chapter 3 I summarise climate information collected from the field sites described in Chapter 2. This climate data, primarily collected from permanent weather stations gives a detailed portrait of the climate of the area, but is based on conditions outside the forest canopy,

and is equivalent to the climate experienced at the canopy surface. To gain a better understanding of the climate experienced by epiphytes I present data collected on the microclimate within the forest canopy from three sites along this transect representing the main ecological zones. I will use the climate data to answer the questions:

1. What are the main climate patterns along the altitudinal gradient?
2. Are there different microclimates at different heights within a forest (e.g. In different Johansson zones (Johansson 1974))?
3. Are conditions inside the canopy sufficiently different from conditions at the canopy surface to provide a clear basis for niche differentiation?

In Chapters 4 and 5 I will quantify the two aspects of bromeliad ecology, their diversity and their biomass. In Chapter 4 I will look at patterns of diversity, both α - and β -diversity and compare these across altitudes. I will also make comparisons between bromeliad and woody species diversity, and look for ecological zones in either group of plants. The main questions I will address in this section are:

- Are there altitudinal patterns in the diversity of bromeliads on the eastern slope of the southern Peruvian Andes?
- Are the patterns in the altitudinal transect similar to those in other altitudinal transects?
- Does the turnover of bromeliads reflect ecological zones of the forests?

In Chapter 5 I will look at the distribution of the biomass of all vascular epiphytes, including bromeliads, along this altitudinal transect. While biomass and diversity are often related, they are not intrinsically linked, and any relationship needs to be tested rather than assumed. Here I use the recently produced SVERA protocol (Wolf, Gradstein & Nadkarni 2009) to measure epiphyte biomass in thirteen permanent sample plots. I then fit models to predict epiphyte

biomass using abiotic and biotic factors, as well as comparing the contribution of epiphyte biomass to total forest biomass. I will address the following questions:

- How does epiphyte biomass vary with altitude?
- Which environmental factors are important in determining epiphyte biomass?
- How much do vascular epiphytes contribute to the biomass of the montane ecosystem?

In Chapter 6 I will try to establish if species of bromeliads are limited to distinct ecological zones based on shoot morphology and physiology as a consequence of plant water-relations. This represents an examination of the importance of adaptations to low water availability on a regional scale. I hope to answer the questions:

- Is there variation in water-availability for epiphytic bromeliads along the altitudinal gradient?
- Are different adaptations to water capture and use more prevalent at certain altitudes?
- Are adaptations to water-availability sufficient to explain ecological zones of species along the altitudinal gradient?
- Is there an altitudinal limit for species with CAM photosynthesis?

Typically bromeliad species with CAM photosynthesis are present in the lowland Amazon, but absent from the wet eastern slopes of the Andes. This means that to gain a more detailed understanding of the importance of CAM photosynthesis I will expand the area of study from the regional to the continental scale. In Chapter 7 I will look at the importance of CAM photosynthesis across the entire range of the bromeliads. With a large dataset of carbon isotope ratios from the leaves of Bromeliaceae species, I will use herbarium specimens and local floras to look for a relationship between the distributions of species with CAM photosynthesis compared to species with C_3 photosynthesis. I will answer the following question:

- Which environmental factors are responsible for the observed distribution of bromeliad species with CAM photosynthesis on a continental scale?

In the discussion (Chapter 8) I will summarise the findings of the other chapters and discuss these findings in the context of the ecology of vascular epiphytes along an altitudinal transect.

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2. FIELD SITES

2.1 INTRODUCTION

In this introductory section data is presented on the field sites used in this study. The field sites are located in southern Peru, in or close to Manu National Park and Tambopata National Park (Figure 2.1). A summary of the physical and biological properties of the permanent sample plots (PSPs) and plotless sampling locations are presented and each individual study site is discussed in the context of the site in which it belongs. Work in both Manu National Park and Tambopata National Park was completed as part of the Andes Biodiversity and Ecosystems Research Group (ABERG; <http://darwin.winston.wfu.edu/andes/>) long-term forest monitoring program (Malhi *et al.*, 2010).

In this section sites will be discussed in terms of the vegetation classes that occur along the elevation transect, and these vegetation classes will be compared to traditional vegetation classifications of Grubb (Grubb *et al.*, 1963; Grubb & Whitmore, 1966) and Holdridge (1967). The ecological classification used here divides the site into four zones, the lowland rainforest (LRF), tropical montane forest (TMF), tropical montane cloud forest (TCF), and Puna grasslands. The division of forests for this site is based on species composition, illustrated in Chapter 4 and summarised in Table 2.1 with some input from a previous classification of the area (Pro-Manu, 2000).

The Andes are some of the youngest mountains on the planet, and their uplift around 20 million years ago led to dramatic change in the South American continent (Hoorn *et al.*, 2010). The mountains create a large variation in climate over a short physical space. There is a large difference between the dry western slopes and wet eastern slopes, marked by differences (including in the Bromeliaceae) in altitudinal distributions of plants which occur on both slopes

(Gilmartin, 1973). The ABERG transect focuses on the wet eastern slope of the Andes, an area of high biodiversity value (Myers *et al.*, 2000). The area is also home to “tropical montane cloud forest”, a special vegetation zone, which covers a small proportion of the earth’s surface, but has a unique ecology and high level of endemic species (Myers *et al.*, 2000).

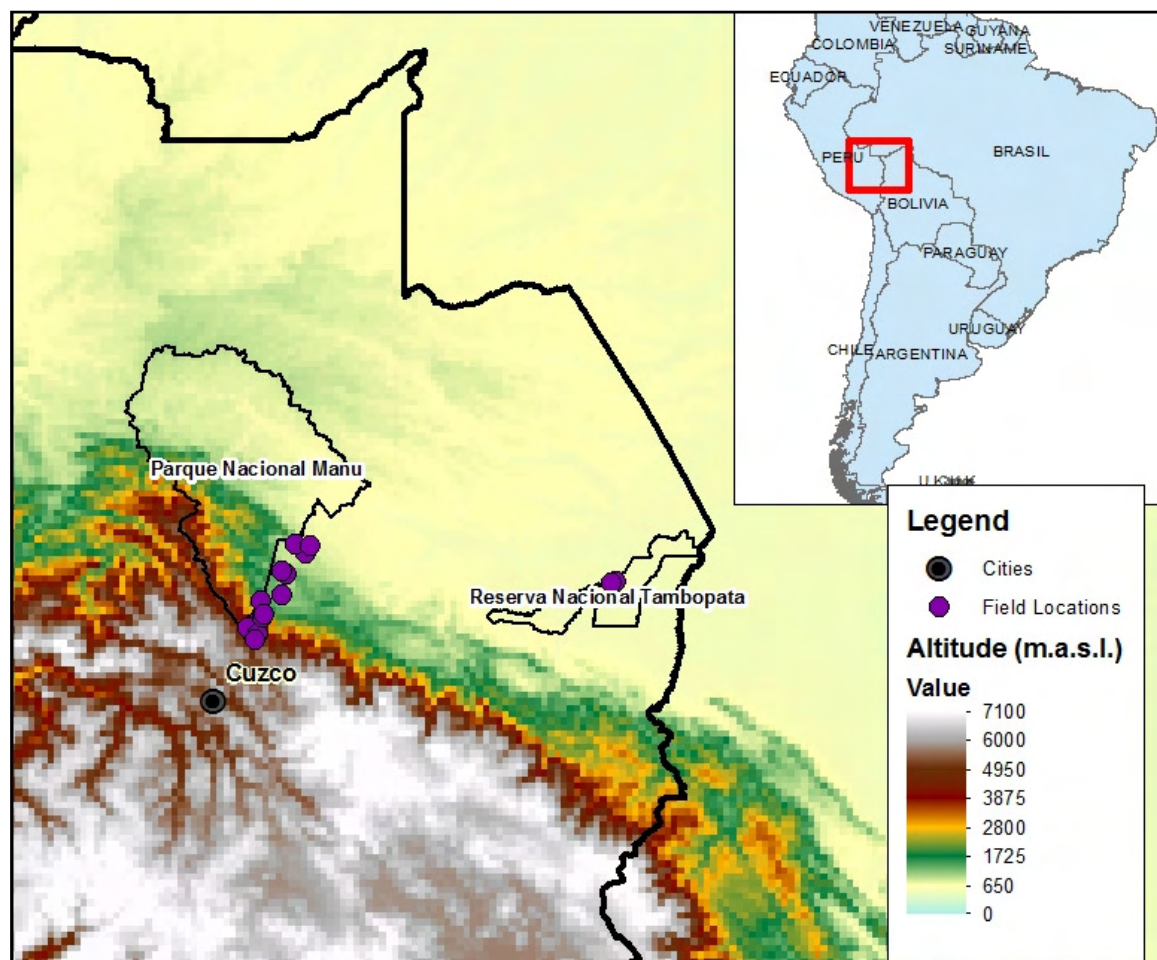


Figure 2.1. Topographic map of Peru showing the location of field sites used in this study and the two national parks in which some of the field sites are located.

Table 2.1. Comparison of vegetation types from this transect to those from the literature

Vegetation type in this study and altitude	Comparison with Grubb and Whitmore (1966)	Comparison with Holdridge (1967)
Lowland rain forest (LRF): 180 m to 1000 m	Same as 'lowland rainforest'	The areas up to 600 m altitude fall on the sub-tropical wet forest and sub-tropical rain forest boundary
Tropical montane forest (TMF): 1000 m to 2000 m	Similar to 'lower montane forest' but more seasonal due to sub-tropical location	Super-humid lower montane and premontane rainforest for transect above 600 m up to montane forest at 2500 m
Tropical montane cloud forest (TCF): 2000 m to 3500 m	Similar to 'upper montane forest'	Super-humid montane rainforest extends down to annual mean temp of 12C at TU5 (2500 m)
Puna grassland: above the tree line around 3500 m	Not discussed.	Climate conditions equivalent to subalpine rainforest and wet-forest reflecting the anthropogenic nature of the grasslands.

2.2 GENERAL CHARACTERISTICS OF THE PLOTS AND SITES

The ecology of the Andes is a complex combination physical and biological interactions (Gradstein *et al.*, 2008). A big driver of the ecology are the frequent landslides which occur on the steeper slopes, especially during the wettest months from January to March (Kessler, 1999). Landslides result in almost complete removal of the soil, especially in more precipitous areas, effectively resetting the succession and there are ongoing studies to determine the frequency and intensity of these events (K. Clark, unpublished data) (Figure 2.2). Much of the montane forest will be in some stage of post disturbance succession. The forests are also subject to fire (Román-Cuesta *et al.*, 2011), particularly at higher altitude, and anthropogenic deforestation particularly for conversion to agriculture (Pro-Manu, 2000).

Hydrology plays an important role in Andes; watercourses from all the field sites ultimately drain into the Amazon. The sites from the highest altitude down to 1000 m are within the Kosñipata Valley (Figure 2.3). The plot at 1000 m, along with the Manu Learning Centre and Pantiacolla sites are in the valley of the larger Tono River into which the Kosñipata drains, and which ultimately joins the Manu River (Figure 2.3). The lowest altitude plots at

Tambopata are by the Tambopata River, a major river which drains the entire Manu National Park watershed along with others.



Figure 2.2. A large landslide the occurred in 2009 along the Trocha Union ridge on the edge of the permanent sample plot at 3250 m. The landslide cleared a large area of the mountain side for about 750 m to the bottom of the valley.

Permanent sample plots (PSPs) were established at 18 locations by the ABERG group following the method of Phillips *et al.* (2003). For convenience, these 18 plots are split into 7 sites, the site being a collection of plots within the boundary of one landowner. The altitude, slope, aspect and substrate are summarised in Table 2.2. In the plots, each stem over 10 cm DBH has been tagged with a numbered steel tag, and a vouchered specimen collected and kept in a field herbarium in Cuzco, Peru. Information on DBH of each stem was recorded in 2003 and repeated in 2007 by the ABERG research group. Details of the woody plant composition, including number of stems, number of species and the most common species are included in Table 2.3. At each site, some plotless sampling of bromeliads was carried out, to supplement

data collected from permanent research plots. Details of locations of plotless sampling are included in the detailed discussion of each site and summarised in Table 2.4.

Table 2.2 Physical details and location of Permanent Sample Plots used in this study.

Site	Plot	Altitude (m)	Latitude	Longitude	Slope (°)	Aspect	Geological substrate
Trocha Union	TU1	3380	-13.1135	-71.6071	41.7	W	Paleozoic shales-slates
Trocha Union	TU2	3200	-13.1107	-71.6045	30.5	W	Paleozoic shales-slates
Wayqecha	WAY	3025	-13.1904	-71.5871	29.2	E	Paleozoic shales-slates
Wayqecha	ESP	2850	-13.1759	-71.5949	31.0	SW	Paleozoic shales-slates
Trocha Union	TU3	3020	-13.1092	-71.5977	18.3	W	Paleozoic shales-slates
Trocha Union	TU4	2740	-13.1068	-71.5894	19.3	W	Paleozoic shales-slates
Trocha Union	TU5	2520	-13.0943	-71.5744	15.6	W	Paleozoic shales-slates
Trocha Union	TU7	2025	-13.0735	-71.5589	40.3	W	Paleozoic shales-slates
Trocha Union	TU8	1850	-13.0705	-71.5557	39.0	W	Granite batholith
San Pedro	SAN1	1750	-13.0472	-71.5425	19.3	SE	Paleozoic shales-slates
San Pedro	SAN2	1500	-13.0491	-71.5368	21.3	SE	Granite batholith ¹
Tono	TON	925	-12.9547	-71.5535	8.5	Flat	Alluvial terrace
Pantiacolla	PAN	580	-12.6495	-71.2625	0.0	Flat	Alluvial terrace
MLC	MLC	500	-12.7889	-71.3905	0.0	Flat	Alluvial terrace
Tambopata	TAM3	190	-12.8303	-69.2705	2.8	Flat	Pleistocene alluvial terrace
Tambopata	TAM4	180	-12.8385	-69.296	5.7	Flat	Holocene alluvial terrace

¹(Y. Malhi, pers. comm.)

Table 2.3. Details of biological characteristics of plots. Raw data unpublished from the ABERG research group.

Site	Plot	Number of stems >10 cm dbh	Number of species	Dominant species (number of stems)	Forest disturbance
Trocha Union	TU1	586	36	<i>Weinmannia microphylla</i> (124); <i>Miconia</i> sp. (94); <i>Symplocos quitensis</i> (65)	Primary
Trocha Union	TU2	779	56	<i>Weinmannia bangi</i> (129); <i>Miconia</i> sp. (78); <i>Prunus huantensis</i> (66)	Primary
Wayqecha	WAY	1139	55	<i>Weinmannia crassifolia</i> (406); <i>Clusia cretosa</i> (124); <i>Clusia flaviflora</i> (54)	Primary
Wayqecha	ESP	706	67	<i>Weinmannia latifolia</i> (154); <i>Clusia poeppigiana</i> (88); <i>Prunus integrifolia</i> (55)	Primary
Trocha Union	TU3	559	45	<i>Clusia cretosa</i> (135); <i>Clusia trochiformis</i> (88); <i>Weinmannia</i> sp. (60)	Primary
Trocha Union	TU4	887	56	<i>Cyathea delgadii</i> (115); <i>Weinmannia</i> sp. (79); <i>Clusia</i> sp. (69)	Primary
Trocha Union	TU5	1034	64	<i>Cyathea delgadii</i> (324); <i>Clusia</i> sp (78); <i>Weinmannia bangi</i> (77)	Primary
Trocha Union	TU7	82	95	<i>Alzatea verticillata</i> (163); <i>Cyathea lechleri</i> (74); <i>Ilex villosula</i> (69)	Primary
Trocha Union	TU8	1150	105	<i>Cyathea lechleri</i> (127); <i>Clethra revoluta</i> (103); <i>Clusia</i> sp. (73)	Primary

Field sites

San Pedro	SAN1	909	195	Cyathaceae sp. (152); <i>Tapirira</i> sp. (48); <i>Alzatea verticillata</i> (41)	Primary
San Pedro	SAN2	837	179	Lauraceae sp. (71); Cyathaceae sp. (64); <i>Tachigali setifera</i> (53)	Primary
Tono	TON	404	112	<i>Perebea guianensis</i> (42); <i>Virola elongata</i> (37); Lauraceae sp. (34)	Primary
Pantiacolla	PAN	498	135	<i>Pseudosenefeldera inclinata</i> (41); <i>Coussapoa parviflora</i> (32); <i>Hevea</i> <i>brasiliensis</i> (26)	Historic selective logging
MLC	MLC	N/A	N/A	N/A	Secondary
Tambopata	TAM3	542	156	<i>Pourouma minor</i> (44); <i>Pseudolmedia</i> <i>laevigata</i> (22); <i>Bixa arborea</i> (19)	Primary
Tambopata	TAM4	668	194	<i>Iriartea deltoidea</i> (123); <i>Socratea exorrhiza</i> (58); <i>Rinorea viridifolia</i> (32)	Primary

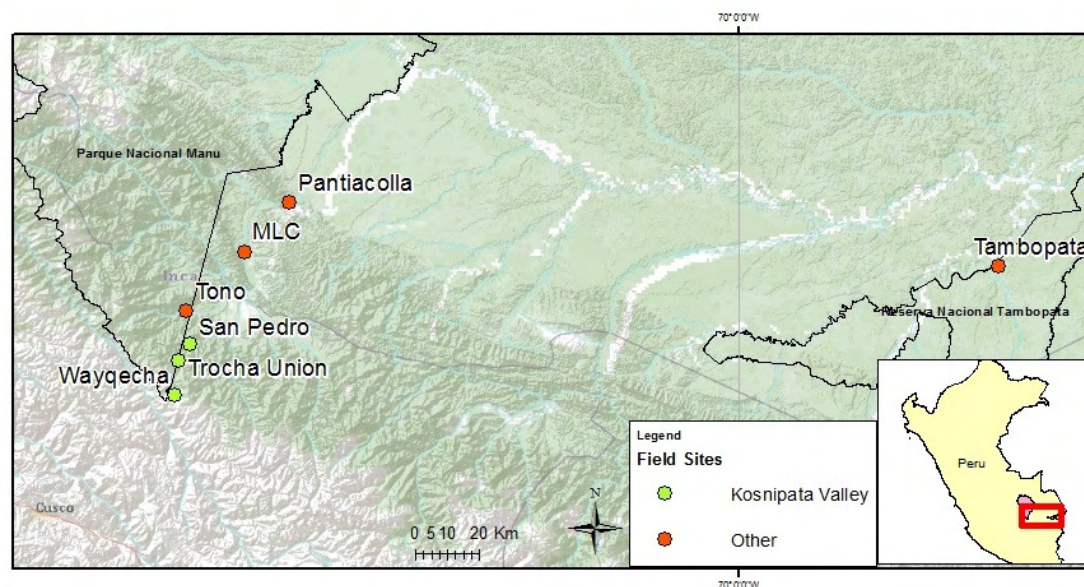


Figure 2.3. Location of 7 field sites with the three sites in the Kosñipata Valley indicated.

Table 2.4. A summary of the plotless sample locations used in this study.

Site	Plotless Sample Name (code)	Details
Manu National Park - Puna	Treeline (TL)	Small, often isolated patches of forest in the matrix of Puna grassland dominated by high-altitude species with short stature
Wayqecha	Trocha Oso (WAYoso)	A linear trail running around the site at approximately 2800 m, passing mainly through open secondary vegetation and some areas of <i>Alnus</i> forest in more sheltered valleys
Wayqecha	Trocha Mariposa (WAYmp)	A small riparian woodland area at the base of a small ridge and the confluence of two streams, at 2250 m

San Pedro	Road (SANrd)	Riparian forest adjacent to the Union River that has opened up by the construction
San Pedro	Trail (SANtr)	The forest along the ridge between the two plots, the slope is steep with shallow soil and frequent stands of bamboo suggesting recent disturbance due to landslides
Tono	Pongo Qoñec (JBO)	Transition forest at around 700 m. For more details see Huamantupa-Chuquimaco (2010)
MLC	Primary forest (MLCpf)	An area of primary lowland rainforest approximately 3 km from the main MLC site
Pantiacolla	Mirador (PANmir)	A small band of elfin forest on the Pantiacolla foothills of the Andes at approximately 900 m.
Pantiacolla	Secondary forest (PANsf)	Secondary forest on the floodplain of the river, with a high proportion of <i>Cecropia</i> spp. and bamboo.

2.3 DETAILED DESCRIPTION OF SITES

2.3.1 LOWLAND RAINFOREST

The lowland rainforest is an extensive vegetation type that occurs on undisturbed land throughout the lowlands up to approximately 1000 m, corresponding exactly to the ‘lowland rainforest’ of Grubb (Grubb *et al.*, 1963; Grubb & Whitmore, 1966). Climate recorded from the plots show that with approximately 4000 mm rainfall and PET ratio of approximately 0.25 these sites fall on the boundary of tropical wet forest and sub-tropical rain forest based on Holdridge’s life zones (Holdridge, 1967). At the ABERG sites, the lowland Amazon in southern Peru is classified as Southwest Amazonian moist forest by Olsen *et al.* (2001) and an Andean super-humid zone (Killeen *et al.*, 2007). Relative to the plots at higher altitude, the lowland tropical rainforest is characterised by higher NPP (Girardin *et al.*, 2010), higher soil respiration (Zimmermann *et al.*, 2009) and higher stem respiration (Robertson *et al.*, 2010). This creates a high turnover of carbon throughout the system and the largest carbon store is in the woody plant material (Malhi *et al.*, 2006). The rapid decomposition on the forest floor is enhanced by the abundance and diversity of termites (Palin *et al.*, 2011). Four sites with five PSPs were located in the lowland rainforest.

SITE: THE MANU LEARNING CENTRE (MLC)

The Manu Learning Centre (MLC) is home to one permanent research plot established in 2009 (500 m elevation) and is located close to the town of Salvación but on the opposite banks of the River Tono (Figure 2.4a). Most of the site is secondary forest (Figure 2.4b), including the PRP. There are trails extending into ancient woodland, where some plotless sampling was carried out (MLCarea). The site is being developed as a model for combined conservation and sustainable tropical land use (<http://www.crees-expeditions.com>).

SITE: PANTIACOLLA

Pantiacolla is a private reserve, with a tourist lodge run by a company of the same name (<http://www.pantiacolla.com>). It is home to one plot (600 m) (Figure 2.4d). The name Pantiacolla is derived from the local names for the small mountain chain, the front-range of the Andes, where the site is located. A hike of 6.5 km from the lodge allows access to the top of the Pantiacolla ridge, on which is elfin forest. Part of the trail passes through white-sand forest, growing on the dry, nutrient poor white sand soil (M. Silman, pers. comm.). The permanent research plot is located on the clay soils, in the continually-wooded but selectively-logged forest. Two plotless sample areas were used from this site, one in the floodplain forest close to the river (PANsf) on flat terrain about 400m. The other plotless sample area (PANmir) was a small strip of elfin forest on the ridge of the Andean foothills at about 900 m altitude (Figure 2.4c). The elfin forest is identified as being exposed on ridge-tops giving rise to short-stature forest (Grubb & Whitmore, 1966).



Figure 2.4. Images of the MLC and Pantiacolla sites (a) the MLC site is located close to the Tono River; (b) understory of the secondary forest in the PSP at MLC; (c) a view of the LRF looking north from the Pantiacolla foothills ridge; (d) the understory of the primary forest in the PSP at Pantiacolla.

SITE: TAMBOPATA NATIONAL PARK (EXPLORER'S INN)

Tambopata National Park is home to eight main permanent research plots from the RAINFOR network (Malhi *et al.*, 2002) in different forest types adjacent to the Tambopata River (Figure 2.5a). The RAINFOR plots are accessed from the permanent lodgings at the Explorer's Inn (<http://www.explorersinn.com/>). Two plots have been extensively studied as part of the ABERG project (Girardin *et al.*, 2010), and both of these were the plots used in this study (here referred to as Tambopata 3, 'TAM3' (Figure 2.5b), at 180 m and Tambopata 4, 'TAM4' at 210 m elevation) (Figure 2.3). Detailed descriptions of the vegetation of these plots can be found in Malhi *et al.* (2002). The forest is primary lowland rainforest, and large areas of the site are subject to regular flooding by the river. The area is also covered by extensive trails.

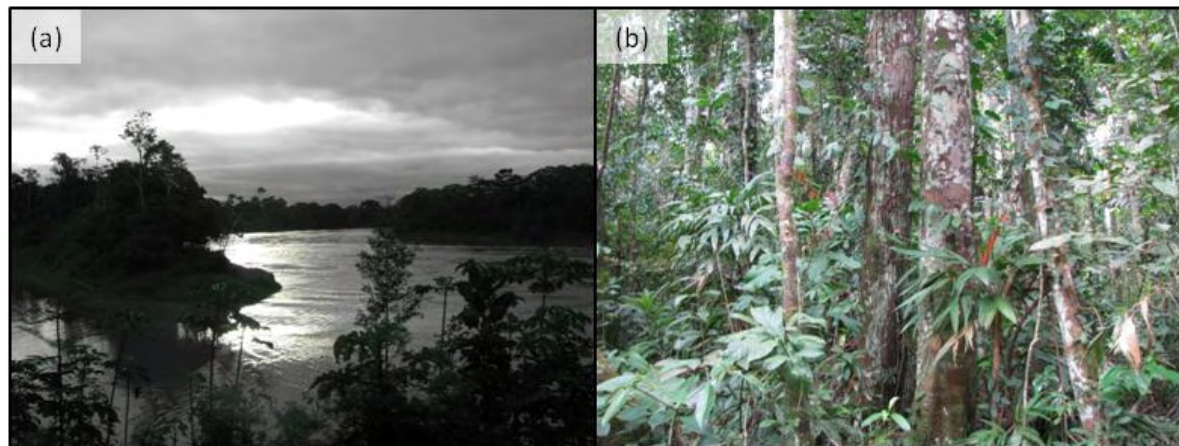


Figure 2.5. Tambopata site, (a) the Tambopata river close to the PSP TAM4; (b) the forest understory in the PSP TAM3.

SITE: MANU NATIONAL PARK - TONO

Tono is the site of one permanent research plot at 1000 m elevation (Figure 2.3). The land is inside the boundary of Manu National Park, and access was via the guard station at Tono Alto. The forest is primary forest (Figure 2.6a) and unlike plots at higher altitude, palm trees are a significant part of the canopy at this site (Figure 2.6b). Natural disturbance also leads to growth of large bamboos (mainly *Guadua* spp.) (Figure 2.6c). This forest is included as LRF, but falls close around the zone of transition between LRF and TMF, and could be considered as part of either. Just outside the national park close to Tono, an additional plotless sample (JBO) was included at Pongo Qoñec, in the forest around the Jardín Botánico de Orquídeas. The forest in this area is described in detail in Huamantupa-Chuquimaco (2010).

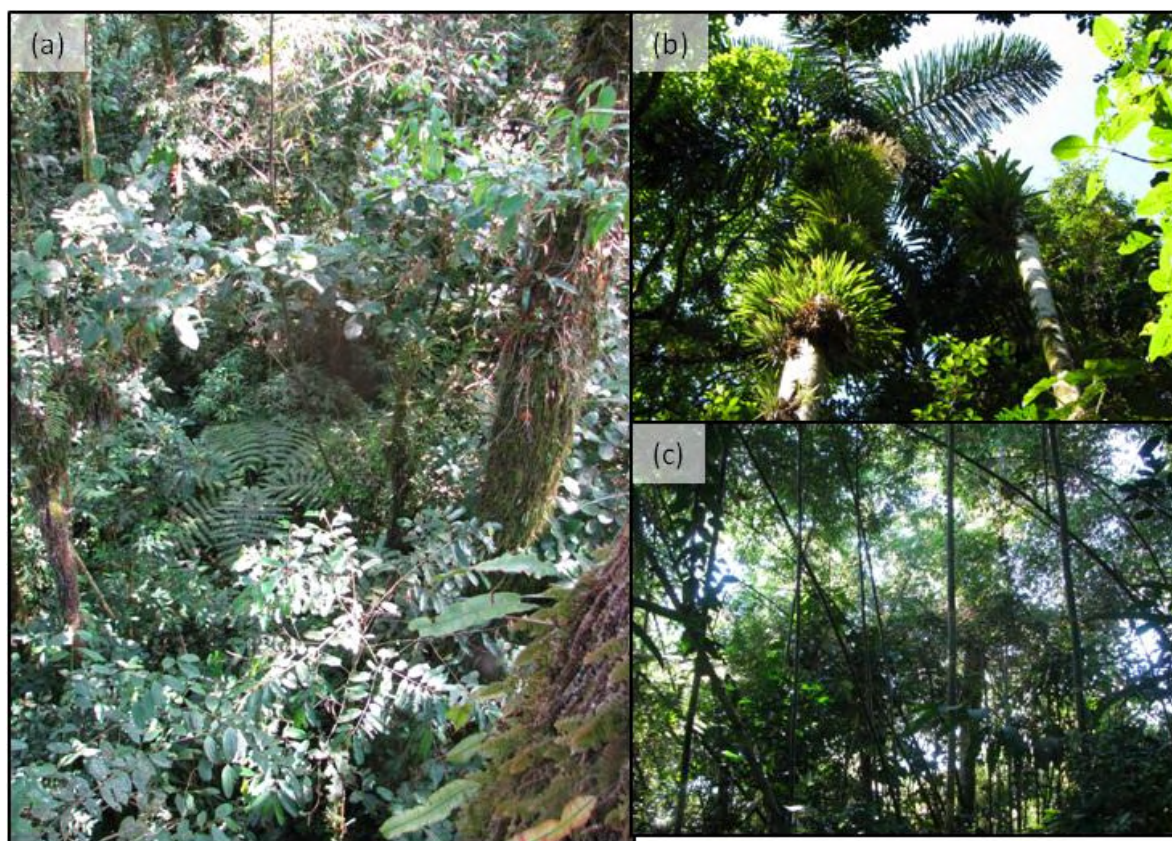


Figure 2.6. Images of the Tono site; (a) looking down into the PSP from the forest canopy; (b) the large palm trees (including this *Iriartea deltoidea*) are a striking feature of the lowland rainforest and often support vascular epiphytes; (c) an area of *Guadua* cf. *weberbaueri* (Bamboo) inside the plot.

2.3.2 TROPICAL MONTANE FOREST

The tropical montane forest (TMF) falls between the cloud base and the lowland forest, and is equivalent to the 'Lower Montane Forest' of Grubb (Grubb *et al.*, 1963; Grubb & Whitmore, 1966). The transition from LRF to TMF is summarised in Grubb and Whitmore (1966) as varying between 700 m for Caribbean islands and 1350 m for the Colombian Andes, based primarily on cloud immersion and water-availability. For Holdridge's life zones, the precipitation and PET ratio classify the TMF sites as lower-montane and pre-montane super-humid rain forest (Holdridge, 1967). A plot along this transect, but not used in this study, at 710 m shows composition significantly different from both LRF and TMF plots (Huamantupa-

Chuquimaco, 2010). For the purposes of this work, 1000 m is used to represent the start of TMF.

At the upper elevation of TMF, significant cloud immersion leads to a vegetation adapted to lower PET, the tropical montane cloud forest (TCF). This change occurs between 1500 m and 1750 m providing the upper boundary of the TMF. TMF is characterised by lower NPP and respiration than LRF (Girardin *et al.*, 2010), but still has termites present and is intermediate between LRF and TCF in carbon turnover times (Girardin *et al.*, 2010). One site with two PSPs is located in the tropical montane forest. Some of the lower altitude plots that are part of the Trocha Union site may also represent TMF, but for convenience at this stage they are included in the TCF section.

SITE: SAN PEDRO

The land around San Pedro exists outside the zone of strict protection of Manu National Park (Figure 2.3). The small amount of flat land around the river between 1400 m and 1600 m has often been cleared to build tourist lodges and private residences, the area being famed for the mating displays of the Cock-of-the-rock (*Rupicola peruviana*), as well as a convenient resting place between Paucartambo and Pillcopata. The two research plots in San Pedro (Figure 2.7a,b) are on a ridge above the tourist lodges (Figure 2.7d). The steep ascent of the trail has made the land inaccessible for development, and the forest is primary forest, although the trail connecting the plots at 1500 m and 1750 m often has dense bamboo patches, indicating recovery from recent landslides. Plotless sampling was carried out along this trail (SPtrail). Accommodation at San Pedro was provided by InkaNatura (<http://www.inkanatura.com/>), and around their property they have developed an extensive trail network. Plotless sampling was carried out on land around the Union river at 1500 m (SProad). In March 2010 the area around San Pedro suffered from extensive landslides.



Figure 2.7. Images of the San Pedro site; (a) the understory of the PSP at 1500 m; (b) the understory of the PSP at 1750 m; (c) a view of the ridges on the opposite side of the valley from the PSPs; (d) a view looking south from San Pedro (back towards the top of the transect).

2.3.3 TROPICAL MONTANE CLOUD FOREST

The tropical montane cloud forest (TCF) ecology is tied to extensive cloud immersion (Grubb & Whitmore, 1966; Richards *et al.*, 1996) and is the same vegetation type as Grubb's 'Upper Montane Forest' (Grubb *et al.*, 1963; Grubb & Whitmore, 1966). Extensive cloud immersion creates very low PET so the vegetation rarely has to cope with extensive drought periods (Grubb & Whitmore, 1966). The lower precipitation and temperatures mean these forests correspond to Holdridge's super-humid montane rain forest, and the precipitation and temperature are always above that of the subalpine zones (Holdridge, 1967). The only exception is the plot at Wayqecha, where the lower rainfall means the site is probably best

classified as wet forest rather than rainforest. Consistent with Grubb and Whitmore (1967) the upper and lower limits of TCF are tied to upper and lower limits of cloud immersion. The cloud base changes throughout the year, but in the Kosñipata Valley there is a distinct change between 1500 m and 1750 m providing the lower limit of this vegetation zone. The TMCF is characterised by the slow decomposition of organic material leading to large carbon stocks in the soil (Girardin *et al.*, 2010), and this is accentuated by the absence of termites (Palin *et al.*, 2011). Two sites with 10 plots are located in the tropical montane cloud forest.

SITE: WAYQECHA

Wayqecha is the site of two plots. It is a private conservation concession, owned by the Association for the Conservation of the Amazon (ACA) and the Peruvian counterpart Asociación para la Conservación de la Cuenca Amazónica (ACCA; <http://www.acca.org.pe/>). The concession is 563 ha, and covers terrain from 3400 m to 2250 m in elevation. The land also includes parts of two tributaries to the Kosñipata River (Rio Allpacancha and Rio Huallpayunca), and their intersection. Much of the land was formerly deforested for use in agriculture. Regeneration of forest has occurred in the last 40 years, but much of the vegetation remains in transition (Figure 2.8a). Two plots were located at the Wayqecha site (the Wayqecha ‘WAY’ and Esperanza ‘ESP’ plots), placed in areas that have been forested continually during the agricultural exploitation of the neighbouring land (Figure 2.8b). Two plotless samples were made at Wayqecha, both along trails. ‘Trocha Oso’ (WAYoso) runs around the middle part of the site at about 2750 m, through both primary and secondary forest areas. ‘Trocha Mariposa’ is located on the lowest part of the site, between 2250 m and 2500 m, running down a ridge to the junction of two rivers and is covered with short, open vegetation except for the riparian zone of the river.



Figure 2.8. Images of the TCF sites; (a) the secondary forest at Wayqecha; (b) accessing the canopy in the 3000 m PSP (WAY) at Wayqecha; (c) the high-altitude forest along the Trocha Union; (d) the understory of the PSP at 2750 m (TU4) showing the large phytotelm bromeliads typical at this altitude.

MANU NATIONAL PARK – TROCHA UNION

The Trocha Union is an ancient Inca trail, connecting the high Andes to the lowland Amazon.

The part of the trail used in this study passes inside the national park boundary at Tres Cruces around 3600 m altitude (Figure 2.3), and leaves again as it intersects the road from Paucartambo to Patria around 1600 m, just south of the San Pedro site. The trail passes quickly from Puna into the TCF along the ridge of a mountain spur (Figure 2.8c). The TCF along the Trocha Union is ancient woodland (Figure 2.8d), although frequent landslide disturbance of the steeper parts may mean the forest is in a natural disturbance regime. A linear transect of 8 plots (one every 250 m elevation), were placed just off the trail. Of these 8 plots, only 7 were used

extensively as the plot at 2250 m (TU6) had too high a slope to be accessed safely. One other plot, TU2 at 3250 m had recently lost about 20% of ground area to a large landslide (Figure 2.2).

2.3.4 MONTANE GRASSLAND

The Puna grassland (Figure 2.9a), extends from the mountain peaks (c. 5000 m) down to the tree line. Within the grassland are scattered patches of trees, most of them protected from the fires due to topography (Figure 2.9c). The tree line varies around 3600 m to 3200 m across the area of study. The tree line is mainly anthropogenically determined, primarily by fires and maintained by extensive cattle grazing (Román-Cuesta *et al.*, 2011). There is also an 'upper limit' to the cloud zone (although in reality this is more likely to be a gradient), at which the total cloud immersion time drops significantly (Figure 2.9b). Above this zone plants are exposed to high levels of solar radiation and UV light during the day and cold temperatures during the night. While large areas of the Puna are dominated by two grassland communities, a *Festuca dolichophylla* - *Calamagrostis vicuñarum* community and a *Stipa ichu* - *Calamagrostis vicuñarum* community (Pro-Manu, 2000), the Puna is actually complex mosaic of vegetation types (Figure 2.9d).

MANU NATIONAL PARK – QURQURPAMPA, ACANAJO AND TRES CRUCES

Here, data on the Puna was collected from a linear transect inside the boundary of Manu National Park, located between two guard stations along the western edge of the park. This area is used for grazing, despite existing inside the boundaries of the park, and is also subject to frequent fires (Román-Cuesta *et al.*, 2011). Around the Puna grassland are isolated patches of trees (Figure 2.9c), and several of these were also sampled for bromeliad species making a plotless sample (Treeline).

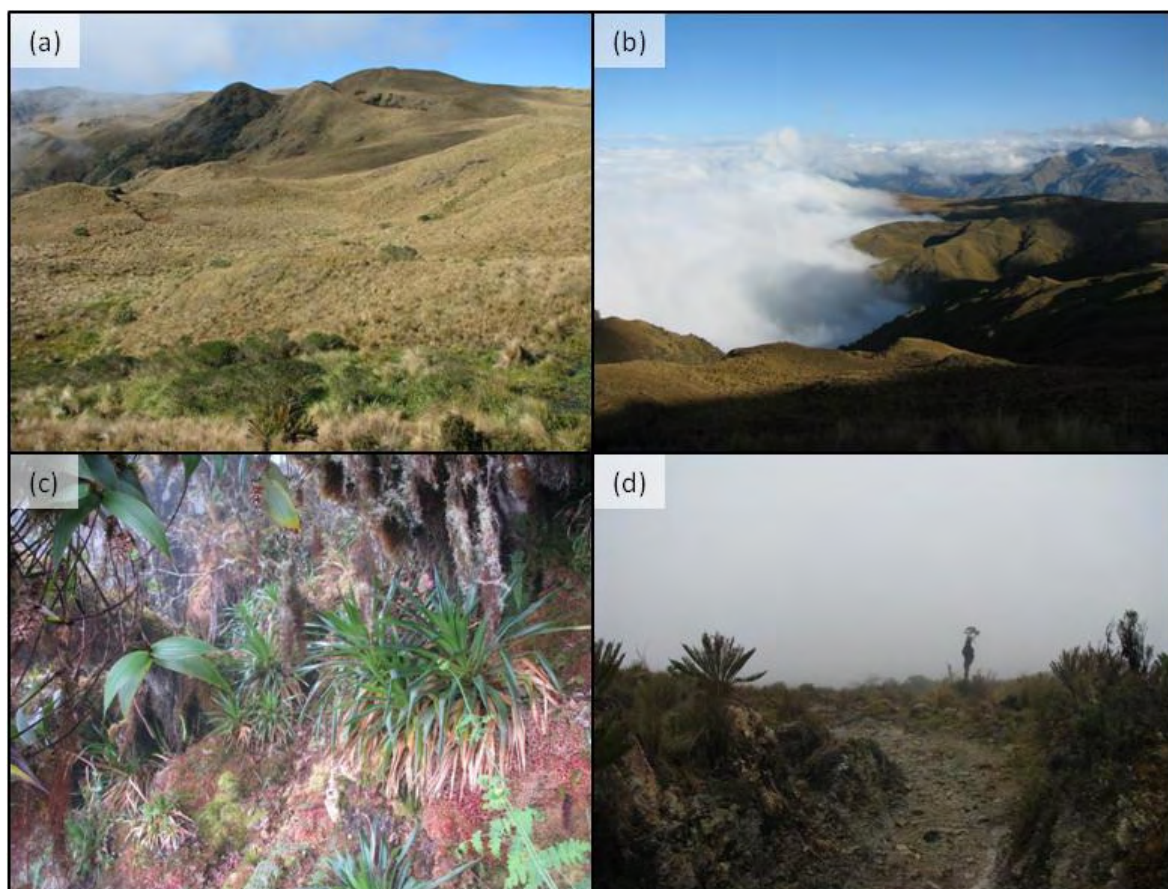


Figure 2.9. Images of the Puna grasslands; (a) a view south looking along the ridge at the highest altitudes of Manu National Park; (b) the Puna grassland are frequently above the upper level of cloud immersion; (c) an isolated patch of forest in the Puna with many epiphytes and *Sphagnum* spp.; (d) the Puna grassland is actually a complex mosaic of phytosociological communities including areas with high densities of cycads.

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3. CLIMATE AND FOREST MICROCLIMATE ALONG AN ALTITUDINAL GRADIENT

3.1 ABSTRACT

An understanding of variation of climate is essential to understanding the ecology of montane elevation transects. The field sites are part of the Manu-Tambopata superhumid zone (Killeen *et al.*, 2007), and receive high annual rainfall, but some elevations also have high cloud cover, reducing evapotranspiration. Temperature variation along the gradient is predominantly driven by altitude. The climate shows three distinct seasons, the dry season, the transition season and the wet season. I used climate sensors to record differences between the climate outside the forest, and climate beneath the forest canopy (forest microclimate). I found the microclimate is buffered within the forest, protecting plants from extremes of temperature and VPD, and preventing plants below the canopy experiencing ‘physiologically challenging’ conditions. The extent of the difference from the canopy surface to below-canopy climate depends on forest structure. This is important for vascular epiphyte distribution, as the conditions experienced within the canopy are less stressful than typical outside-canopy climate data indicates, and sites at the canopy surface can experience much more stress than microsites within the canopy.

3.2 INTRODUCTION

The climate on the eastern slope of the Andes shows strong spatial variation and broad-scale patterns are mixed with a high level of local variation due to complex topography. Climate has a direct influence on the metabolism, productivity and carbon cycling of the forest (Zimmermann *et al.*, 2009; Girardin *et al.*, 2010; Robertson *et al.*, 2010; Zimmermann *et al.*, 2010). It also affects species distributions (Rapp, 2010; Palin *et al.*, 2011) which can impact on forest ecology.

The climate is especially important to epiphytes (Chapter 1). The limits of the cloud zone, total annual rainfall and the extent of any dry periods will be very important at various stages of the life-cycle of the vascular epiphytes.

Climate is typically recorded from weather stations installed in open areas that record conditions typically experienced in the air above the exposed surface (usually the canopy top or above a grass surface). It is well known that conditions beneath the forest canopy are different from the conditions in the open, and these conditions are referred to as the forest microclimate. In this chapter I aim to establish the patterns of climate along the altitudinal gradient and to record the microclimate at three sites along the altitudinal gradient. After a brief review of information published on the climate relevant to the study area, I hope to address the following questions using *in situ* data collected during fieldwork:

- What are the main climate patterns along the altitudinal gradient?
- Are there different microclimates at different heights or locations within a forest (e.g. In different 'Johansson zones' (Johansson, 1974)?
- Are conditions inside the canopy sufficiently different from conditions at the canopy surface to provide a clear basis for niche differentiation?

The area of study, between 12° S and 13° S, falls into the Manu-Tambopata area identified as an Andean super-humid zone (Killeen *et al.*, 2007). Rapp (2010) found three distinct seasons across the field sites; the austral summer wet season from November to March ('wet season'), the austral winter dry season from May to July ('dry season') and the austral spring dry-wet transition from August through October ('transition season'). The seasons are marked by changes in rainfall and cloud formation patterns. In the dry season cloud forms at lower elevation and insolation and VPD increase with increasing altitude. The lapse rate is higher in the dry season. In transition season cloud forms at high altitude and insolation and

VPD decrease with increasing altitude. The wet season cloud patterns are similar to those in the transition season, but there is a higher amount of cloud at all elevations, which reduces the size of the gradients by reducing insolation reaching the ground.

The annual extent of cloud immersion is important to epiphytes as it increases water availability while reducing the VPD and exposure. The seasonal variation in the altitude at which cloud immersion occurs will be important for both vascular and non-vascular epiphytes. Many bryophytes and plants have adapted to intercept the water from fog. I would expect to see more species adapted to fog interception in areas with more extensive periods of cloud immersion, although the importance of these adaptations would be mitigated if the daily and monthly rainfall were sufficiently high.

3.2.1 ALTITUDINAL TRENDS

The linear decrease in annual mean temperature with increasing altitude is a well established pattern across montane areas due to the physical relationship between air pressure and the properties of gasses (Korner, 2007). The most common variation between different sites is the lapse rate, or size of the decrease with altitude. In the Kosnipata Valley the lapse rate changes between seasons, but on average is 5.22 °C per 1000 m (Rapp, 2010).

Precipitation does not follow the same linear pattern as temperature. Rainfall is not directly tied to altitude, and although it will often show altitudinal trends, these are not linked to physical distance above sea level. In the Kosnipata Valley the annual rainfall peaks at 1000 m (annual precipitation > 5000 mm) (Rapp, 2010). There is a linear decrease with increasing altitude above 1000 m, with the highest altitude station recording 980 mm of rainfall at 4000 m. The 1000 m peak occurs because this elevation is the zone of convergence between cool dry Andean air descending the slopes at night, and warm moist Amazonian air. The warm moist air is forced upwards by the cold front, resulting in frontal rainfall peaking in the early hours of the

morning. For the sites above 1500 m the monthly potential evapotranspiration is always less than the monthly rainfall total, so any plant water deficits would only be of short duration (Rapp, 2010). In the lowlands, the mean annual rainfall is more variable geographically, but is always less than 5000 mm.

Cloud formation is critical to montane ecology, as it determines forest types as discussed in Chapter 2 (Grubb & Whitmore, 1966; Holdridge, 1967). Additionally the fog input has important impacts on epiphyte and bromeliad distribution and abundance (Sugden, 1981; Gehrig-Downie *et al.*, 2011). The presence of a 'cloud zone' occurs roughly between 1500 m and 3000 m and is characterised by extended daily periods of fog. Data on cloud formation, persistence and altitudinal trends is scarce, and a sustained effort is underway to obtain more accurate data (Halladay, unpublished data). Data on cloud cover (but not immersion) is available from two stations at Rocotal (2500 m) and Chontachaca (700 m). The data shows a high frequency of cloud cover over at both sites, with cloud present over 80 % of the time on average. At Rocotal there is daily variation, with cloud cover lower in the morning than the afternoon and evening, but the same is not true at Chontachaca (Halladay, unpublished data). It is likely that there is substantial additional precipitation input through fog interception above 1500 m elevation, but this fog input has not yet been quantified (Y. Mahli, pers. comm.).

3.2.2 TEMPORAL TRENDS

To establish the daily and annual trends, data from three intensively studied sites is presented here, along with data from Rapp (2010). Two of the sites, Wayqecha (elevation 3000 m) and San Pedro (elevation 1500 m), are part of the ABERG network, and the data collection is discussed in Girardin *et al.* (2010). The third site is a sensor maintained by a local NGO (Asociación para la Conservación de la Cuenca Amazónica) at the Los Amigos Biological Station (elevation 400 m) and the data was accessed through the Atrium Biodiversity data portal (atrium.andesamazon.org).

At Wayqecha (TCF) the mean annual temperature was around 12 °C and total rainfall was 1800 mm (Figure 3.1). The temperature does not vary much throughout the year. The annual climate at San Pedro (TMF) is similar to Wayqecha; the daily mean temperature wet season is around 19 °C with the dry season (May – July) mean daily temperatures dropping to 17 °C or colder (Figure 3.1). At the latitude of 12° S the sites experience less than 1.5 hours variation in daylight hours between the solstices. For the LRF the annual temperature variation was small, and rainfall showed similar patterns to the other sites, although the total annual rainfall was higher (Figure 3.1). The availability of light (photosynthetically active radiation, PAR) is higher in January – the sun being directly overhead and the photoperiod lasting for longer. Some moderation of the difference in peak intensity will be caused by the increased cloud cover in January, but the amount of radiation is still higher. The changes in cloud cover showed similar patterns to rainfall; at Chontachaca (700 m) the cloud cover reached a minimum of 74 % in July and a maximum of 90 % in the wet season. At Rocotal (2500 m) the cloud cover was much lower in the dry season reaching a low of 53 % in July and 94 % in February.

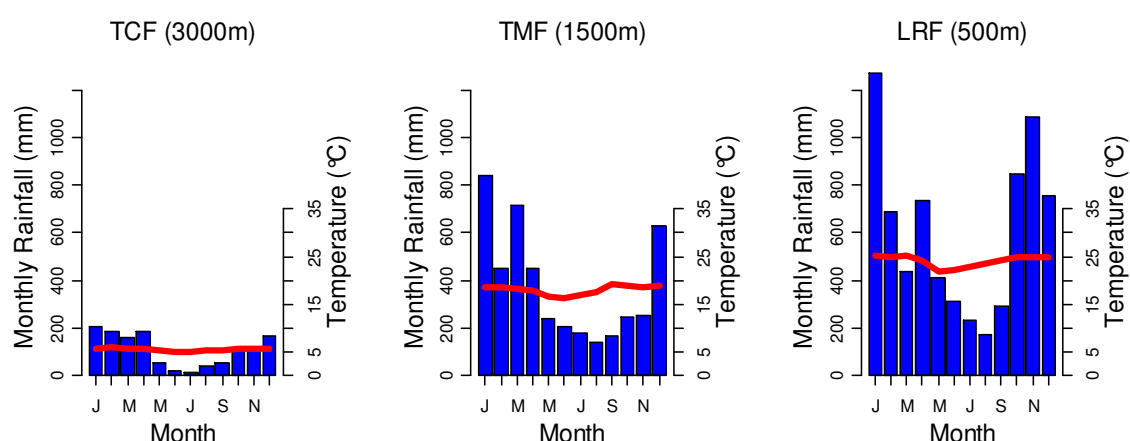


Figure 3.1. Climate diagrams for three sites along the elevation transect represent the three main forest types, tropical montane cloud forest (TCF), tropical montane forest (TMF) and lowland rainforest (LRF). Temperature is monthly mean temperature. Calculations from the author based on data described in Girardin *et al.* (2010).

3.2.3 MICROCLIMATE

While there is a significant amount of data available on the above-canopy climate, there is significantly less information on the climate within the forest canopy. The climate recorded above the canopy, or externally in open areas is assumed to be representative of climate at the canopy surface, here I use the term 'above-canopy' for clarity, but this climate recorded is most relevant biologically at the canopy surface. Rapp (2010) showed that at all altitudes the forest floor is sheltered, with vapour pressure deficits (VPD) reduced significantly compared to above the forest canopy (mainly because the daytime temperature peak is much lower in the shady sub-canopy). This effect is maintained across the altitudinal gradient. In the tropical montane cloud forest, VPD at the canopy surface rarely reached levels which are challenging for cloud forest plants (1.0-1.2 kPa); the understory never reached these levels. The VPD in the understory remained below 0.2 kPa for most of the year at all sites, only rising to 0.5 kPa in the dry season at sites below 2000 m. No data on VPD was collected for sites below 1500 m.

Further information on the microclimate is available from soil temperature and moisture content. Mean annual soil temperature is in general 1-2 °C cooler than the above-canopy air temperature, due to the canopy shelter from daytime radiation (van de Weg *et al.*, 2009). Soil moisture content showed no strong seasonal patterns, and mean annual water content was between 15 and 40 % for all sites. Spikes in water content were only seen during intense periods of rain, more common in, but not necessarily restricted to, the wet season (Zimmermann *et al.*, 2009; Zimmermann *et al.*, 2010).

3.3 METHODS

3.3.1 FIELD SITES

Intensive microclimate data was collected at three sites representing the three main forest types, tropical montane cloud forest (TCF) at Wayqecha (3000 m), tropical montane forest

(TMF) at San Pedro (1500 m) and lowland rain forest (LRF) at the Manu Learning Centre (500 m) (see Chapter 2 for description of sites; all sites have permanent climate stations installed close to the research plots.). For comparison to long term climate, sites were selected close to permanent weather stations. At Wayqecha the permanent weather station is located in a clearing close to the permanent research plot (Chapter 2). A site was selected at the tree line. The tree line site was close to the PRP and to the external permanent climate station. Due to technical issues, data on solar radiation outside the canopy was only available from the Wayqecha permanent weather station.

In San Pedro the permanent station is located in a clearing of 2 ha, kept free of vegetation, close to the research centre, however the aspect of the site is facing about 25 °S relative to the plot where the microclimate data was collected, and this may have lead to some of the differences with the permanent station data. At the MLC the permanent automatic weather station was not functional at the time of this study and climate data was recorded manually. Detailed annual climate data was taken from the nearby climate station at Salvacion, 5 km to the south, but at the same altitude. Onsite data for temperature and RH was collected using a Tingtag sensor installed at the site of the non-functional permanent weather station.

3.3.2 MICROCLIMATE DATA

Microclimate data was collected over 6 consecutive days at each of the three sites. The measurements were taken during May 2010, at the onset of the dry season, but with occasional days showing weather patterns more typical of the wet season. At Wayqecha the data was collected from 11:00 on 03/05/2010 to 11:00 on 09/05/2010. At San Pedro, the data was collected from 10:45 on 10/05/2010 to 11:30 on 16/05/2010. At the MLC data was collected from 11:30 on 17/05/2010 to 15:15 on 23/05/2010 (Figure 3.2).

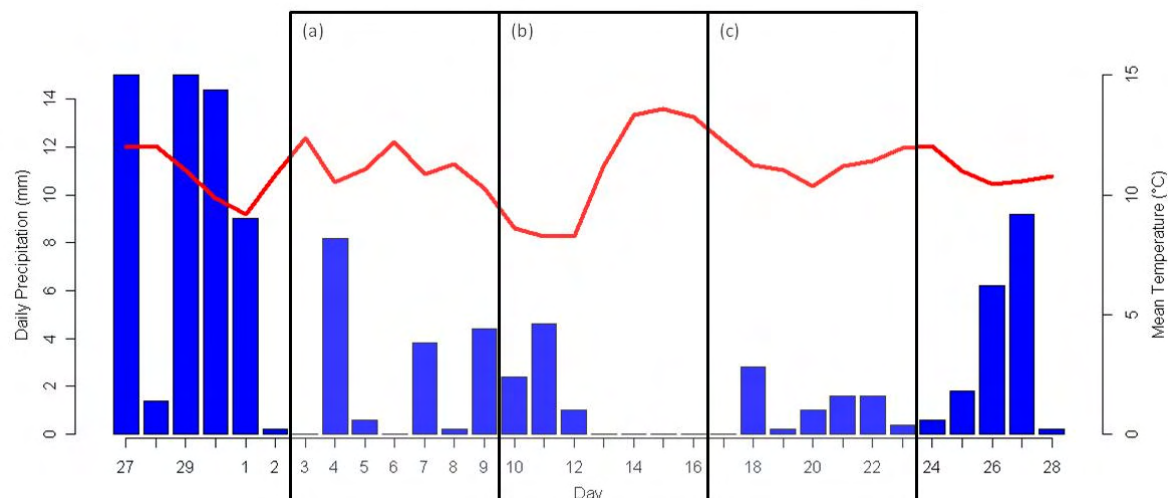


Figure 3.2 Time periods for microclimate recordings overlaid on the daily temperature and precipitation data for Wayqecha. Windows refer to (a) Wayqecha, (b) San Pedro and (c) MLC.

Solar radiation was aggregated over a five minute interval using a Skye SKS 1110 pyranometer (Skye Instruments Ltd., Powys, UK). Data on solar radiation is only presented for the TCF site (Wayqecha) as no comparable above-canopy data was available for the other two sites. Air temperature and relative humidity were recorded using four Tingtag Plus 2 TGP-4505 sensors (Gemini Data Loggers (UK) Ltd., Chichester, UK). The measurements were instantaneous measurements, taken every three minutes.

At each site the sensors were suspended from a single tree on a climbing rope. The sensors were tied with thin plastic string to the climbing ropes, to give a separation of at least 10 cm from the rope in order to minimise localised humidity effects caused by the rope. Trees were chosen with relatively clean trunks and as little vegetation between the canopy and forest floor as possible. The sensor was suspended away from the main trunk, to avoid the changes in microclimate caused by bryophyte layers on the trunk (Figure 3.3). At Wayqecha two combined temperature and RH sensors were installed in the permanent research plot. The lowest sensor was installed at 2 m from the ground. The upper sensor was installed at 10 m and the top of the canopy was measured at 14 m. In addition the pyranometer was installed at 6 m. In San Pedro

the Tinytag sensors were installed at 1.6 m, 6.6 m, 9.5 m, and 13.3 m with the top of the canopy at 18 m. At the MLC the sensors were installed at 2 m, 11.4 m and 16.2 m and the top of the canopy was at 20 m. The sensor at the tree line was installed at 1 m in a tree of 2 m height.

3.3.3 STATISTICS

Data from the TinyTag sensors was downloaded and processed in the TinyTag Explorer software (Version 4.6). Data from the Skye Datahog was downloaded using SkyeLynx software (Version 1.2). The RH data was converted to vapour pressure deficit (VPD) for each instantaneous measurement following the methods described in Rapp (2010) and Yoder *et al.* (2005), as VPD is more relevant to plant water relations in the humid tropics than relative humidity. The data on temperature was used to calculate the saturation vapour pressure and the actual vapour pressure. The difference represents the vapour pressure deficit (VPD). To test the relative importance of water content of the air and temperature in determining RH I used the methods described in Yoder *et al.* (2005) and the gas law.

Instantaneous 3 minute measurements of temperature were also averaged to produce daily means of day (06:00 to 18:00) and night (18:00 to 06:00) and daily temperatures. The maximum and minimum instantaneous temperatures recorded from each sensor were averaged over the 6 days for all sites. Differences between above canopy temperature and within canopy temperature were calculated for each instantaneous 3 minute recording. The differences were then averaged daily, and for the day and night. The same calculations were used for the VPD data. Data on solar radiation was recorded in megajoules (MJ) and summed for each day.

Data from the microclimate measurements was used to test the importance of actual humidity (AH) and temperature in determining relative humidity (RH). AH and temperature

were used to predict RH in a general linear model (GLM) and where significant the relative contribution of each (t -values) was compared.

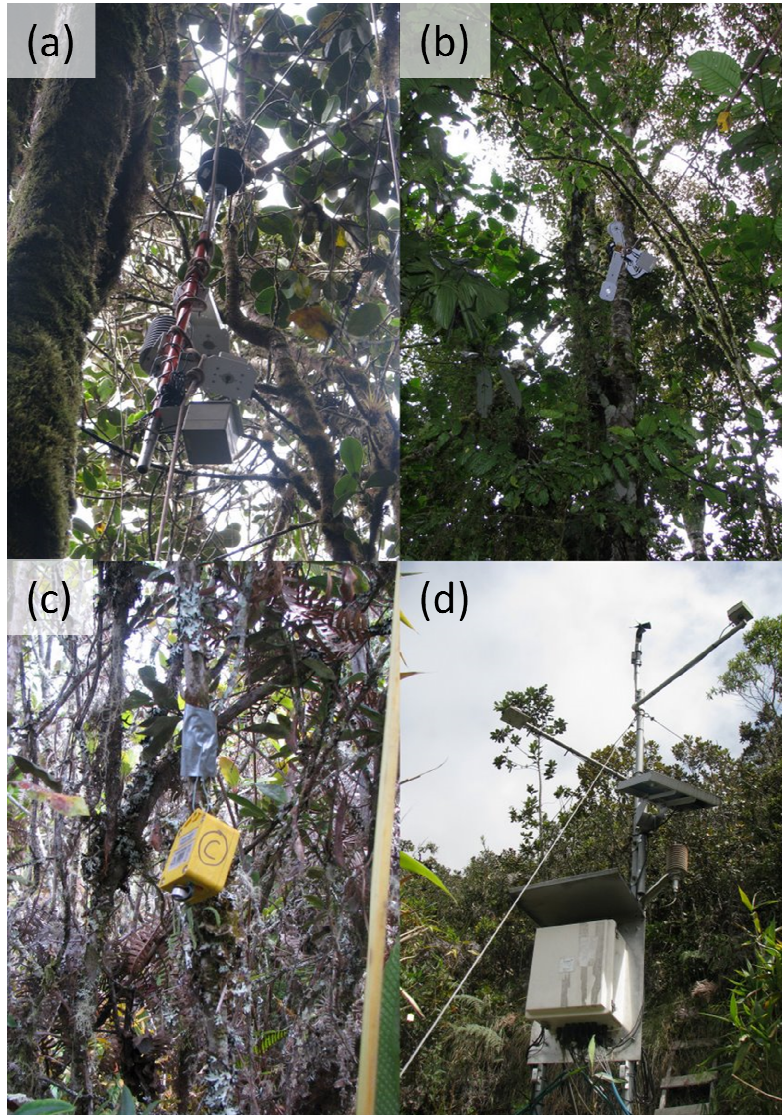


Figure 3.3. Set-up of weather sensors (a) in Wayqecha, (b) in San Pedro (c) at the tree line and (d) the permanent weather station in Wayqecha.

3.4 RESULTS

3.4.1 TEMPERATURE

I found consistent differences in mean and maximum daytime temperatures above the canopy and within the canopy. There was no consistent evidence for the stratification of temperatures within the canopy, and from the upper canopy to the forest floor. At Wayqecha the difference in mean daytime temperature above and below the canopy was between 4 °C and 6 °C, and at San Pedro and the MLC the difference was 2 °C to 4 °C. There was significant stratification within the canopy at San Pedro, with the forest floor around 1 °C lower than the top canopy.

As well as differences in daily means, the exposure of different strata to short term extremes will also be biologically relevant. In Wayqecha the maximum temperature above the canopy was around 15 °C higher than that in the lowest strata of the forest (Above canopy $T_{\max} = 31.3 \pm 3.1$ °C, Forest floor $T_{\max} = 15.7 \pm 1.8$ °C.) (Figure 3.4). At MLC the maximum above-canopy temperature was similar to that at Wayqecha, but the difference with the forest floor was smaller (Above canopy $T_{\max} = 33.9 \pm 1.6$ °C, Forest floor $T_{\max} = 24.7 \pm 1.0$ °C). The maximum temperatures represent a peak, and the temporal extent, as well as the magnitude, will be important in determining their impact on plants (Figure 3.5).

Above and within canopy temperatures also differed at night time in Wayqecha and San Pedro, but not at the MLC (Figure 3.4). The gradient was opposite to the day time pattern, with within-canopy temperatures higher than above the canopy. At Wayqecha the difference was 1 °C from above the canopy to both the upper canopy and forest floor. In San Pedro the difference was much lower, less than 0.5 °C. Wayqecha is subject to occasional night time ground frosts and climate data from 2008 to 2010 shows air temperature occasionally dropped below 5 °C (Rapp, 2010), which is cool enough to indicate ground frosts, although this depends on calm,

clear conditions. The cover created by the canopy would be sufficient to prevent ground frosts under the forest canopy.

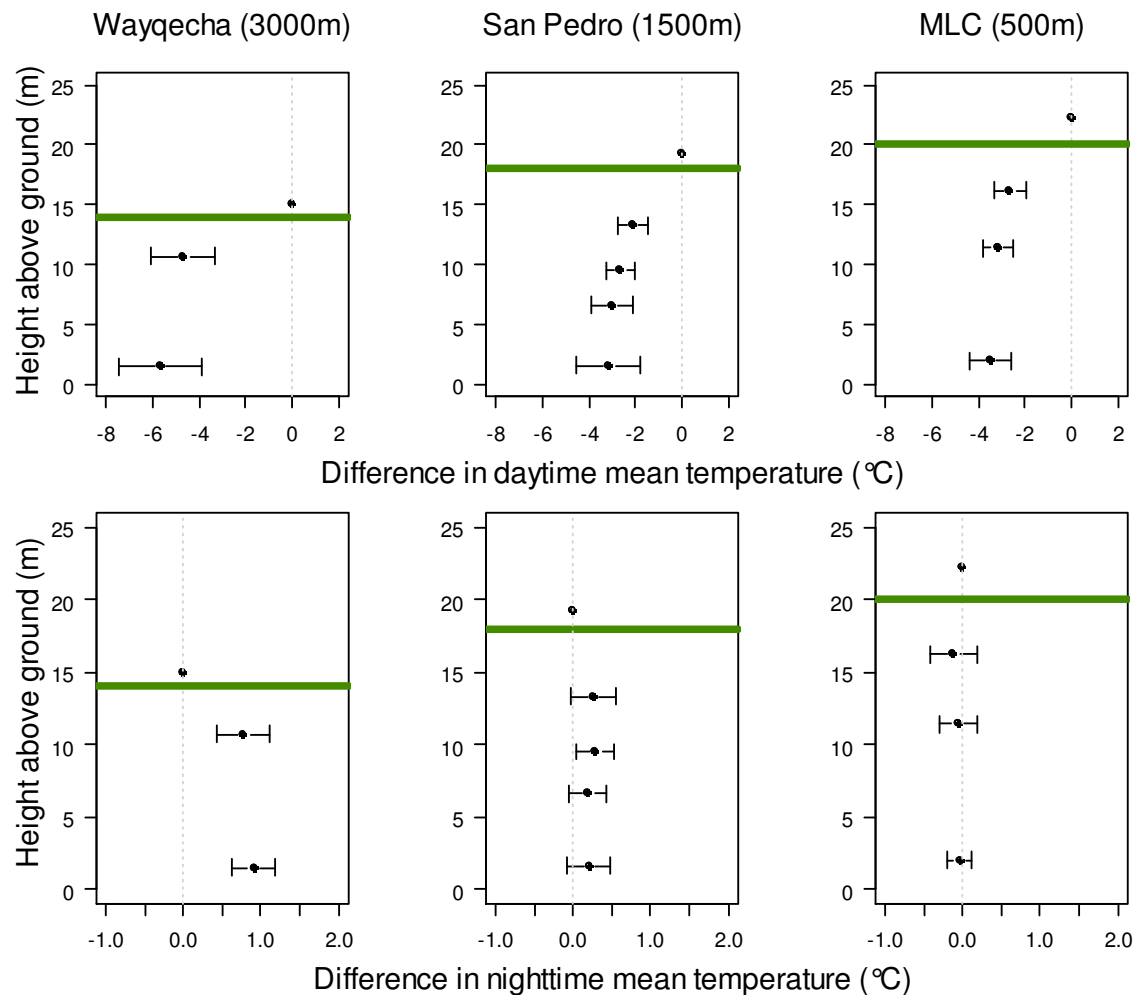


Figure 3.4. Difference in temperature at different heights above the ground. The values are calculated as the instantaneous difference between the above canopy value and the value at each height. Mean canopy height marked with green line. Errors show 95% confidence interval of mean except there the confidence interval is too small to be clearly illustrated.

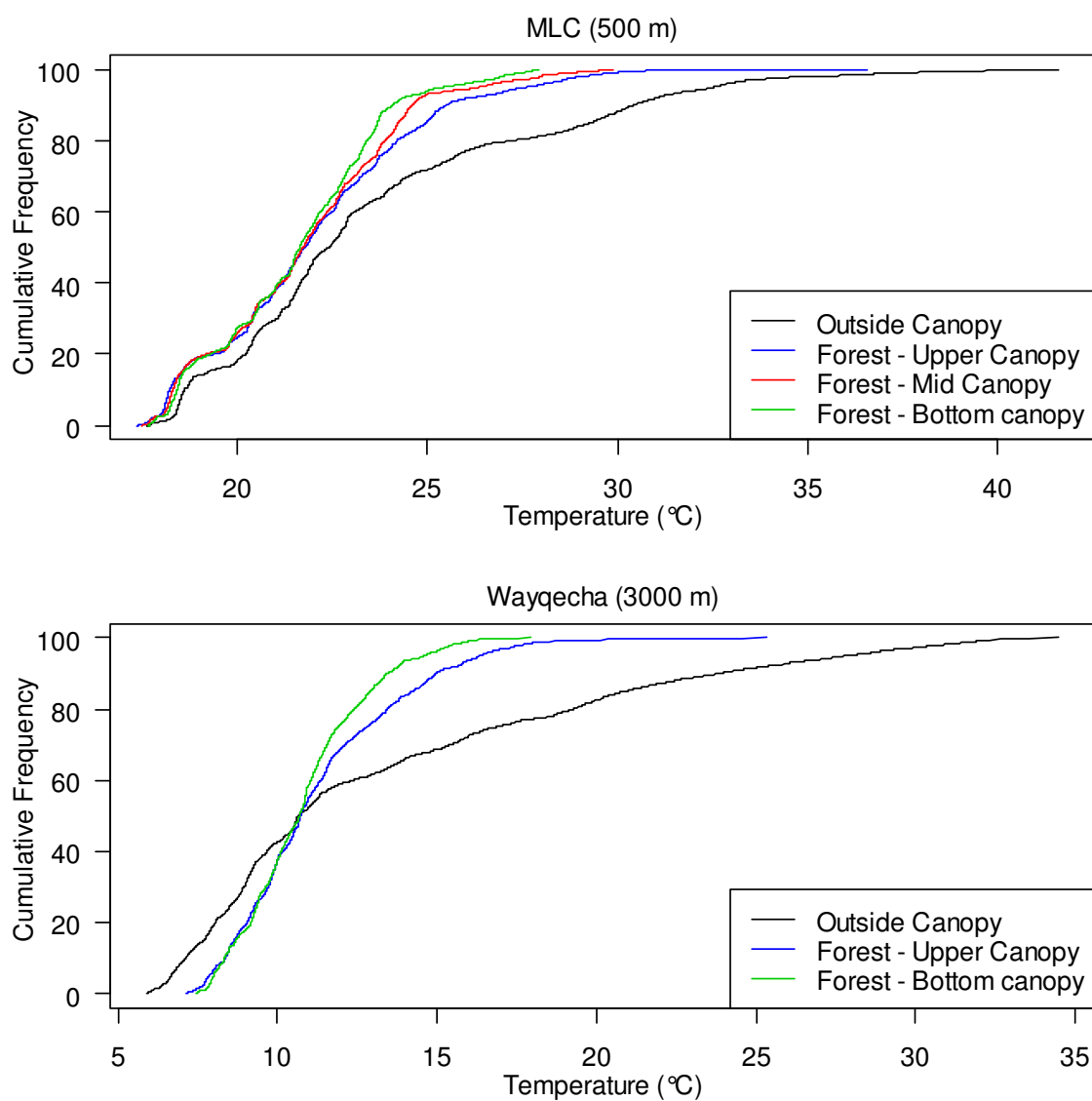


Figure 3.5. Cumulative frequency curves of instantaneous measurements of temperature taken at 3 minute intervals over 6 days

3.4.2 RELATIVE HUMIDITY AND VAPOUR PRESSURE DEFICIT

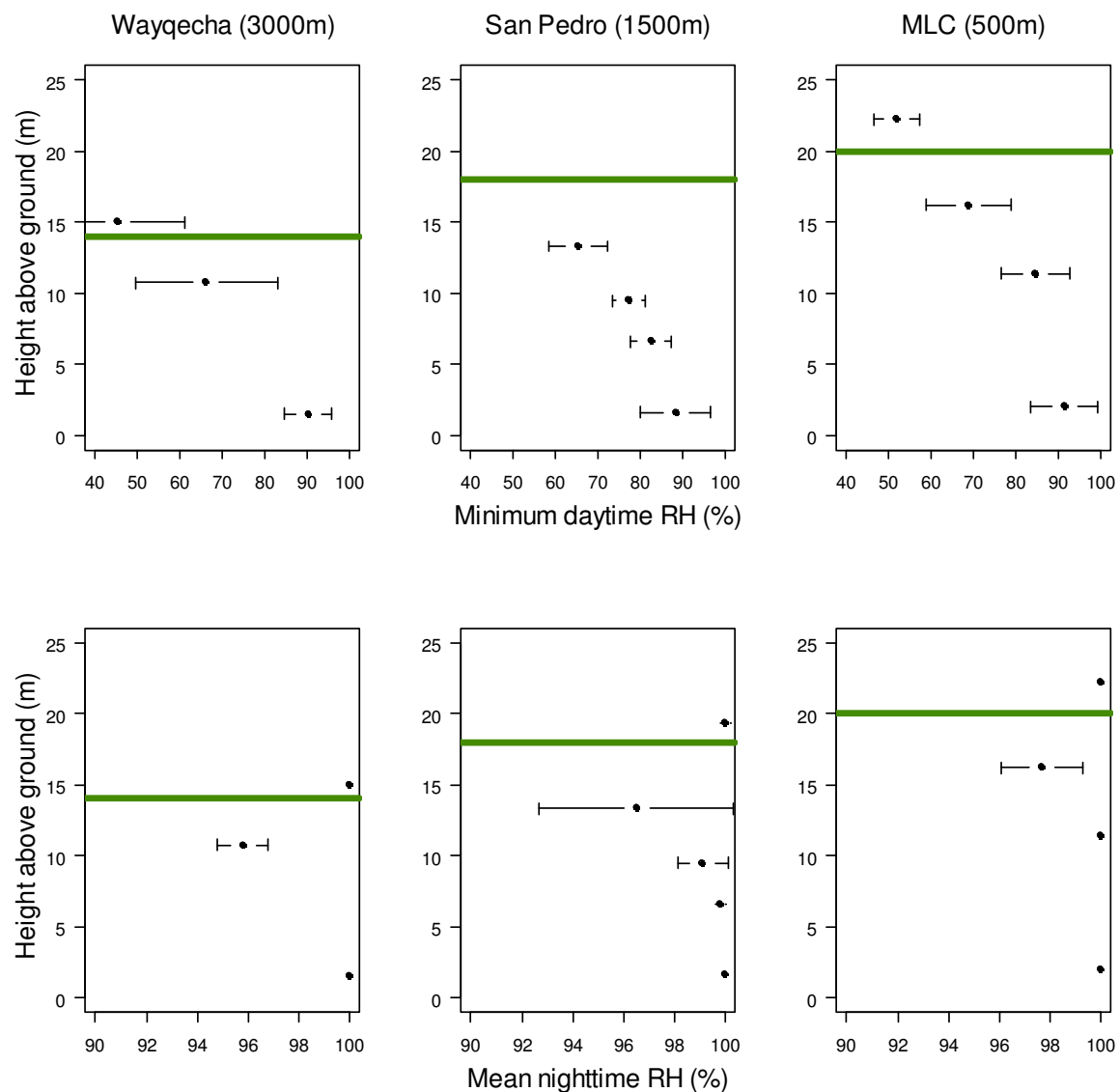


Figure 3.6. Daytime and nighttime humidity from the three microclimate sensors. Values are mean $\pm$ 95 % confidence interval, except where the confidence interval is too small to be illustrated.

The field sites showed a large difference across the canopy for both RH and VPD (Figure 3.6 and Figure 3.7). VPD stratified from above to below the canopy, but showed little stratification within the canopy (Figure 3.7). The forest floor at all three sites showed a difference in mean daytime VPD of about 0.5 kPa (Wayqecha: $VPD_{diff} = -0.56 \pm 0.10$ kPa; San Pedro: $VPD_{diff} = -0.24 \pm$

0.05 kPa; MLC: $VPD_{diff} = -0.52 \pm 0.36$ kPa) from the above canopy mean. The maximum VPD at both Wayqecha and the MLC exceeds 2.5 kPa (Wayqecha: $VPD = 2.82 \pm 0.32$ kPa; MLC: $VPD = 2.73 \pm 0.39$ kPa) but is lower in San Pedro ($VPD = 0.73 \pm 0.12$ kPa). Below the canopy the maximum VPD is significantly lower, although the upper canopy at Wayqecha and all strata at the MLC show some daytime VPD which exceeded 1.0 kPa. Changes in RH can result from both changes in temperature and in absolute humidity. We calculated absolute humidity for all sites and found that for Wayqecha, absolute humidity is the most important factor determining RH, but at the other sites, the contributions of AH and temperature were similar (Table 3.1).

At night time the above canopy VPD drops to 0 kPa, and RH is 100 % with very little variation (Wayqecha: $RH = 99.96 \pm 0.04$ %; San Pedro: $RH = 100.00 \pm 0.10$ %; MLC: $RH = 99.97 \pm 0.02$ %). This is due to complete saturation of the cool night air. The VPD at the forest floor is also 0 kPa throughout the night at all 3 altitudes. However, the upper canopy showed a consistent positive VPD difference at night, and relative humidity dropped below 100 % (Wayqecha: $RH = 97.7 \pm 0.8$ %, $VPD = 0.05 \pm 0.02$ kPa; San Pedro: $RH = 96.5 \pm 0.2$ %, $VPD = 0.06 \pm 0.03$ kPa; MLC: $RH = 95.8 \pm 0.5$ %, $VPD = 0.06 \pm 0.02$ kPa) (Figure 3.6 and Figure 3.7).

Table 3.1. The importance of actual humidity (AH) and temperature (T) in determining relative humidity (RH). The t value shows the strength of the predictor from the GLM, which takes the form $RH = AH + T$. The strongest predictor in each case is highlighted in bold.

		AH		T	
Site	<i>df</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Upper canopy					
Way	2873	109	<0.001	-35	<0.001
SP	2892	393	<0.001	-307	<0.001
MLC	2952	497	<0.001	-360	<0.001
Forest floor					
Way	2873	320	<0.001	-106	<0.001
SP	2892	446	<0.001	-652	<0.001
MLC	2952	811	<0.001	-881	<0.001

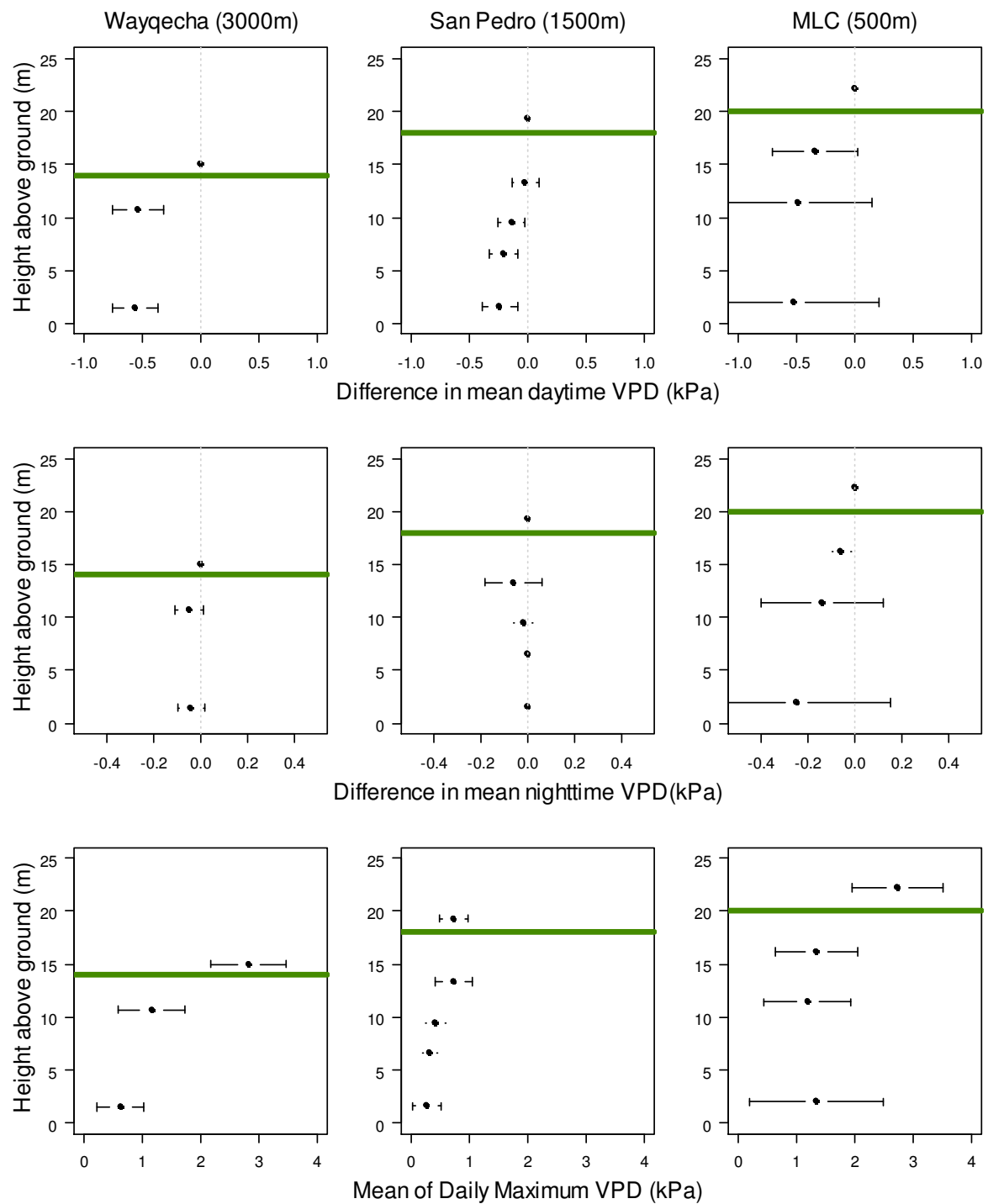


Figure 3.7. VPD data for 3 sites. Differences are shown from above canopy values. Values are mean $\pm$ 95 % confidence interval except where confidence intervals are too small to illustrate clearly.

3.4.3 RADIATION

In the TCF the total radiation recorded at 10 m height within a canopy of 14 m total height varied between 11% and 14% of the total radiation received at the top of the canopy over the five days. There was large variation in total solar radiation between days, and this variation was found both above and below canopy. However, the proportion of radiation that penetrated the canopy remained constant (Table 3.2). For a more detailed discussion of the light microclimate see Rapp (2010).

Table 3.2. Total solar radiation recorded above and below the canopy in the TCF (Wayqecha site, 3000 m). The sensor was 6 m from the ground and the main canopy was at 14 m.

Day of recording	Number of measurements	Mean daytime solar radiation above canopy (MJ)	Mean daytime solar radiation within canopy (6 m from ground) (MJ)	% solar radiation transmission
1	144	31712	3596	11.3
2	144	36758	5151	14.0
3	144	43481	5883	13.5
4	144	21991	2427	11.0
5	144	34926	3903	11.2

3.4.4 TREE LINE MICROCLIMATE

Microclimate was recorded at 1 m in stunted trees at the tree line, where the canopy was at about 2 m high. The microclimate in the understory of these small, shrubby trees showed similar patterns to the microclimate of the canopy top at Wayqecha (at the same altitude). However, the VPD was much larger during the day than the forest floor in Wayqecha (Figure 3.8). The mean daily VPD inside the canopy never exceeded 0.6 kPa, and was well below the 1 kPa which is challenging to established cloud forest plants (Rapp 2010). Temperature also closely follows the top canopy at Wayqecha, but is about 4 °C warmer than the top canopy, and 5 °C warmer than the forest floor during the hottest part of the day.

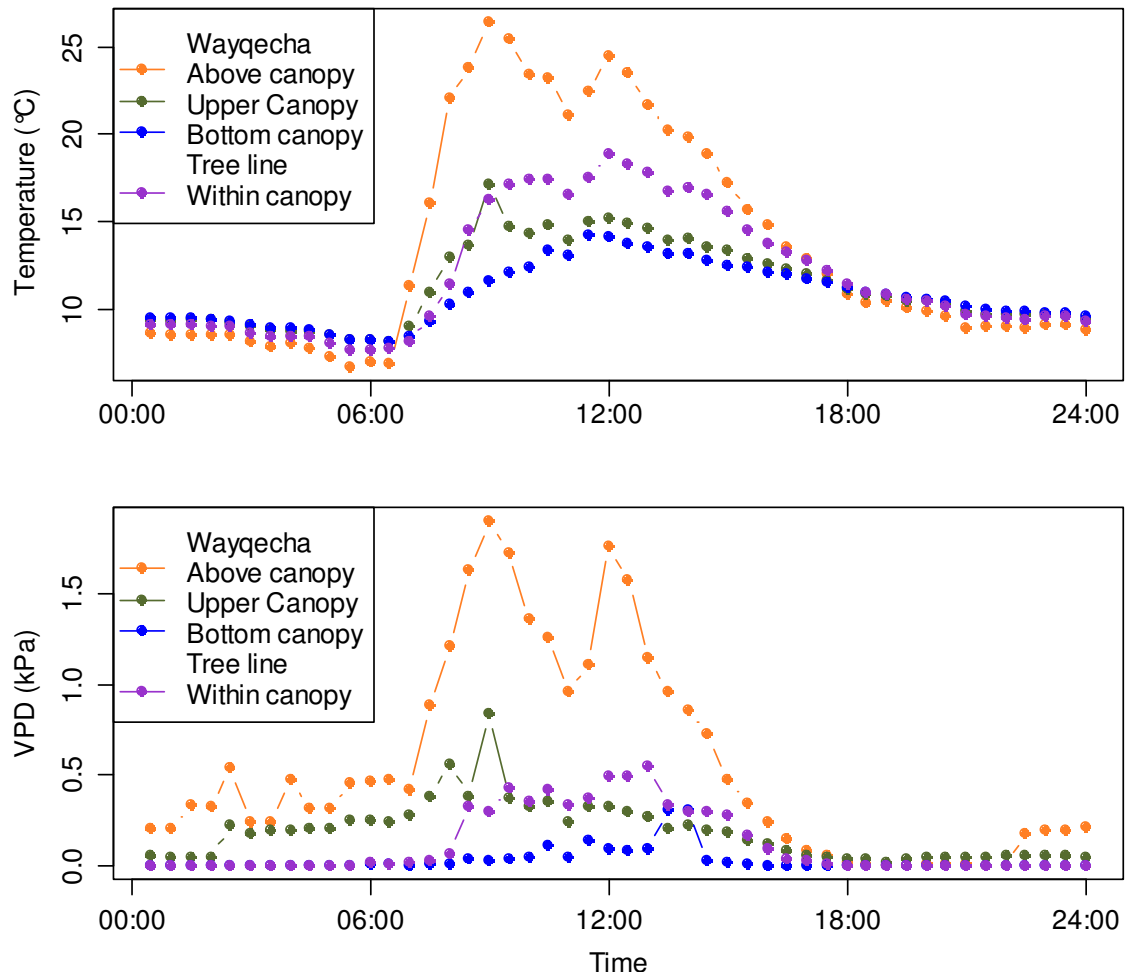


Figure 3.8 Daily patterns of temperature and VPD in the cloud forest (Wayqecha, 3000 m) and at the tree line approximately 250 m north of the plot (at the same altitude). Values are the mean of six days of measurements.

3.5 DISCUSSION

The data presented here is consistent with previous studies of microclimate documenting the significant impact of the forest canopy on prevalent climate below the upper surface of the canopy. This influence occurs primarily due to interception of radiation by canopy leaves, and the evapotranspiration of water from canopy leaves. The canopy also acts to trap a layer of air, except in very strong winds, which can maintain the higher humidity generated by evapotranspiration. The combination of lower radiation and higher moisture

content combine to make the forest understory cooler, darker and more humid during the daytime. At all three sites studied here daytime temperature was lower beneath the canopy than above it during the day, consistent with microclimate measurements at other sites (Thompson & Hinckley, 1977; Walsh, 1995; Szarzynski & Anhuf, 2001; Cardelús & Chazdon, 2005; Motzer, 2005). The differences in temperature were strongest with peak daytime temperatures (Figure 3.5). These decreased in a large step from above the canopy to within the canopy. Within the canopy there was either small or no change between the top canopy and the forest floor. At night the canopy at Wayqecha also acted to prevent heat loss by reducing radiative cooling (Sakai & Larcher, 1987), meaning the temperature under the canopy was warmer than above it. The VPD was also stepped from above to below the canopy during the daytime, with lower VPD found inside the canopy. There was little evidence for distinct microclimatic strata within the canopy at any site, but a more detailed recording of microclimate, *sensu* Cardelús and Chazdon (2005), would be needed to determine if Johansson zones (Johansson, 1974) were more critical in terms of substrate type or microclimate.

The magnitude of differences across the canopy for both temperature and VPD are strongest at Wayqecha. Wayqecha shows the largest difference in day and night temperatures of all the sites, and the large daily fluctuation may lead to greater lag of temperature between above canopy and within canopy temperatures. Adaptation to a greater temperature range is important in species responses to the environment, and species which experience a greater daily range are more likely to tolerate long-term changes in climate (Deutsch *et al.*, 2008), and this might suggest that epiphytes at Wayqecha should be more tolerant of climate change.

Night time microclimate gradients are only seen at the highest altitudes. At Wayqecha the understory air temperature remains higher for the duration of the night than the temperature of the air above the canopy as it has lower radiative losses (Sakai & Larcher, 1987).

At Wayqecha, the canopy is much lower, and the daytime radiation heats the soil significantly more than at lower altitudes. The soil will retain heat longer than the canopy, so warmer below-canopy night time temperatures are only seen in the short-stature TCF, and not in the taller TMF or LRF. The presence of the canopy will be sufficient to protect plants during a mild frost. Bromeliads are generally not tolerant of frost, except for a few terrestrial species with special adaptations (Benzing, 2000), and extensive frosts are known to cause mortality in epiphytic bromeliads (Benzing, 2000). By avoiding freezing conditions in the understory, species may be able to grow at higher altitude than if the ground was not protected by the canopy.

Humidity and VPD also change significantly below the canopy surface. The initial change from above the canopy to within the canopy occurred at all sites, consistent with patterns seen in other forests (Thompson & Hinckley, 1977; Walsh, 1995; Szarzynski & Anhuf, 2001; Cardelús & Chazdon, 2005). For humidity there was a small effect within the canopy, with humidity increasing linearly from the top canopy to the ground. This effect is due in part to lower temperatures beneath the canopy, but absolute humidity shows daily cycles. This means some of the increase in RH beneath the canopy is due to increased water from evapotranspiration. The increased water combined with the lower wind velocities under the canopy creates a more humid environment close to the forest floor. The increased humidity in the forest understory at all altitudes is sufficient for most plants to avoid water deficits throughout the year. This will mean that despite changing climate outside the forest, in the understory the regeneration niche is buffered against the worst effects of climate. This is important during establishment of epiphytes, as small plants lose water to the environment faster and for phytotelm bromeliads, the buffered microclimate will result in fewer days without a supply of water in the phytotelm (Zotz & Thomas, 1999).

Radiation data recorded from inside and above the canopy at Wayqecha shows there is strong filtering of radiation through the canopy. Wayqecha, as a cloud forest site, has a lower leaf area index (LAI) than sites at lower altitude, so filtering of radiation would be expected to be weakest. I found that radiation reaching the mid-forest layer was between 11 and 14% of radiation above the canopy. This is comparable to the amount of solar radiation penetrating into the mid-canopy of the crowns of 30 m tall *Lecythis* trees in Costa Rican cloud forest (Cardelús & Chazdon, 2005). Levels of radiation penetrating the canopy in the LRF reported in the literature are much lower (Walsh, 1995; Dial *et al.*, 2006). Solar radiation at 10% of above canopy levels may not be limiting to bromeliads, and protection from photoinhibition would also be beneficial to plants in the cloud forest (Griffiths & Maxwell, 1999; Benzing, 2000).

The reduced influence of stratification at the tree line is a result of the more open canopy, and the much shorter stature of tree. This means the microclimate is more 'challenging' to plants, and is likely to slow the growth of forest trees, although values never reached those which are challenging to cloud forest trees (Rapp, 2010). Slower growth would hinder regeneration of forest trees at the tree line. The lack of a suitable regeneration niche for forest trees may contribute to both the current dynamics and resistance to future change of the tree line. It suggests efforts to artificially raise the tree line to protect species from increasing temperatures may need to focus on providing more water and lower temperatures to encourage the growth of forest species.

3.5.1 CONCLUSIONS

There is a consistent difference between the climate above and below the canopy at all sites along this elevation transect. The canopy creates an environment which is more humid, cooler and darker during the day. This would benefit plants of the understory, and encourage faster growth. The only exception would be where light is limiting, but I do not have sufficient data to test this. While data from climate stations is useful in assessing plant physiology, data on the

microclimate may be more relevant to understanding regeneration and growth of plants inside the canopy at all altitudes.

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4. DIVERSITY AND TURNOVER OF BROMELIADS ALONG A 4000 M ELEVATION GRADIENT IN THE PERUVIAN ANDES

4.1 ABSTRACT

Patterns of α -diversity of epiphytes, and bromeliads in particular are well studied. Patterns of β -diversity are less-well studied. Bromeliad diversity data along an altitudinal transect on the eastern slope of the Andes in Southern Peru was collected from permanent sample plots (PSPs) and the wider landscape. Along this transect α -diversity of bromeliads was highest at the 1500 m in TMF, consistent with other studies, although species richness was higher in the TCF between 2500 m and 3000 m. The α -diversity of bromeliads across this transect was similar to the diversity of woody species in families that have higher species richness in the TCF, but lower than other families except in the TCF. Analysis of bromeliad species composition of both PSPs and plotless sampling showed ecological zones can be delimited for bromeliads comparable to those for woody species, and matching climate-based ecological zones typically delimited for the eastern slope of the Andes. These ecological zones are supported by β -diversity peaks at 1250 m and 2250 m, although the turnover between ecological zones is masked by turnover within the zones. The β -diversity of other families is very variable but averaged over all woody species, shows a decrease with increasing altitude, matching the general pattern of β -diversity in bromeliads.

4.2 INTRODUCTION

Bromeliads are a keystone family in the Andes biodiversity hotspot and understanding patterns in diversity, and how this relates to other taxa, helps us to understand how they fit into the ecosystem (Benzing 2000). General patterns of epiphyte diversity are well established from

across South America (Gentry & Dodson 1987b), and the diversity of the family Bromeliaceae has been closely studied in the Andes (Kessler 2002). Kessler (2002) showed the importance of scale in studying epiphyte diversity; epiphytic bromeliads in particular are known to have high diversity in a single location (α -diversity) and low species turnover between habitats (β -diversity) giving rise to low diversity over large areas (γ -diversity) (Ibisch *et al.* 1996). This means that while bromeliads can contribute significantly to total forest phytodiversity at local scales, they are rarely a significant contributor at larger scales.

Bromeliad diversity roughly matches that of overall vascular epiphyte diversity on most scales and sites (Gentry & Dodson 1987b), and are therefore a useful group to use to make inferences about the vascular epiphyte community where no taxon specific information is available. Data available in the literature can be summarized to make the following predictions about both vascular epiphyte and bromeliad diversity in montane environments:

1. α -diversity in the Neotropics is highest in lower-montane forests (Gentry & Dodson 1987b; Hietz & Hietz-Seifert 1995; Ibisch *et al.* 1996; Kessler 2002; Krömer *et al.* 2005);
2. this mid-altitude peak may arise because of low diversity at both the highest and lowest altitudes;
 - a. low diversity at the highest altitude due to cold temperatures, particularly frost (Hietz & Hietz-Seifert 1995; Kessler 2002; Krömer *et al.* 2005);
 - b. low diversity in lowland rainforest due to high temperatures and low humidity (Gentry & Dodson 1987b; Kessler 2002; Krömer *et al.* 2005) but this can be mitigated in areas with high rainfall and low seasonality (Kreft *et al.* 2004) or high fog occurrence (Obregon *et al.* 2011);
3. the mid-altitude peak may also be a result of the random distribution of species in a bounded domain (Cardelús, Colwell & Watkins 2006);

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4. diversity is lower in more disturbed forest due to poor phorophyte structure and loss of microclimate gradients (Barthlott *et al.* 2001; Krömer & Gradstein 2003).

Whilst patterns in α -diversity are well established, the turnover of species between sites (β -diversity) is less well understood for bromeliads and epiphytes in general. β -diversity is generally acknowledged to be low as a result of the ability of epiphytic species to disperse widely to find suitable habitat (Ibisch *et al.* 1996). Higher rates of β -diversity are correlated with habitat heterogeneity (Larrea & Werner 2010). The β -diversity of neotropical trees has been studied more intensively, with the increasing availability of large-scale data sets (Condit *et al.* 2002; Malhi *et al.* 2002). Across the Amazon β -diversity of trees can be predicted by distance and rainfall, which are co-variant, but around half of the variation is unexplained (Condit *et al.* 2002). Local adaptation to changes in rainfall (Davidar *et al.* 2007) and soil types (Fine & Kembel 2011) have been shown to be important for β -diversity of trees.

One factor driving β -diversity is grouping of species into different habitats, and moving from one habitat to another would lead to a peak in β -diversity. Discrete assemblages of epiphytes were found at the scale of individual trees by Kelly *et al.* (2004), Zotz, Bermejo and Dietz (1999) and Flores-Palacios and García-Franco (2008). Bromeliad species are known to form separate groups on a broader scale in the Andes in response to precipitation and exposure (Gilmartin 1973; Sugden 1981), and this is the scale in which bromeliad zones will be assessed in this study. Continental-scale zones of different bromeliad composition, better referred to as biogeographic regions, have also been shown on a broad scale in relation to evolutionary history (Givnish *et al.* 2011).

To gain a complete picture of bromeliad diversity data from the altitudinal transect in Southern Peru will be used to address questions about the diversity of bromeliads. This will be achieved by answering the following questions:

- What is the α -diversity in this transect and how can it best be represented?
- Do patterns in α -diversity differ from predictions from the literature?
- How does bromeliad β -diversity vary with altitude and how does it compare to other families in this transect?

4.3 METHODS

4.3.1 FIELD SITES

Data was collected along the altitudinal transect on the eastern slope of the Andes from 200 m to 3500 m altitude in the states of Cuzco and Madre de Dios in southern Peru, with most sites (those above 1000 m) located in the Kosñipata Valley. Annual mean temperatures are highest at lowest altitudes (25.5°C at 200 m) and decrease linearly with increasing altitude (7.7°C at 3500 m). Precipitation is highest at intermediate altitudes (4900 mm year at 1500 m) and decreases in both directions. Figure 4.1 shows the location of permanent research plots and plotless sample areas used for sampling bromeliad diversity. Details of the plots, their climate, physical geography and biological factors can be found in Chapter 2. As described in Chapter 2, the forest is classified into three different types, lowland rainforest (LRF) below 1000 m, tropical montane forest (TMF) from 1000 m to 1750 m, and tropical montane cloud forest (TCF) from 1750 m to the upper limit of forests, around 3500 m.

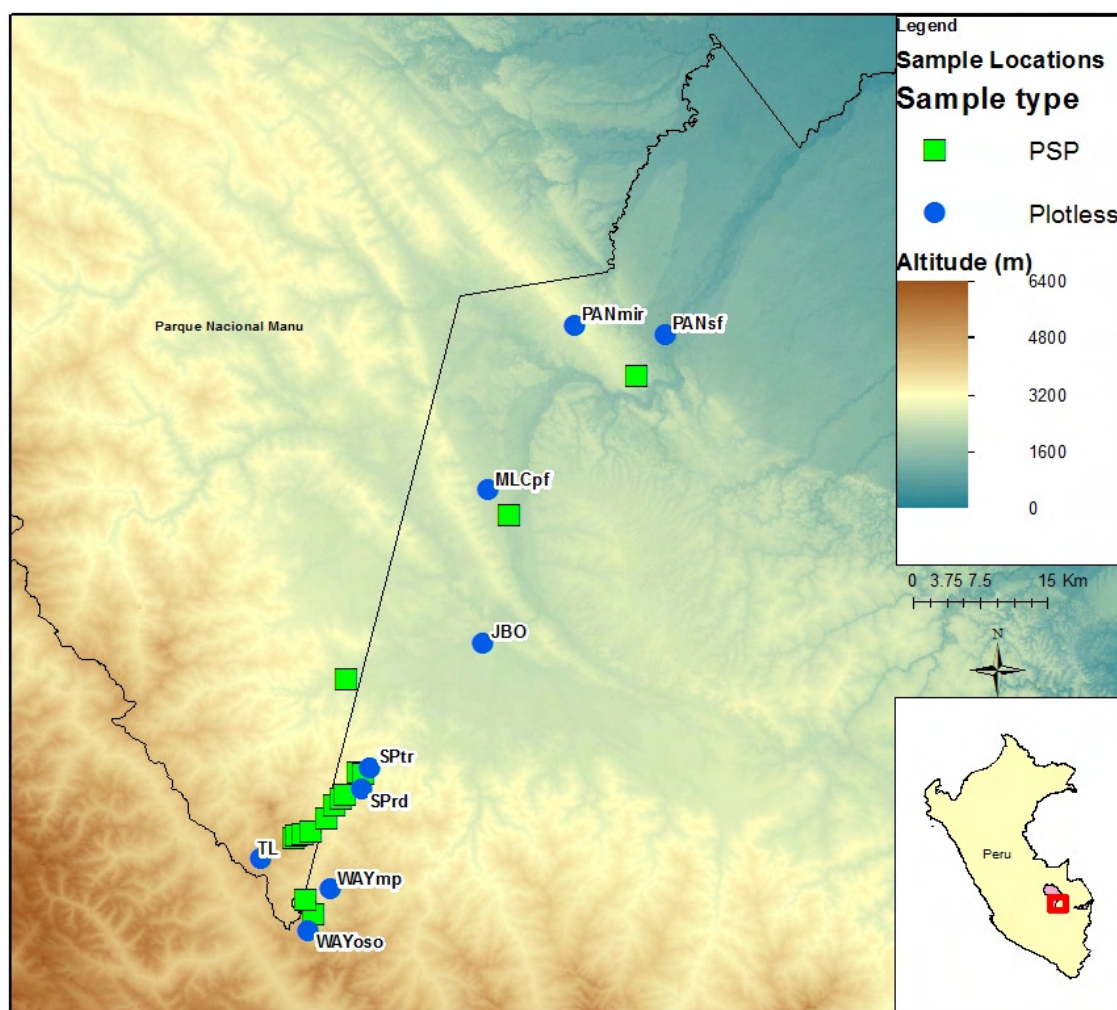


Figure 4.1. Location of Permanent Sample Plots (green squares – names as Chapter 2) and plotless samples (blue circles) in the main part of the field site. The two PSPs in Tambopata are not shown on this map, they are located approximate 200 km to the east.

4.3.2 DATA COLLECTION

Data on the distribution of Bromeliaceae at the field sites was collected during field surveys conducted over 3 years. Species inventory data was collected in fourteen permanent research plots. Plotless sampling was also carried out in areas outside the permanent research plot, where trees and bromeliads were sampled haphazardly. Field records were backed up with data on Bromeliaceae from Zevallos (2008), herbarium specimens from the Vargas herbarium, Cuzco (VAR), and from the Atrium biodiversity portal (atrium.andesamazon.org). Research effort for the area outside plots was calculated by summing the total distance of trails

walked (summed over the three years, up to 20km) at each 500m altitudinal band (Table 4.1). When searching the wider area and between plots there is an inevitable relationship between search effort and the number of species discovered (Table 4.1). In the Kosñipata valley, the area between 1500 m and 1000 m is the hardest at which to access primary forest and consequently the diversity of bromeliads recorded at this altitude is the lowest.

Table 4.1. Distance of trails searched at each altitude, used as a proxy for research effort.

Altitude (m)	>3000	3000-2500	2500-2000	2000-1500	1500-1000	1000-500	500-150
Trails searched (km)	>20	>20	10	15	<2	>20	15
Number of species	14	22	24	22	12	21	14

Species accumulation curves were constructed based on abundances recorded during systematic exploration of five subplots (20 × 20 m) from each of six permanent research plots. Each subplot was exhaustively searched and all adult bromeliads were recorded. Juvenile bromeliads were ignored because it was often not possible to identify them. Estimated species richness was then calculated from the species abundance data using the Chao 1 statistic (Chao 1984) and the extrapolation of species accumulation curves. As no plots fully captured diversity total species richness at each altitude was derived by combining plotless sampling with plot data and interpolating species ranges.

4.3.3 DIVERSITY STATISTICS

Diversity statistics based on permanent research plot data were calculated in the R statistical package (R Core Development Team 2005). Fisher's α was used to calculate α -diversity for all groups (Hayek & Buzas 1997). Fisher's α (α) is a dimensionless parameter calculated using the equation:

$$S = \ln \alpha \left(1 + \frac{n}{\alpha} \right) \quad (1)$$

where S is species richness and n is the number of individuals in the plot. Bromeliad α -diversity was compared to the 12 most species rich families of woody plants (Table 4.2). Since most of these families had the highest species richness in the LRF, an additional three families with higher richness in the TCF were also included.

Table 4.2. Species richness (including morphospecies) for Bromeliaceae and 15 of the more diverse families of woody species based on data from permanent sample plots (data for trees >10 cm dbh only).

Family	Species Richness														
Plot	Transect total	TAM4	TAM3	TON	SP2	SP1	TU8	TU7	TU5	TU4	ESP	WAY	TU3	TU2	TU1
Altitude (m)	-	180	200	1000	1500	1750	1850	2000	2500	2750	2850	3000	3000	3250	3450
Habitat type	-	LRF	LRF	TMF	TMF	TMF	TCF	TCF	TCF	TCF	TCF	TCF	TCF	TCF	TCF
Bromeliaceae	69*	4	2	7	8	6	-	7	6	7	6	8	5	6	3
Annonaceae	39	16	7	4	12	7	3	2	0	0	0	0	0	0	0
Cecropiaceae	23	5	7	6	5	4	1	0	1	0	0	0	0	0	0
Clusiaceae	31	6	2	2	8	4	7	4	2	3	3	3	3	3	3
Cunoniaceae	12	0	0	0	0	2	2	4	3	4	6	6	4	2	1
Cyatheaceae	18	0	0	1	3	2	7	8	7	7	7	2	3	5	2
Euphorbiaceae	41	6	6	5	13	11	8	6	5	3	0	0	0	0	0
Fabaceae	68	25	18	14	9	10	2	1	0	0	0	0	0	0	0
Lauraceae	65	15	13	1	2	2	16	10	4	7	9	7	4	7	1
Melastomataceae	51	1	7	2	13	14	6	2	4	6	5	3	7	9	5
Moraceae	41	16	10	9	9	6	3	0	1	0	0	0	0	0	0
Myrsinaceae	14	3	1	0	0	0	0	1	0	5	3	4	2	4	4
Myrtaceae	23	4	0	2	3	9	5	4	2	0	1	0	0	0	0
Rubiaceae	55	6	7	8	17	14	3	7	4	3	1	1	1	0	1
Sapotaceae	23	9	8	8	5	2	1	1	0	0	0	0	0	0	0
Theaceae	14	0	1	0	3	0	0	1	6	3	1	1	2	1	0

*includes species found outside the permanent research plots.

To test if patterns in the distribution across the elevation gradient differed from neutral patterns, I used a mid-domain effect (MDE) neutral model using RangeModel (Colwell 2008). The model uses the measured size of the range of all species found in this transect and arranges them randomly. One hundred repeat runs were used to predict species richness and the reported errors associated with the model are all two standard deviations of the mean. The assumption of a mid-domain effect, leading a peak at mid-elevation, arises from the random distribution of species' ranges within a bounded domain. The theoretical boundaries in the altitudinal transect may occur at high altitude as the tree line prevents further upwards spread of epiphytic species. A theoretical boundary in the lowlands is more difficult to imagine, but the low epiphyte biomass (Chapter 5) in the LRF suggests vascular epiphytes do not easily expand their ranges into the lowland Amazon in this area.

Correlation between plot diversity and total number of species in the wider areas were calculated in R software package (R Core Development Team 2005). As the plots are not evenly distributed in space, correlation was also tested using Dutilleul's adjusted degrees of freedom (Dutilleul 1993). A general linear model (GLM) was constructed to see if Fisher's α (α) could be predicted by a combination of environmental variables. The GLM was of the form:

$$\alpha = T + P + S + A + FS \quad (2)$$

where T = annual mean temperature, P = total annual precipitation, S = slope, A = aspect, FS = forest structure, approximated as the stem surface area index (SSAI) following Chambers *et al.* (2004) with modification for TMF and TCF following Robertson *et al.* (2010).

β -diversity was calculated using two indices. The Sørensen index ($\beta_{sør}$) is widely used to calculate species turnover (Anderson *et al.* 2011) and can be expressed as the formula:

$$\beta_{s\theta r} = \frac{2a}{A+B} \quad (3)$$

where a is the number of species shared between the two plots and A and B are the total number of species in each plot. The Sørensen index is dependent on sample richness, with larger difference between sites with more samples. As a richness-independent measure the β -similarity index (β_{sim}) (Kreft & Jetz 2010) was also calculated using the following formula:

$$\beta_{sim} = 1 - \left(\frac{a}{\min(b,c) + a} \right) \quad (4)$$

where a is the number of shared species, b and c are the number of species unique to each of the two plots being compared. These indices were calculated using the abundance data collected from permanent research plots. Altitudinal comparisons were made using pairwise values between adjacent plots.

Species ordination plots were produced using the Non-metric Multidimensional Scaling (NMDS) method with the Jaccard dissimilarity index used to calculate pairwise distances of species composition difference. NMDS uses only rank information and maps this into non-linearly into ordination space. NDMS can handle non-linear species responses of any shape and effectively and robustly find the underlying gradients. The importance of ten variables were assessed in relation to NMDS output; these were altitude, annual mean temperature, annual precipitation, plot slope, plot aspect, Fisher's α of the relevant species group, stem surface area, mean tree height, total tree height and vascular epiphyte biomass (from Chapter 5). The relationship between the ordination plots and environmental gradients was estimated using the 'envfit' function of the vegan package in R, only variables where $P_{r>r} < 0.01$ were displayed on the graphs. Ellipses were fitted to the plotless sample based on classification as one of three forest types, with the ellipses showing 2 standard deviations of the group mean.

4.4 RESULTS

4.4.1 SAMPLING MEASURES AND ALPHA-DIVERSITY

Both the Chao 1 statistic and species accumulation curves for the six intensively sampled plots show that sampling in a 1 ha permanent research plots did not capture the full diversity of bromeliads at each altitude (Table 4.3) as expected for epiphyte surveys (Flores-Palacios & García-Franco 2001).

Table 4.3. Observed (S_{obs}) bromeliad species richness recorded from intensive sampling of five sub-plots in six of the permanent research plots at different altitudes with estimated richness based on the Chao statistic (S_{chao1}) and species accumulation curves ($S_{\text{ACE}} \pm 1$ standard error).

Plot	Way	TU4	TU7	SP2	TON	PAN
S_{obs}	8.00	8.00	5.00	6.00	9.00	4.00
S_{chao1}	9.00	8.50	6.00	6.00	10.00	4.00
S_{ACE}	9.84 ± 1.66	9.56 ± 1.50	7.80 ± 1.40	6.00 ± 1.15	10.33 ± 1.49	4.70 ± 0.79

By interpolating species ranges from plotless sampling, the estimate of species diversity at any given altitude increased significantly. Most of the diversity is made up by epiphytes, with terrestrial species present in very low numbers across this transect (Figure 4.2). The total diversity (epiphytes and terrestrials combined) did not differ significantly from the MDE null model over most of the altitudinal transect (Figure 4.2, values falling outside the 95% confidence interval show where species richness deviated from the MDE null model at the $p = 0.05$ level), as is consistent with other studies (Cardelús, Colwell & Watkins 2006). This implies that the eastern slope of the Andes behaves as a bounded domain, with the species-poor lowlands providing one barrier and the transition from wet eastern slope to dry inter-Andean valley the other barrier. Interpolated species ranges showed a maximum species richness of 20 species between 2500 m and 3000 m.

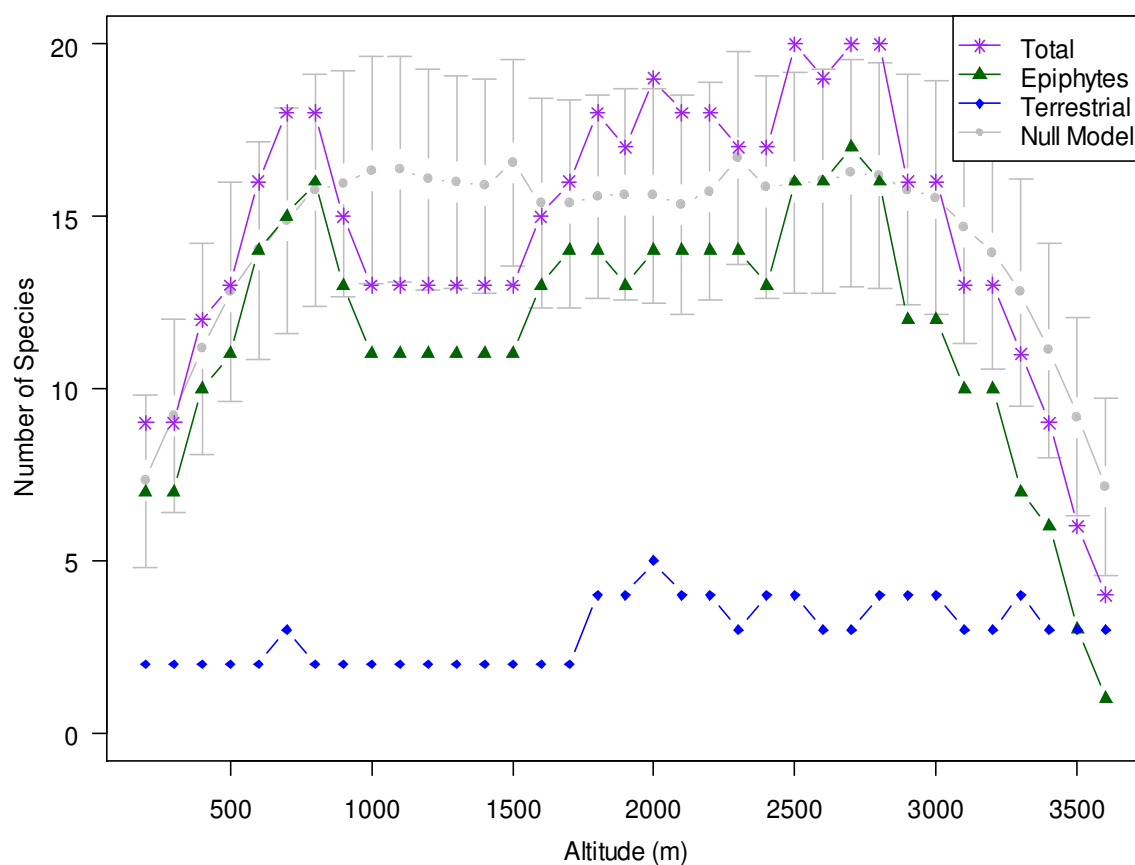


Figure 4.2. Total number of bromeliad species estimated at each 100 m elevation interval using interpolated altitudinal ranges based on plotless sampling. The total diversity is divided into epiphytes (purple) and terrestrial (blue) species based on predominant growth habit. The grey line shows the predicted total diversity at 100 m altitudinal steps using the MDE null model. The predicted diversity is shown $\pm 95\%$ confidence interval.

Fisher's α calculated based on plot data shows the greatest diversity at 1500 m (plot SP2) just below the boundary of high cloud immersion. α -diversity in the LRF was much lower than the diversity of LRF specialists (e.g. Fabaceae, Moraceae) (Figure 4.3a) and TMF specialists (Figure 4.3b), but higher than TCF specialists (Figure 4.3c). In the TMF bromeliad diversity was lower than TMF specialists (e.g. Myrtaceae) and similar to the generalist family Lauraceae (Figure 4.3b). Bromeliad diversity in the TCF was comparable higher than other families in most plots, including specialists in the TCF (e.g. Cyatheaceae, Cunionaceae, Theaceae). Across the transect bromeliad α -diversity was similar to families with higher species richness in the

TCF such as the Cyatheaceae and Theaceae, but also to the Lauraceae, with no particular affinity to forests type.

There is no correlation between Fisher's α for all trees combined and Fisher's α for bromeliads (Spearman's rank, $\rho = -0.363$, $p = 0.223$) suggesting no direct link between host species diversity and epiphyte diversity that could result from species specific interactions.

4.4.2 MODELLING ALPHA-DIVERSITY

In common with other studies of bromeliads and vascular epiphytes, the peak of diversity was found at 1500 m based on Fisher's α (Figure 4.3). This altitude has often been shown to have very high epiphytic species richness, despite being below the altitudes with the lowest humidity, and may result simply from random arrangement of species in a bounded domain (the mid-domain effect). However, using interpolated species ranges, the highest species richness (2500-3000 m) coincided with the peak in relative humidity along this transect between 2500 m and 2750 m (Rapp 2010). Very few correlations were found between factors predicted to influence epiphyte diversity, and the diversity recorded along this transect. The GLM combining climate, biological and physical properties of the plots was only able to explain 45.8% of the variation in the data set. There was weak positive correlation between Fisher's α for bromeliads and the stem surface area index when spatial autocorrelation is taken into consideration (Spearman's, $r = 0.322$, $p^* = 0.05$, where p^* is the significance value based on degrees of freedom adjusted using Dutilleul's method to account for spatial autocorrelation) suggesting a link between disturbance and bromeliad diversity. While this effect is known in anthropogenically disturbed sites, in this instance the disturbance is primarily through naturally-occurring landslides.

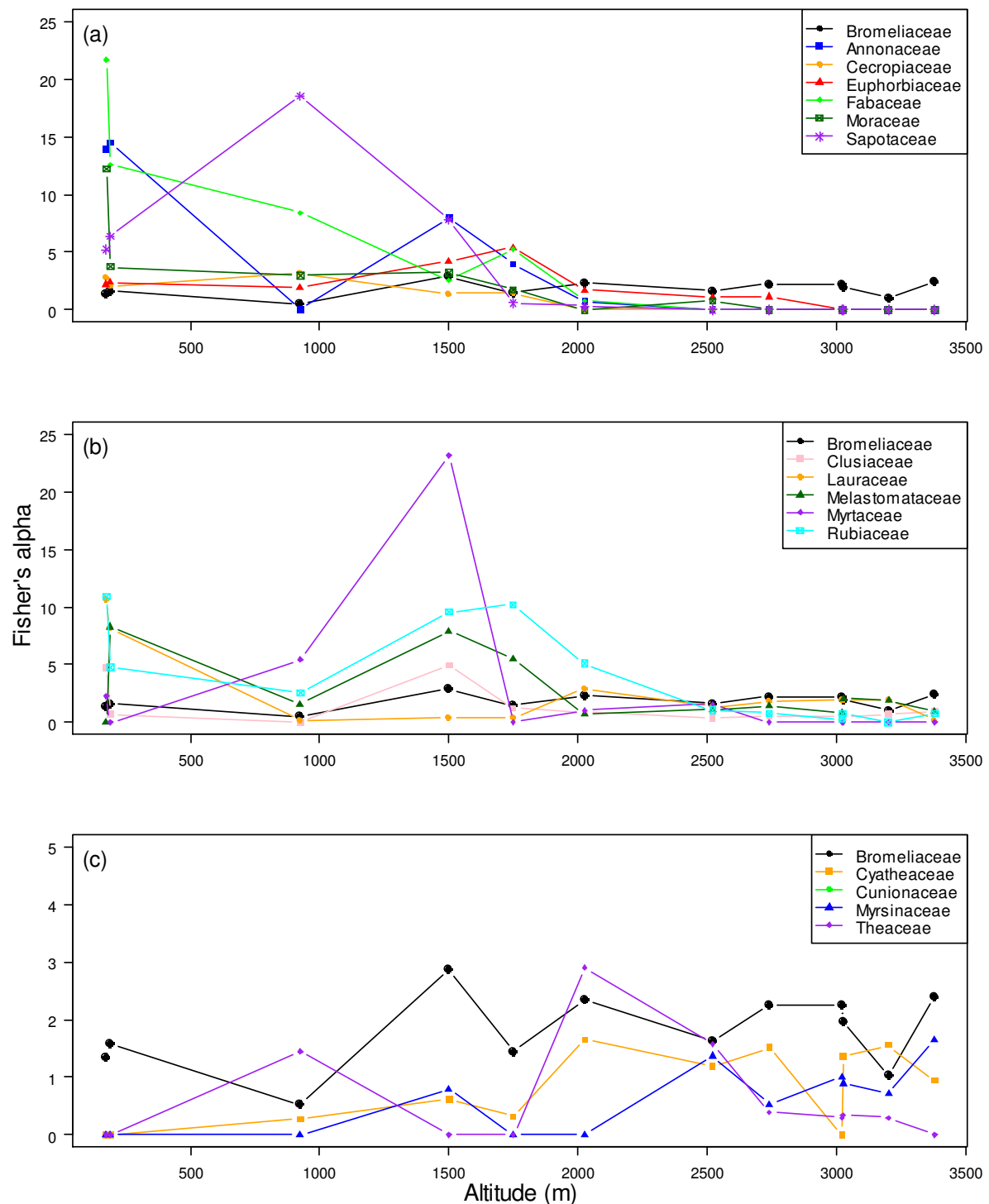


Figure 4.3. Fisher's α plotted against altitude for Bromeliaceae (black circles) and some of the more species-rich families found along the transect, separated into (a) families with higher species richness in the lowland rainforest (LRF), (b) families with higher species richness in the tropical montane forest (TMF) or no obvious peaks of richness, and (c) families with higher species richness in the tropical montane cloud forest (TCF). Note the y-axis in part (c) is on a different scale to the other parts.

Table 4.4. Co-efficients from the GLM given in equation (1). No coefficients are able to explain a significant proportion of the variation in Fisher's α .

	Coefficient Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.57×10^{-1}	1.65	-0.095	0.927
Precipitation	-9.69×10^{-5}	2.61×10^{-4}	-0.372	0.721
Temperature	3.53×10^{-2}	6.57×10^{-2}	0.537	0.608
Forest Structure	6.26×10^{-4}	3.80×10^{-4}	1.646	0.144
Aspect	-2.24×10^{-3}	2.87×10^{-3}	-0.779	0.461
Slope	1.65×10^{-2}	1.15×10^{-2}	1.426	0.197

4.4.3 BETA-DIVERSITY

For bromeliads β_{sim} shows a decreasing turnover of species with increasing altitude (Figure 4.4), although there are two peaks at 1000 – 1500 m and 2000 - 2500 m. Individual tree families showed a wide variety of patterns in turnover. There were no consistent patterns for families with higher richness in any of the three main forest types. When all tree species are combined there is a constant decline with altitude using the β -similarity index, but with a less severe decline at high altitudes when compared to bromeliads (perhaps due to the larger total number of species) (Figure 4.4).

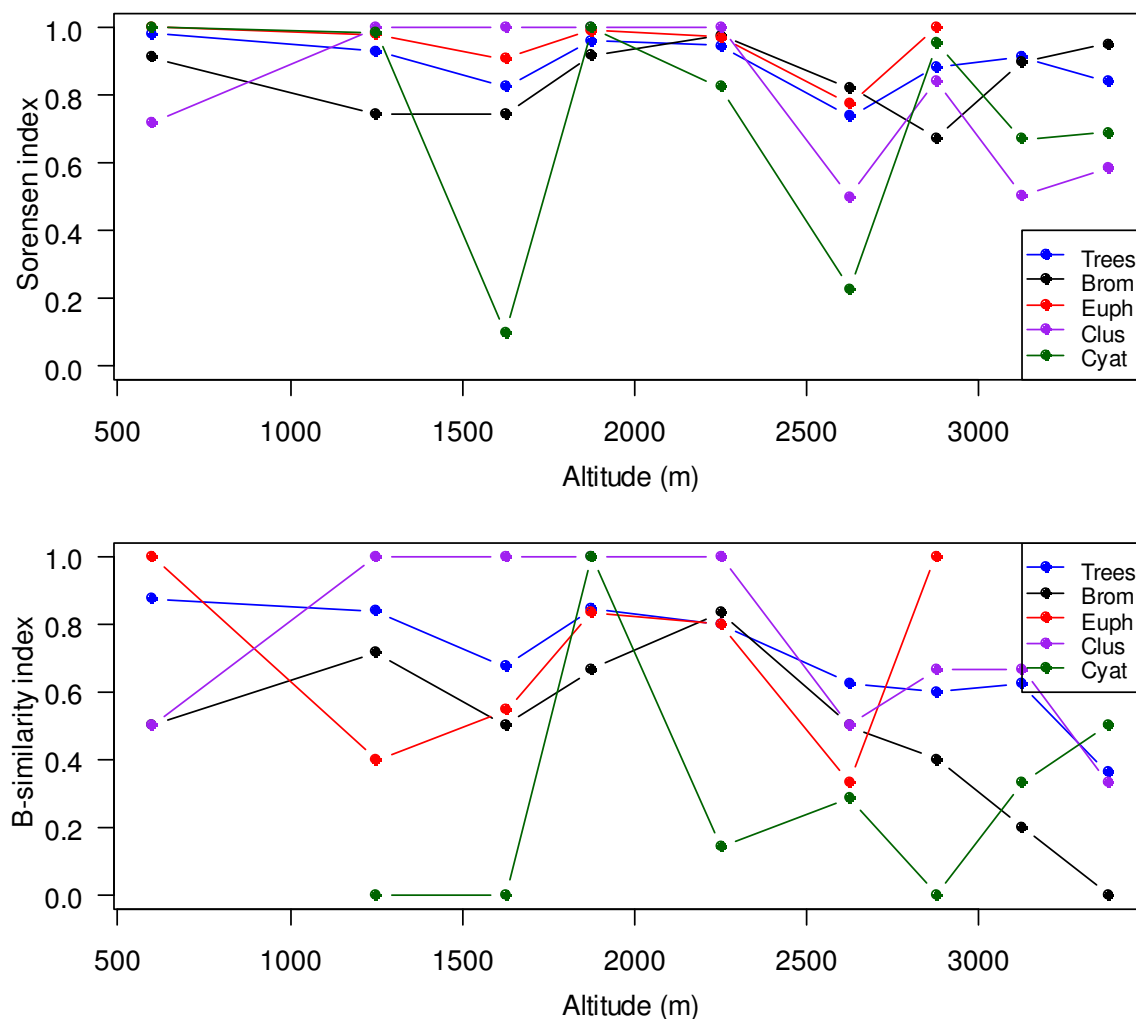


Figure 4.4. β -diversity along the continuous altitudinal transect. Values are calculated using (a) Sørensen index and (b) the β -similarity index, and are calculated for bromeliads, three representative families of woody species and all tree species combined. Points are plotted for the mean altitude of the two plots between which the represent the similarity. Abbreviations used in the legend, Brom = Bromeliaceae, Euph = Euphorbiaceae, Clus = Clusiaceae, Cyat = Cyatheaceae.

4.4.4 NMDS ANALYSIS

Ordination of sites based on bromeliad species composition in permanent research plots (Figure 4.5a) shows a similar organisation to the one based on bromeliad species from plotless sampling (Figure 4.5b). The plotless sampling includes more species, and so it shows a more distinct pattern. Axis 1 in both of these analyses shows a strong correlation with altitude (and the co-variable temperature) and three distinct groups represent the lowland rainforest (LRF),

tropical montane forest (TMF) and tropical montane cloud forest (TCF). Plots at TU5 and TU7 (Figure 4.5b) appear intermediate between the TMF and TCF groups. The plotless sampling shows that despite being classified as TMF, the plot at 1000 m (TON) has a species composition typical of lowland tropical rainforest. The pattern for woody species is similar (Figure 4.5c); although here the 1000 m plot (TON) is more intermediate between the TMF and LRF. Only three environmental variables showed a significant relationship with the NMDS axes for trees, annual precipitation and two measures of tree structure (sum of tree heights and stem surface area index), although these may simply reflect underlying altitudinal gradients. These plots show that overall there is a strong altitudinal component to species composition and for both bromeliads and trees, there is constant turnover and shared species across adjacent plots.

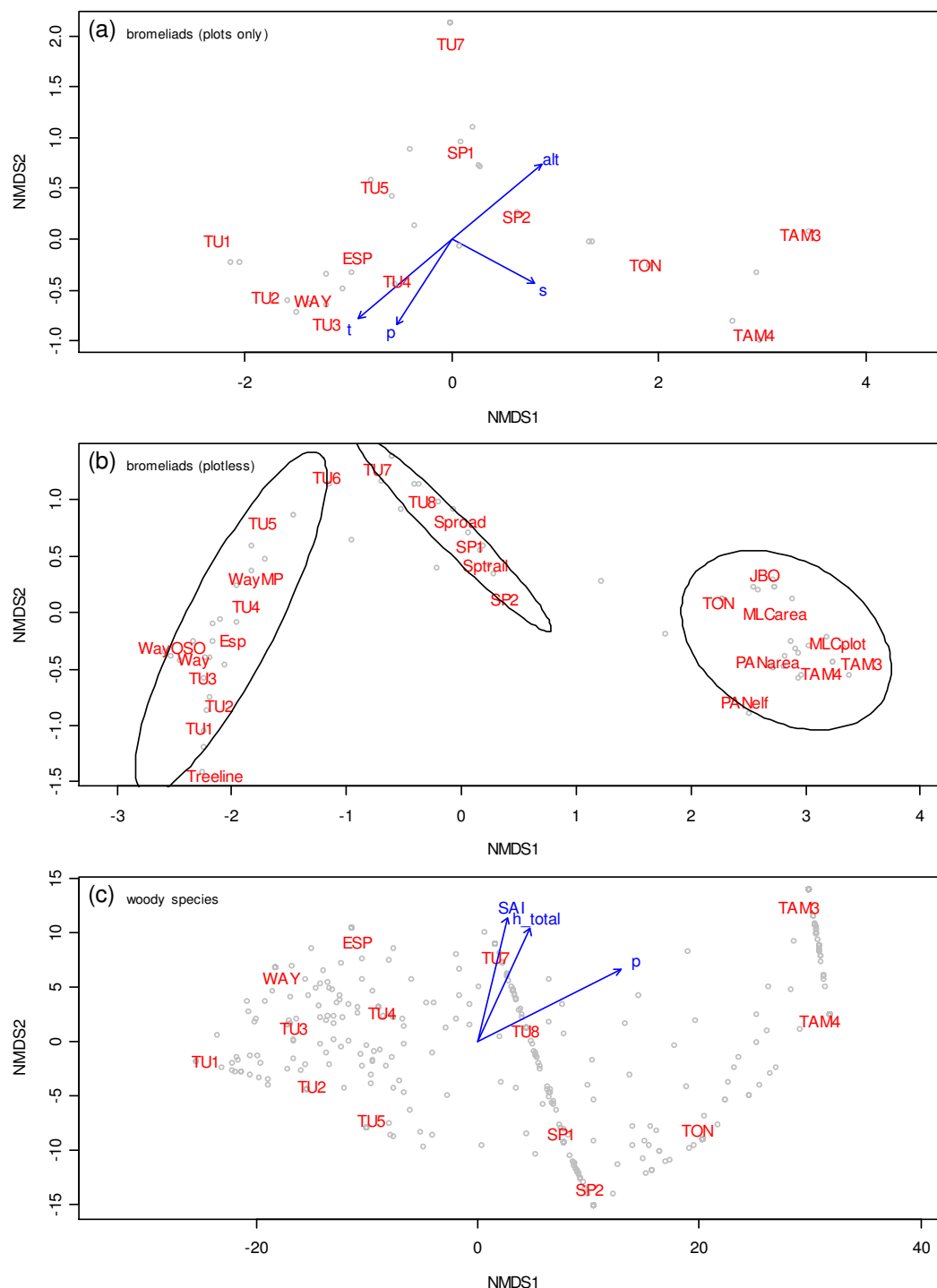


Figure 4.5. Plots of the first two axes of NMDS analysis of the species composition of 14 permanent research plots and sites based on plotless sampling for (a) bromeliad species from plot data only, (b) bromeliad species based on plotless sampling and (c) woody species from species inventories for the permanent research plots. Plot names and plotless site names are represented by red text. Grey dots show the location of individual species in the ordination, the species names for bromeliads are illustrated on repeats of these plots in Chapter 6. Abbreviations of environmental variables (shown in blue) are: alt = altitude, h_{total} = sum of height of all trees in plot, p = annual precipitation, SAI = stem surface area index (plot total), t = annual mean temperature.

4.5 DISCUSSION

4.5.1 HOW DO PATTERNS OF ALPHA-DIVERSITY COMPARE TO PREDICTIONS AND VALUES FROM THE LITERATURE?

The α -diversity of vascular epiphytes and bromeliads has been well studied and patterns established across the Neotropics (Gentry & Dodson 1987b) and for more specific locations (Freiberg & Freiberg 2000; Kessler 2002; Krömer & Gradstein 2003). While most studies cite climate factors as driving diversity, the steep climate gradients of the Andean slopes provide a 'bounded domain'. This leads to the emergent property for diversity that observed patterns closely match those arising from randomly placing species within these boundaries (Cardelús, Colwell & Watkins 2006). The same property of diversity is observed here, as species richness does not differ significantly from the MDE null model (Cardelús, Colwell & Watkins 2006; Colwell 2008). This effect is attributed to the random overlap of ranges with a bounded domain; however the low α -diversities at the highest and lowest altitudes could be attributed to climate and biotic factors, rather than random distribution of species.

The decrease in α -diversity and species richness at high altitudes is most likely due to decreasing availability of host trees and the increasing occurrence of frost, which will damage phytotelm bromeliads (Benzing 2000; Krömer *et al.* 2005). There is a dramatic change in climate either side of the ridge that separates the wet eastern slope of the Andes from the much drier inter-Andean valley to the west. Of all the bromeliad species observed in this study only terrestrial *Puya* are found growing across the ridge. The decrease in α -diversity and species richness of bromeliads seen at low altitude is most likely related to climate; the low diversity of epiphytes in the lowland Amazon is well known phenomenon (Reitz 1965; Gentry & Dodson 1987b). High evapotranspiration leads to increased water stress, limiting the growth of epiphytes (Krömer *et al.* 2005). Lowland Amazon areas which receive more rainfall or high fog input often have higher epiphyte diversity and biomass, supporting the hypothesis that water is

the limiting factor (Freiberg & Freiberg 2000; Kreft *et al.* 2004; Obregon *et al.* 2011). The limitation of diversity as a result of climate factors is supported by the low vascular epiphyte biomass at low altitude (Chapter 5).

The location of a mid-altitude peak along this transect was different using Fisher's α and species richness. Fisher's α showed a peak at 1500 m, the same as is widely reported for other studies (Krömer *et al.* 2005; Cardelús, Colwell & Watkins 2006; Krömer, Kessler & Herzog 2006). The constant species richness, with a more subtle peak of 20 species between 2500 m and 3000 m, is more consistent with findings from Bolivia where there was a plateau of bromeliad diversity across most of the transect, from 500-3000 m (Krömer *et al.* 2005). For local floras, species richness of between 10 and 30 species seems common (Kelly *et al.* 2004; Cardelús, Colwell & Watkins 2006; Krömer, Kessler & Herzog 2006; Krömer, Kessler & Gradstein 2007), but a detailed comparison between sites was not possible due to the different methodologies used in each study.

4.5.2 SPECIES TURNOVER AND PLOT COMPOSITION

Altitudinal transects present strong climate gradients in a small geographic space. This leads to conflicting drivers of species turnover. Strong climate gradients can lead to high turnover and the shorter distances make it easier to disperse beyond edge of a profitable range. Bromeliads (like epiphytes in general) have been shown to have a low β -diversity, so that despite high α -diversity, they rarely contribute significantly to landscape scale (γ) diversity. In this study we found that bromeliad β -diversity was lower than tree β -diversity, but not by a large amount. The Andes are known to be rich in epiphytes (Gentry & Dodson 1987a), and this comparison on the scale of Andean valleys, as here, show the increased contribution to overall diversity in this landscape. The β -diversity for both trees and bromeliads was higher in the lowlands than in the TCF plots. It is difficult to compare the Bromeliaceae to other families of woody species as each family has unique patterns of β -diversity caused by individual features of their biology.

The NMDS ordination shows that with sufficient sampling, bromeliads form three groups roughly assignable to LRF, TMF and TCF. This pattern is less obvious from the permanent research plot data, where there are fewer species, and the plots appear more evenly spaced. Including climate data in the ordination shows temperature and precipitation to have very similar gradients in relation to species composition. In woody species, precipitation is the only climate variable forms a gradient significantly correlated with species composition, a pattern found for woody species in Asian tropical rainforests (Davidar *et al.* 2007).

The three groups of bromeliad species composition match the forest classification based on tree species and climate from Grubb *et al.* (1963) for Andean forests in Ecuador. They also roughly correspond to the zones of epiphyte diversity identified for Peru by Ibisch *et al.* (1996), except in this transect there is no distinction between Ibisch's 'sub-Andean' and 'Amazonian' rainforest categories. The classification of TONO (1000 m) as having a species composition similar to LRF fits with a distribution of LRF up to 1200 m reported in Grubb *et al.* (1963), and contradicts the suggestion from the introduction (Chapter 2) that it be classified as TMF. The separate montane communities, closely matching the distinction between TCF and TMF, appear to be divided around 2000 – 2500 m, corresponding to a peak in β -diversity between these altitudes. The change in species composition here is higher than the lower limit of the 'cloud zone'. The discord between the change in species composition and the cloud level may reflect the fact that the area between 2000 m and 1750 m has been subject to historic landslides (supported by lower plot biomass and tree stature) and the more open, disturbed forest could have been re-colonised by species tolerant of warmer conditions (those from lower altitudes). The division in bromeliad composition at this altitude is matched by the tree flora, with the plots TU5 (2500 m) and TU7 (2000 m) forming of separate groups. However, for trees there is no corresponding peak in β -diversity, suggesting the presence or absence of a few key species is responsible for the contrasting species composition.

4.5.3 CONCLUSIONS

Along this elevation transect bromeliads form three distinct communities separated by altitude. These communities can be roughly referred to corresponding climate defined forest types, as lowland rainforest (LRF), tropical montane forest (TMF) and tropical montane cloud forest (TCF). The presence of these three groups of bromeliad species roughly corresponds to the same, less clearly defined groups in trees. There are peaks of β -diversity between the three communities when using sample-size-independent measure of turnover, although there is still turnover of species within communities. α -diversity was highest in the TMF at 1500 m matching other epiphyte studies, but species richness was highest in the TCF although species richness matched predictions of the MDE null model. Diversity was low in the lowland rainforest which is likely to be a result of climate factors.

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5. BIOMASS OF VASCULAR EPIPHYTES ALONG AN ALTITUDINAL TRANSECT IN THE PERUVIAN ANDES

5.1 ABSTRACT

Neotropical montane forests are known for the prevalence of vascular epiphytes, but quantifying the amount of vascular epiphytes can reveal underlying processes controlling the abundance of vascular epiphytes. I use a recently published standardised method for estimating vascular epiphyte biomass in a non-destructive way, and make suggestions on adapting this method for use in 1 ha permanent sample plots (PSPs). Data collected from thirteen PSPs along an altitudinal transect on the Eastern slope of the Peruvian Andes shows vascular epiphyte biomass peaks in the TCF with a value of 4220 kg ha⁻¹ at 3250 m, a higher altitude than other comparable studies. The vascular epiphyte biomass is significantly lower in LRF than in either the TMF or TCF. Vascular epiphyte biomass in the TCF is significantly more variable than the other ecological zones, and this correlates with steeper slopes and higher natural forest disturbance. Environmental variables were poor at explaining variation in vascular epiphyte biomass, and this suggests it is not in equilibrium with the environment. Vascular epiphytes do not make a significant contribution to forest biomass, reaching a maximum of 4% of total canopy biomass.

5.2 INTRODUCTION

Vascular epiphytes play a key role in the Tropical Andes biodiversity hotspot (Myers *et al.* 2000). They are keystone species (Benzing 2000; Wittman 2000; Jabiol *et al.* 2009) and influence ecosystem processes (Nadkarni 1984; Veneklaas *et al.* 1990; Benzing 2000; Hölscher *et al.* 2004; Kelly *et al.* 2004; Nadkarni *et al.* 2004; Kohler *et al.* 2007; Martinson *et al.* 2010).

Epiphytes exist in a stressful niche in which productivity is severely constrained by their physical environment, particularly by climate (Benzing 1998; Nadkarni & Solano 2002; Zotz & Bader 2009), and are threatened by the climate change already occurring in the eastern Andes (Feeley *et al.* 2011).

Vascular epiphyte biomass varies across multiple scales, from single branches (Freiberg & Freiberg 2000) to across ecosystems (Kohler *et al.* 2007). In this study we focus on epiphyte biomass at the stand level, looking at differences between 1 ha plots. At this scale, the effects of macro-climate should be observable over the influence of microclimates within single trees. Climatic factors are widely cited to drive vascular epiphyte biomass, and water availability is known to correlate with vascular epiphyte biomass at the stand level (P'ocs 1980; Gehrig-Downie *et al.* 2011; Obregon *et al.* 2011) despite the fact many vascular epiphyte species are drought tolerant. It is likely that temperature also plays an important role too, particularly with respect to the limiting factors of strong seasonal variation and freezing temperatures (Zotz 2005). At the scale of this study it is important to control for the effects of local topography (Werner *et al.* 2012) and disturbance history of the forest (Barthlott *et al.* 2001; Nkongmeneck, Lowman & Atwood 2002; Wolf 2005; Hietz, Buchberger & Winkler 2006; Werner & Gradstein 2009).

Despite the large volume of research on Neotropical vascular epiphytes there is not a uniting theory on the causes of variation in vascular epiphyte biomass. One reason for this may be insufficient sampling locations across the continent (Figure 5.1) but there is also a real need for a standard set of methods to make VEB studies comparable (Wolf, Gradstein & Nadkarni 2009). The SVERA protocol (Wolf, Gradstein & Nadkarni 2009) provides a useful standardised method. However the method is time-consuming since a great deal of time is taken enumerating and measuring trees in a 30 m × 30 m plot. The use of existing tree sample plots would

dramatically reduce the time required for this method. The use of one hectare (or bigger) plots is now common practice in forest ecology (Phillips *et al.* 2003) and here an altered form of the SVERA method is proposed for use in permanent sample plots (PSPs).

In this paper the epiphyte biomass across an altitudinal gradient in the Southern Andes (Malhi *et al.* 2010) is quantified using the SVERA protocol modified for use in permanent sample plots. This site is further south than most sites studied previously in South America (Figure 5.1), and is therefore more seasonal. Vascular epiphyte biomass at the plot level was modelled with climate, forest structure and diversity as well as nutrient availability. The carbon storage of vascular epiphytes was compared to other forest components. Finally the biomass on this transect was compared to the biomass reported in different studies across South and Central America.

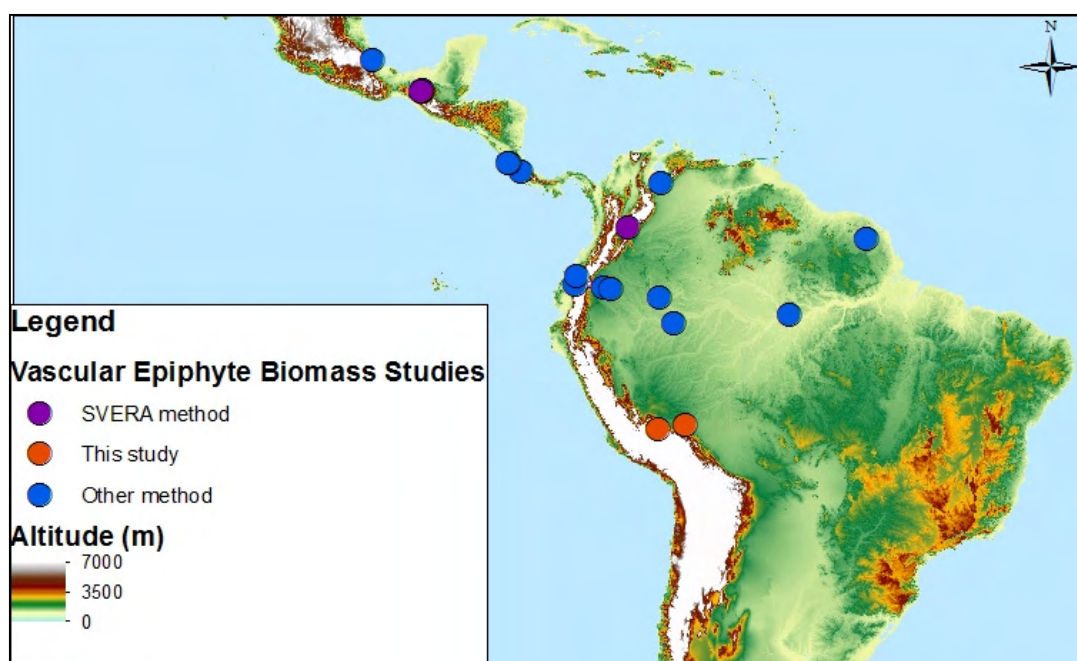


Figure 5.1. Geographic location of Neotropical vascular epiphyte biomass studies (data from this study and Fittkau & Klinge 1973; Nadkarni 1984; Veneklaas *et al.* 1990; Nadkarni & Matelson 1992; Hofstede, Wolf & Benzing 1993; Ingram & Nadkarni 1993; Hietz & Hietz-Seifert 1995b; Freiberg & Freiberg 2000; Barthlott *et al.* 2001; Nadkarni *et al.* 2004; Benavides *et al.* 2005; Benavides, Wolf & Duivenvoorden 2006; Kohler *et al.* 2007; Wolf, Gradstein & Nadkarni 2009; Higuera & Wolf 2010; Gehrig-Downie *et al.* 2011).

5.3 FIELD SITES

Vascular epiphyte biomass was quantified in thirteen permanent sample plots (PSPs) that form part of the Andes Biodiversity and Ecosystem Research Group (ABERG) network in southern Peru (Malhi *et al.* 2010). Fieldwork was carried out from June to August of 2009. The permanent research plots used in this study were 6 from the Trocha Union site (TU1, TU2, TU3, TU4, TU5, TU7), two from the Wayqecha site (WAY, ESP), two from the San Pedro site (SP1, SP2), one from the Tono site (TON), and two from the Tambopata site (TAM3, TAM4). Details of the PSPs are given in Chapter 2. Details of tree species, location, and size are recorded as part of the permanent sampling, and trees were identified using a permanent identification number. Climate variables are taken from existing transect data in Rapp (2010) and Girardin *et al.* (2010) and the annual mean temperature and annual precipitation are summarised in Figure 5.2. Foliar nitrogen and phosphorus were calculated by averaging the values reported in van de Weg *et al.* (2009) by PSP using both the per unit leaf area and per unit leaf mass values.

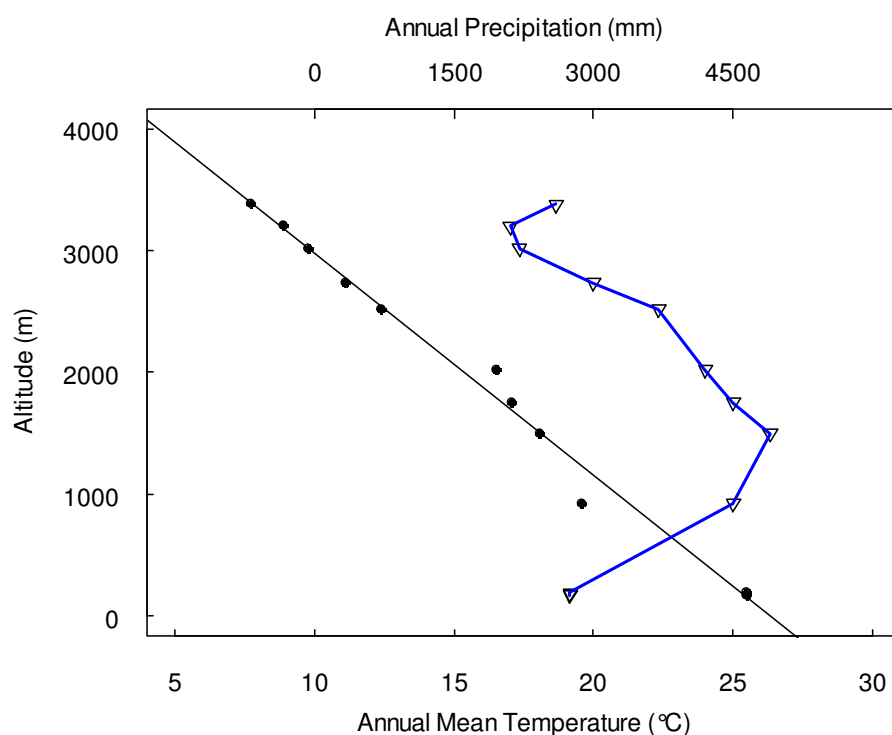


Figure 5.2. Plot climate data showing temperature (filled circles) and precipitation (open triangles) against altitude for ten of the plots used in this study.

5.4 METHODS

Data on epiphyte biomass was collected using the protocol set out by Wolf *et al.* (2009). Here the method is outlined, with the changes made to adapt the protocol from 30 × 30 m plots set out in the original method to the established 1 ha plots on this transect. The epiphyte biomass was estimated non-destructively by selecting 35 trees, distributed across seven size categories based on diameter at breast height (DBH). Initial tree selection was random, and subsequently the nearest neighbour inside the plot was selected. As these forests have high tree diversity a range of tree species were sampled. Tree species is known to influence the diversity and quantity of epiphytes (Callaway *et al.* 2002; Laube & Zotz 2006) and sampling a range of host species therefore reduces any tree species-specific bias. Trees with no vascular epiphytes, such as ant-trees or those with sloughing bark were excluded as they obscure the relationship between tree size and vascular epiphyte biomass (Wolf, Gradstein & Nadkarni 2009). This would not affect plot-level biomass estimates for TCF and TMF as less than 1% of trees fall into this category. The proportion of epiphyte-free trees is only significant below 500 m (at which estimated plot-level biomass is likely to be an over-estimate). For each sampled tree, height was measured using a hypsometer (TruPulse 200, Laser Technology Inc., Colorado, USA), DBH was re-recorded (to compare to existing data) and the total number of 'branching points' were recorded (where at least two branches of over 5 cm DBH emerged from a division point (Wolf, Gradstein & Nadkarni 2009)). For each sample tree the numbers of epiphytes was counted in cohorts based on a measure of plant size most relevant to each physiognomic group. Details of epiphytic taxa and sampling strategy can be found in Section 5.8 along with a detailed explanation of the method to convert counts to plot-level biomass and these methods are summarised in this section. Vascular epiphyte counts were converted to biomass using mean values per size-class from measurements taken on a sample of each cohort. To scale up vascular epiphyte biomass of the sampled trees to total vascular epiphyte biomass of each 1 ha plot, a

log-log relationship was fitted between the measured vascular epiphyte biomass and tree size approximated using DBH and height. Differences in the slope of biomass accumulation between plots were tested using analysis of covariance (ANCOVA). In addition the total surface area of trees was estimated using Chambers' formula (Chambers *et al.* 2004) modified for montane forests (Robertson *et al.* 2010) to derive the stem surface area index (SSAI).

5.4.1 STATISTICAL ANALYSIS

Simple linear models were fitted to the biomass data using linear and quadratic regression with untransformed biomass and log biomass as the independent variable and altitude as the only dependent variable. Linear models of log(biomass) showed the highest r^2 values. A general linear model (GLM) was also fitted to the data. To predict epiphyte biomass using environmental variables from the literature, we used a GLM of the form:

$$biomass = altitude + climate + topography + forest\ structure$$

Nine input variables were reduced to four and included in the model using principal coordinates analysis axes selected using the broken stick method. Only the first axis of each factor contained a significant amount of variation and was used in the final model. The variables combined in climate were mean annual temperature, annual precipitation and mean annual RH. The variables combined in topography were slope and aspect, the variables in structure were mean tree height, sum of all tree heights and stem surface area index. The model was run for total plot biomass and plot biomass per unit surface area of tree. Data on nutrient availability was only available for seven PSPs so correlation between vascular epiphyte biomass and nutrient availability was tested using Pearson's product moment correlation coefficient.

5.4.2 BIOMASS OF PLOTS AND CANOPY

The tree biomass of each plot was calculated from data collected for the ABERG project (Malhi *et al.* 2010). The leaf biomass data was calculated using the leaf area index (LAI) estimated from

hemispherical photos taken in the plots. These photos include all aspects of the canopy including leaves, branches and all epiphytes, and these factors can not be easily separated in the images, and hence this is considered to represent ‘total canopy biomass’. Specific leaf area (SLA) values were taken from Moser *et al.* (2007) who report the following relationship between SLA and altitude for montane sites in Andean Ecuador:

$$SLA = 91.4 - (0.013 \times altitude)$$

where altitude is measured in meters above sea level. Multiplying SLA by LAI gives an estimate of total canopy biomass. This estimate is likely to underestimate total canopy biomass because the leaf area index calculated from hemispherical photos is expected to be lower than the true value due to clumping (Jonckheere *et al.* 2004).

5.5 RESULTS

A total of 13 plots were surveyed using the SVERA protocol. In 12 of the 13 plots, there was significant correlation between tree DBH and vascular epiphyte biomass (Figure 5.3), allowing the total plot biomass to be calculated. There was no significant relationship for plot TAM3, so this plot was not used in further analysis. The slope and intercept of the biomass accumulation curves varied significantly between plots (ANCOVA, $F = 6.62$, $p < 0.001$) showing that colonisation of host trees occurs at different rates in different plots.

The plot at the lowest altitude, at the Tambopata site (TAM4), had significantly lower biomass than the other sites (22 kg ha⁻¹ at Tambopata, compared to 90 – 450 kg ha⁻¹ at other sites) (Figure 5.4). The plot at 3250 m (TU2) has an exceptionally high biomass of 439 kg ha⁻¹, more than twice the mean and 160 kg ha⁻¹ more than the plot with the next highest vascular epiphyte biomass, the 3000 m plot at Wayqecha (Figure 5.4). The plot level biomass has no

spatial structure (Moran's $I = -0.19$, $p = 0.39$) (Figure 5.5) indicating that significant variation in vascular epiphyte biomass can happen over short spaces.

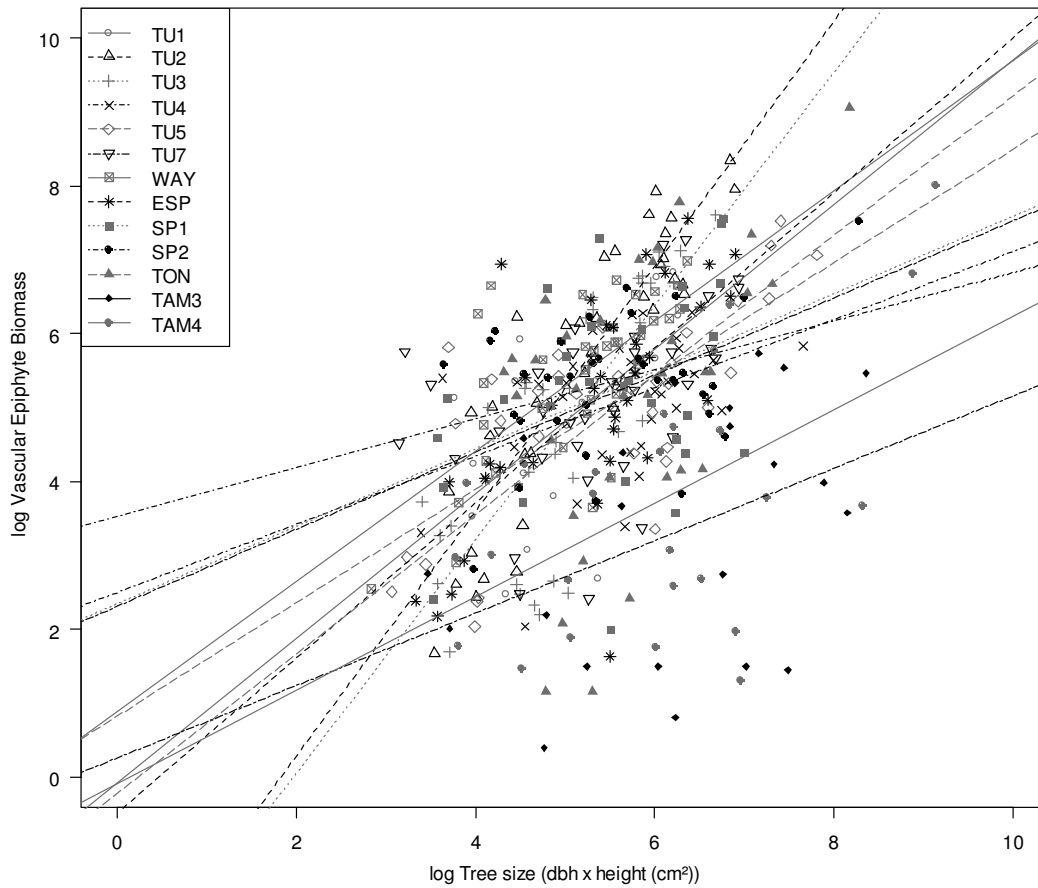


Figure 5.3. Correlation between tree size (measure as DBH multiplied by height based on field measurements from this study) and vascular epiphyte biomass for individual trees in plots. TU1: $\log(\text{biomass}) = -0.071 \times 0.977 \log(\text{tree size})$, $r^2 = 0.36$, $p = 0.006$; TU2: $\log(\text{biomass}) = -3.03 \times 1.66 \log(\text{tree size})$, $r^2 = 0.78$, $p < 0.001$; TU3: $\log(\text{biomass}) = -3.11 \times 1.58 \log(\text{tree size})$, $r^2 = 0.60$, $p < 0.001$; TU4: $\log(\text{biomass}) = 2.50 \times 0.461 \log(\text{tree size})$, $r^2 = 0.18$, $p = 0.008$; TU5: $\log(\text{biomass}) = 0.820 \times 0.767 \log(\text{tree size})$, $r^2 = 0.50$, $p < 0.001$; TU7: $\log(\text{biomass}) = 2.32 \times 0.521 \log(\text{tree size})$, $r^2 = 0.20$, $p = 0.007$; WAY: $\log(\text{biomass}) = 0.879 \times 0.882 \log(\text{tree size})$, $r^2 = 0.46$, $p < 0.001$; ESP: $\log(\text{biomass}) = -0.491 \times 1.05 \log(\text{tree size})$, $r^2 = 0.46$, $p < 0.001$; SP1: $\log(\text{biomass}) = 2.34 \times 0.525 \log(\text{tree size})$, $r^2 = 0.16$, $p = 0.02$; SP2: $\log(\text{biomass}) = 3.53 \times 0.330 \log(\text{tree size})$, $r^2 = 0.13$, $p = 0.04$; Tono: $\log(\text{biomass}) = -0.226 \times 0.944 \log(\text{tree size})$, $r^2 = 0.22$, $p = 0.005$; TAM3: no significant relationship, $r^2 = 0.11$, $p = 0.06$; TAM4: $\log(\text{biomass}) = -0.092 \times 0.633 \log(\text{tree size})$, $r^2 = 0.29$, $p = 0.004$.

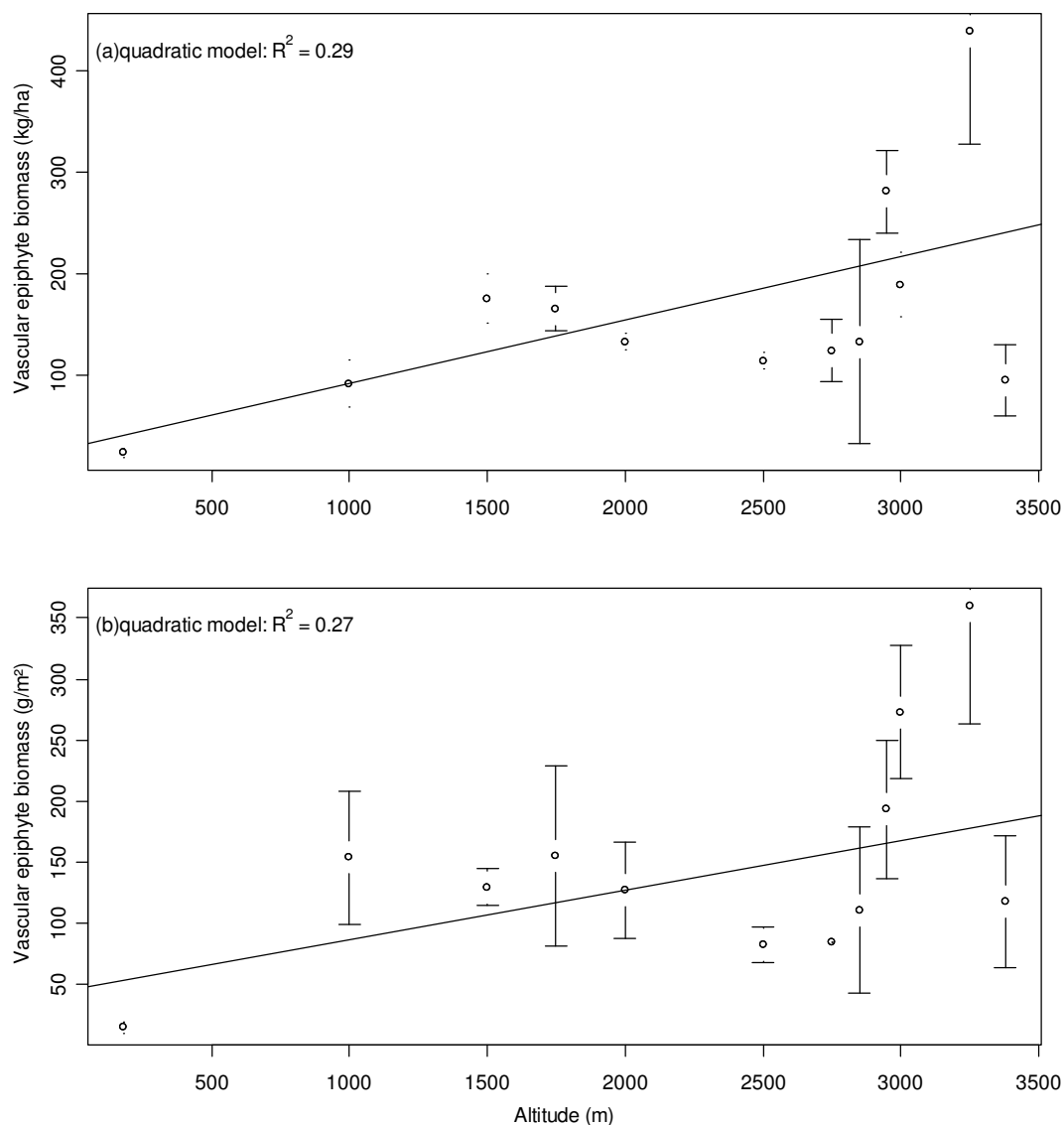


Figure 5.4. Vascular epiphyte biomass, (a) per ha and (b) per m² of bark surface, estimated using the stem surface area index, for all plots measured. Values are mean $\pm$ 95 % confidence interval. Quadratic models fitted to the data with the equations (a) $y = -1.2 \times 10^{-6}x^2 + 0.06x + 28$ and (b) $y = -2.06 \times 10^{-6}x^2 + 0.04x + 46$, where y is the biomass variable and x is altitude. R^2 values are shown in the plot windows.

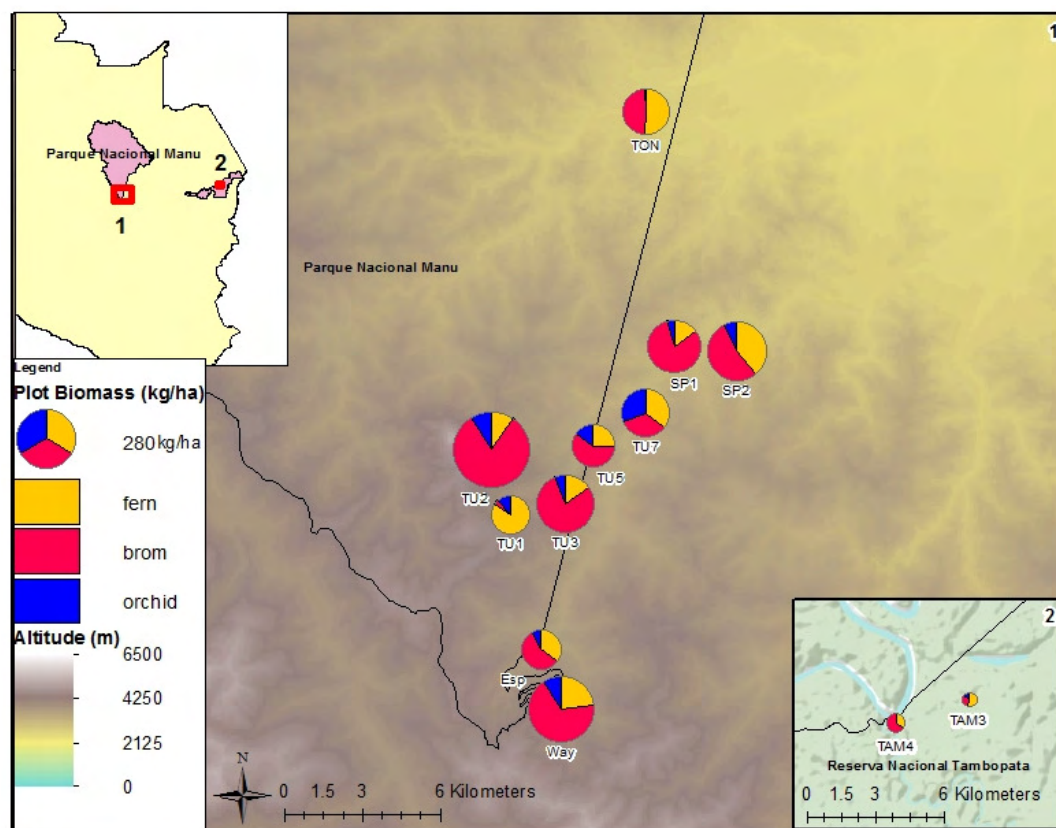


Figure 5.5. Map of vascular epiphyte biomass results showing vascular epiphyte biomass as a proportional pie symbol. Charts are coloured according to the percentage contribution of the three main components of vascular epiphyte biomass (ferns, bromeliads (=brom) and orchids). The map is split into the montane part of the transect (1) and Tambopata (2) is shown as an inset for clarity, the relative locations are indicated on the overview map.

The stem surface area of trees is potentially a limiting factor for epiphyte biomass. While tree height decreased linearly with increasing altitude, the mean DBH showed no significant decrease with increasing altitude (Table 5.1). The SSAI, combining heights and DBH, showed high variability between plots and peaked between 2500 m and 3000 m. The lowest plots (200 m, 1000 m) showed similar SSAI values to the highest elevation plots (>3000 m). There was no correlation between SSAI and epiphytes biomass (Pearson's $r = 0.39$, $p = 0.35$). The vascular epiphyte biomass per unit of SSAI showed the plot TU2 at 3250 m had the highest

ratio of biomass to stem surface of 0.33 kg m^{-2} . The plot TU3, at 3000 m, had the second highest biomass per unit area of 0.19 kg m^{-2} .

Table 5.1. Vascular epiphyte biomass as estimated for the PSPs in this study with some information on the structure and biomass for woody species in the PSPs used in this study.

Location	Altitude (m)	Vascular epiphyte biomass (kg ha^{-1})	95% Confidence interval	Number of trees over 10 cm DBH	Mean tree DBH (cm)	Total tree surface area ($\text{m}^2 \text{ ha}^{-1}$)	Vascular epiphyte biomass (kg m^{-2})	Total above ground biomass (T ha^{-1})	Total Canopy Biomass (T ha^{-1})
TAM4	180	22.7	8.6	675	20.3	1847	12.3	304	4.6
TAM3	200	-	-	547	20.9	1475	-	-	4.9
TON	1000	91.0	60.3	446	23.9	1110	82.0	162	5.8
SP2	1500	175.2	25.3	869	20.7	1700	103.1	199	8.7
SP1	1750	165.0	133.2	926	20.2	1804	91.5	-	11.5
TU7	2000	132.6	56.2	939	16.9	1435	92.4	92	10.5
TU5	2500	113.4	26.2	1004	21.5	1773	64.0	164	10.7
TU4	2750	123.9	28.2	877	19.9	1468	84.4	154	-
ESP	2850	132.1	77.0	709	18.3	1127	117.2	-	-
WAY	3000	280.4	102.0	1144	17.8	1802	155.6	166	10.6
TU3	3000	188.6	53.6	605	19.2	985	191.5	110	10.8
TU2	3250	439.1	127.2	779	20.6	1313	334.5	153	-
TU1	3450	94.2	54.5	582	21.8	1013	93.0	112	-

The GLM was a poor fit, only able to explain 40.0% of the deviance in the total plot biomass and 28.5% of plot biomass per unit surface area. None of the individual variables showed a significantly good fit in the model (Table 5.2). Neither model had significant spatial autocorrelation (plot biomass: Moran's $I = -0.08$, $p = 0.47$; biomass per surface area: Moran's $I = -0.12$, $p = 0.59$). The model residuals showed that biomass was lower than predicted between 2500 and 3000 m, and in the highest altitude plot, at 3500 m. The biomass was much higher than predicted at 3250 m (Figure 5.6). There was also no correlation between vascular epiphyte biomass and foliar nitrogen (Pearson's $r = -0.37$, $p = 0.36$) or foliar phosphorus (Pearson's $r =$

0.09, $p = 0.83$). Since rainfall is only one aspect of the water regime experienced by these plants, it is likely the overall water balance is more strongly correlated with the vascular epiphyte biomass. Low potential evapotranspiration is known to be characteristic in tropical montane cloud forests (Rapp 2010) and while relative humidity was included in the GLM, it was not possible to calculate potential evapotranspiration for most of the PSPs.

Table 5.2. Contribution of environmental variables to the GLM used to model plot biomass.

Variable	Total plot biomass		Plot biomass per surface area	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
altitude	3.4111	0.1073	2.4593	0.1608
climate	0.1229	0.7362	0.0688	0.8007
topography	0.1742	0.6889	0.2573	0.6276
structure	0.9558	0.3608	0.0042	0.9502

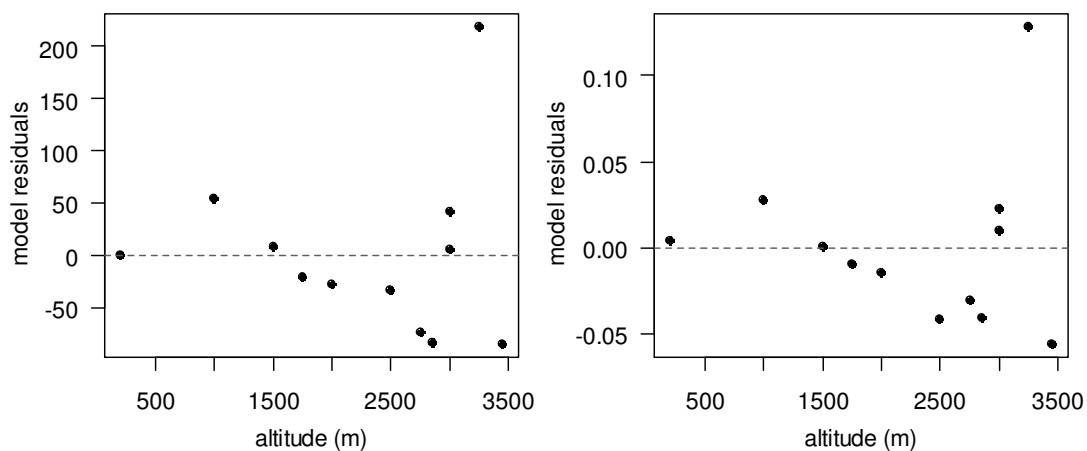


Figure 5.6. Model residuals from the GLM for (a) total plot biomass and (b) plot biomass per surface area of tree

In most plots bromeliads were the vascular epiphyte group with the highest biomass (Figure 5.5). They contributed over 50% of the vascular epiphyte biomass in all plots except TAM3, TU7 and TU1. Of these both TAM3 and TU1 had low vascular epiphyte biomass

compared to other plots. Ferns contributed consistently more than orchids to overall biomass across this transect (Figure 5.5).

The vascular epiphytes represent a very small proportion of forest biomass in these sites (Table 5.1). In all forest plots, the largest pools of biomass are found in the woody material and the soil. Vascular epiphytes have very little woody material, and so contribute negligibly to this. At Wayqecha in the cloud forest there is estimated to be 83 Megagrams C ha⁻¹ (Girardin *et al.* 2010) compared to 0.17 Mg C ha⁻¹ stored in the vascular epiphytes. In the lowland rainforest, vascular epiphytes make an even lower contribution to overall forest biomass, contributing 0.01 Mg C ha⁻¹ to an overall pool of 150 Mg C ha⁻¹ (Malhi *et al.* 2004).

Vascular epiphytes contribute significantly more to the amount of plant material actively involved in photosynthesis. Using values of canopy biomass derived from estimates of LAI and SLA there is a linear increase in canopy biomass from 4.5 Mg ha⁻¹ at 200 m to a plateau of 11.5 Mg ha⁻¹ at 1800 m and about 10 Mg ha⁻¹ in all plots above this. In the lowland rainforest the vascular epiphytes still contribute less than 1% of the total canopy biomass. In the plot at 1000 m and at higher altitude they contribute between 1.5% and 3.5% of the total canopy biomass. These values are likely to be higher when woody material in the canopy is excluded. The percent contribution is similar between the TMF and TCF.

5.6 DISCUSSION

5.6.1 ALTITUDINAL PATTERNS

The biomass of vascular epiphyte reached its peak in the TCF and was also high in the TMF, but there was no consistent trend with altitude (Figure 5.4), in contrast to studies of altitudinal transects elsewhere (Hietz & Hietz-Seifert 1995a; Freiberg & Freiberg 2000). An important feature in the pattern of vascular epiphyte biomass in the plots in this transect was the low

quantity of vascular epiphytes in lowland rainforest, as well as non-vascular epiphytes (Horwath 2011). The reason for the paucity of epiphytes in lowland rainforests is not fully understood, but is most likely to be the result of climatic factors in a similar way to diversity (Krömer *et al.* 2005). The sites at Tambopata have a long dry season (Malhi *et al.* 2004) and are not subject to inundation by low-level clouds (Gehrig-Downie *et al.* 2011). Lowland tropical rainforest sites closer to the equator often show much higher vascular epiphyte biomass, as well as a shorter, or lower intensity, dry season (Kohler *et al.* 2007).

A constant feature of cloud forests is the presence of epiphytes, facilitated by the low evapotranspiration (Gentry & Dodson 1987; Gehrig-Downie *et al.* 2011). In other studies cloud forests occur above a mid-altitude peak in vascular epiphyte biomass, meaning the cloud forest supports a lower vascular epiphyte biomass than mid or lower montane forests (Ingram & Nadkarni 1993; Hietz & Hietz-Seifert 1995a). However in this elevation transect the two highest vascular epiphyte biomass plots were in the cloud forest, TU2 (3250 m, 472 kg ha⁻¹) and Wayqecha (3000 m, 348 kg ha⁻¹).

The plot TU2 has unusually high vascular epiphyte biomass, as is shown in the large residual for the plot in the GLM models. A recent landslide on the northern edge of this plot has dramatically altered microclimatic conditions. The biomass of ferns and orchids are similar to nearby plots but the biomass of bromeliads is much higher. It is possible the landslide has led to an increase in vegetative reproduction and recruitment. Vascular epiphytes in isolated trees suffer high mortality (Werner 2011), but here the forest structure remains intact and the low potential evapotranspiration (PET) combined with increased light levels could have caused rapid vegetative growth of bromeliads. High bromeliad biomass is not uncommon in more exposed environments (Poltz & Zotz 2011). Further investigations would be required to determine the importance of the landslide in the population dynamics of vascular epiphytes,

and to establish if the vascular epiphyte biomass recorded in the TU2 PSP is normal or artificially raised (or even lowered!) by the landslide.

The climate factors used here, annual mean temperature and annual precipitation and relative humidity, were unable to explain much of the variation in the vascular epiphyte biomass per plot and biomass per unit of tree surface area. It is well established that overall water balance is one of the most important factors determining vascular epiphyte biomass (Hietz & Hietz-Seifert 1995a; Kohler *et al.* 2007; Gehrig-Downie *et al.* 2011; Poltz & Zotz 2011), and a more thorough picture of the water regime, particularly including evapotranspiration, of these forests may reveal stronger relationships with vascular epiphyte biomass. Nutrient levels in the vegetation did not affect vascular epiphyte biomass, and it is likely the efficient nutrient uptake in bromeliads (Inselsbacher *et al.* 2007; Winkler & Zotz 2009; Winkler & Zotz 2010) and other epiphytes may mean that nutrient levels are rarely limiting to vascular epiphyte biomass accumulation.

While vascular epiphyte biomass was higher in the TCF and TMF, the high variability in the TCF may relate to the forest dynamics. In the Andes around Manu National Park there is a strong correlation between altitude and the probability of landslides due to steeper terrain at higher altitude (K. Clark, unpublished data), and this would lead to frequent disturbance of the higher altitude plots. It is likely that plots at an early stage of recovery would have few large trees and hence a low stem surface area index (SSAI). If epiphytes biomass is constrained by the amount of available space for colonisation this would explain variation in biomass which is not explained by climate. However, in this instance I might expect to find a strong relationship between SSAI and plot epiphyte biomass. The lack of any strong correlation in this study has two possible explanations: (1) There is a significant lag period between the recovery of forest structural factors and vascular epiphytes. This effect is seen in forest recovering from

anthropogenic disturbance (Nadkarni *et al.* 2004; Benavides, Wolf & Duivenvoorden 2006); (2) Epiphyte communities are not limited by lack of available surface.

In many of the cloud forest plots in this study there is also a thick covering of bryophytes on trunks and branches. This has a two-fold effect, firstly of competing with vascular seedlings for light, but alternatively in maintaining a more humid environment and providing a better surface for seed attachment. Bryophytes biomass peaks in the cloud forest at 2500 m elevation (Horwath 2011), where vascular epiphyte biomass is high and the bryophyte mats contained a significant quantity of vascular epiphyte seedlings (Horwath 2011). This bryophyte peak could be responsible for the high vascular epiphyte biomass in the TCF. This would suggest that along this elevation transect vascular epiphyte biomass is limited by the capacity of species to establish, a feature found in several other geographic locations (Cascante-Marín *et al.* 2008).

5.6.2 VASCULAR EPIPHYTE BIOMASS OF OTHER GEOGRAPHIC LOCATIONS

The data collected here is directly comparable to other studies which have used the SVERA protocol to measure biomass. Wolf *et al.* (2009) found that the biomass in Mexican sites was higher than the amount measured here and the biomass in the Colombian cloud forest was about 1.5 times greater than the plots recorded in this study. However, further studies at the Colombian site showed much lower biomass in slightly disturbed conditions, although the disturbance was anthropogenic rather than natural (Higuera & Wolf 2010).

Biomass data is available for a significant number of other sites around South and Central America. In these studies vascular epiphyte biomass was measured using a variety of methods, and different units of measurements. The maximum reported vascular epiphyte biomass is 8250 kg ha⁻¹ for Monteverde in Costa Rica (Nadkarni *et al.* 2004). Comparing data at other sites requires some adjusting or estimating of values to obtain comparable units, so

values can only be treated as approximations. However, higher vascular epiphyte biomass of 2600 kg ha⁻¹ is reported from the Cordillera de Tillaran in Costa Rica (altitude 1500 m, MAP = 6000 mm year⁻¹)(Kohler *et al.* 2007), 2500 kg ha⁻¹ in Veracruz, Mexico (altitude = 1430 m , MAP = 1600 mm year⁻¹) (Hietz & Hietz-Seifert 1995a), 705 kg ha⁻¹ at Los Santos in Costa Rica (Altitude = 2900 m, MAP = 2800 mm year⁻¹)(Hölscher *et al.* 2004). There are other plots at these sites with higher vascular epiphyte biomass than equivalent plots in this study. Although these sites are wetter than sites in Manu National Park, the site in Veracruz, Mexico is drier, yet still supports a higher vascular epiphyte biomass. This shows that although precipitation is important to vascular epiphytes, there are epiphytes that are well adapted to dry conditions, and can achieve a high biomass in dry sites (Hölscher *et al.* 2004; Poltz & Zotz 2011).

5.6.3 FOREST CARBON CONTEXT

The biomass of vascular epiphytes in the Kosñipata Valley represent a relatively small proportion of forest biomass, in contrast to vascular epiphytes in other geographic locations (Nadkarni 1984). Epiphytes do not invest in long-lasting structural parts (e.g. wood), so their contribution is usually low compared to trees. The importance of the vascular epiphytes in carbon storage schemes, such as REDD or REDD+, which are being developed for the area is limited, and their importance lies in other functions. Lianas inhibit carbon sequestration by trees (Clark & Clark 1990), and there is some evidence that vascular epiphytes may have a similar effect (Benzing 2000), although they are not in direct competition with trees for soil resources in the same way as lianas.

Even the contribution of vascular epiphytes to total canopy biomass (a proxy for photosynthetically active biomass) is below 4% in all plots measured here. The low proportion of biomass combined with low gas exchange rates of vascular epiphytes (Griffiths *et al.* 1986) mean vascular epiphytes will play a minor role in the carbon cycle of the forest at all altitudes along the transect. Nevertheless, recent work on bromeliads has shown that water stored in

tanks can contribute significantly to the methane balance of forests (Martinson *et al.* 2010). The biomass of bromeliads in the montane forests at this site are comparable to the Ecuador site used by Martinson *et al.* (2010), and despite the cooler temperatures at these sites, bromeliad phytotelm might be expected to create a similar quantity of methane gas. This may mean that epiphytic bromeliads contribute disproportionately to greenhouse gas emissions from these sites.

5.6.4 SVERA PROTOCOL

The SVERA protocol tends to provide an overestimate of vascular epiphyte biomass, as trees with no vascular epiphytes are ignored. In TMCF, there is only a negligible proportion of trees over 10 cm DBH that do not host vascular epiphytes; the proportion of epiphyte-free trees is small in TMF below the cloud level, and is only significant in lowland tropical rainforest, which already have very low vascular epiphyte biomass. The paucity of epiphytes in lowland Amazonia is well documented, and the occurrence of vascular epiphytes in these forests is very patchy. The lack of correlation between tree size and its epiphyte load in the TU3 plots means the SVERA protocol can not be used to provide an estimate of vascular epiphyte biomass in this plot, and instead, a more exhaustive technique would be required.

The SVERA protocol provided a practical and repeatable way to quantify vascular epiphyte biomass in many forest types. The modifications here suggested to the method make it a useful tool for quantifying vascular epiphyte biomass in 1 ha permanent sample plots. While the SVERA protocol in Wolf *et al.* (2009) details the establishment of a 30 × 30 m plot, using previously established plots saves a significant amount of time. I found that identifying a minimum of 35 trees, then counting the vascular epiphytes could be completed in 4 to 8 hours, depending on terrain, tree size distribution, and if tree climbing was required to fully assess the quantity of vascular epiphytes accurately. The SVERA method avoids the harmful effects of

stripping sections of branches and trunks or entire trees required by other methods. Since a larger number of trees can be surveyed comparatively quickly the data will better account for the high spatial variability of vascular epiphytes.

While the method explicitly states that trees with no vascular epiphyte biomass should be ignored for the purpose of sampling, I propose an adaptation to account for this. In a 20 m × 20 m sub-plot the permanent tag number of trees of DBH > 10 cm which qualify as 'low vascular epiphyte biomass' can be recorded, and from this data a proportion of trees which fit this category can be calculated and removed from estimates when scaling up. In the absence of this step any plots with a significant proportion of trees with no vascular epiphytes would have epiphyte biomass overestimated.

The SVERA protocol represents an excellent opportunity for sampling vascular epiphyte biomass in a consistent way, and this can be applied to the large number of permanent sample plots now established to make a useful model of vascular epiphyte biomass across the globe, which will be an important step in understanding the significance of epiphytes across ecosystems.

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5.8 APPENDIX 1: SCALING FROM INDIVIDUALS TO PLOTS

5.8.1 DEFINING COHORTS AND COLLECTING SUFFICIENT SAMPLES

Collecting samples of individual taxa to convert epiphyte counts into biomass values was done differently for each physiognomic group. The methods employed are given in detail below and the results summarised in Table 5.3.

Piperaceae are a very small component of epiphyte biomass in this study area (Figure 5.7e). The plants have small succulent leaves distributed alternately along a thin woody stem. Piperaceae show a good correlation between stem length and biomass.

Ferns were abundant on this transect (Figure 5.7c), and contribute significantly to vascular epiphyte species richness. Ferns have a relatively low biomass per unit area, and some species can survive moderate drought in the sporophyte stage. The diversity of ferns is strongly correlated with humidity and rainfall at many sites (Hietz & Briones 1998; Fayle *et al.* 2009). The biomass values obtained from leaf measurements were adjusted to include root biomass. Rhizomes were included as 'roots'.

Orchids came as two types, with leaves emerging from a simple pseudobulb (Figure 5.7a) or with leaves emerging along a compound pseudobulb (Figure 5.7b). For simple pseudobulb species the length of the leaf blade and petiole were added together and weighed together. For the compound pseudobulb, an analysis of a sample of 115 plants showed a strong correlation ($r^2 = 0.50$, $p < 0.01$) between the total length of stem and the plant biomass. As counts from the ground were based on leaf length, and pseudobulbs were not always visible, the pseudobulbs were included as part of the root biomass.

Bromeliad biomass data was pooled over all locations along this transect due to the difficult and destructive nature of sampling the biomass of large bromeliads. Bromeliads were classified into categories by the diameter of the rosette at the widest point. The actual width of

the plant was measured, before being divided into constituent parts for drying and weighing. The biomass of inflorescences was ignored in this study. Although inflorescences can contribute to biomass, especially in large plants, they are transient structures and vary significantly from species to species.

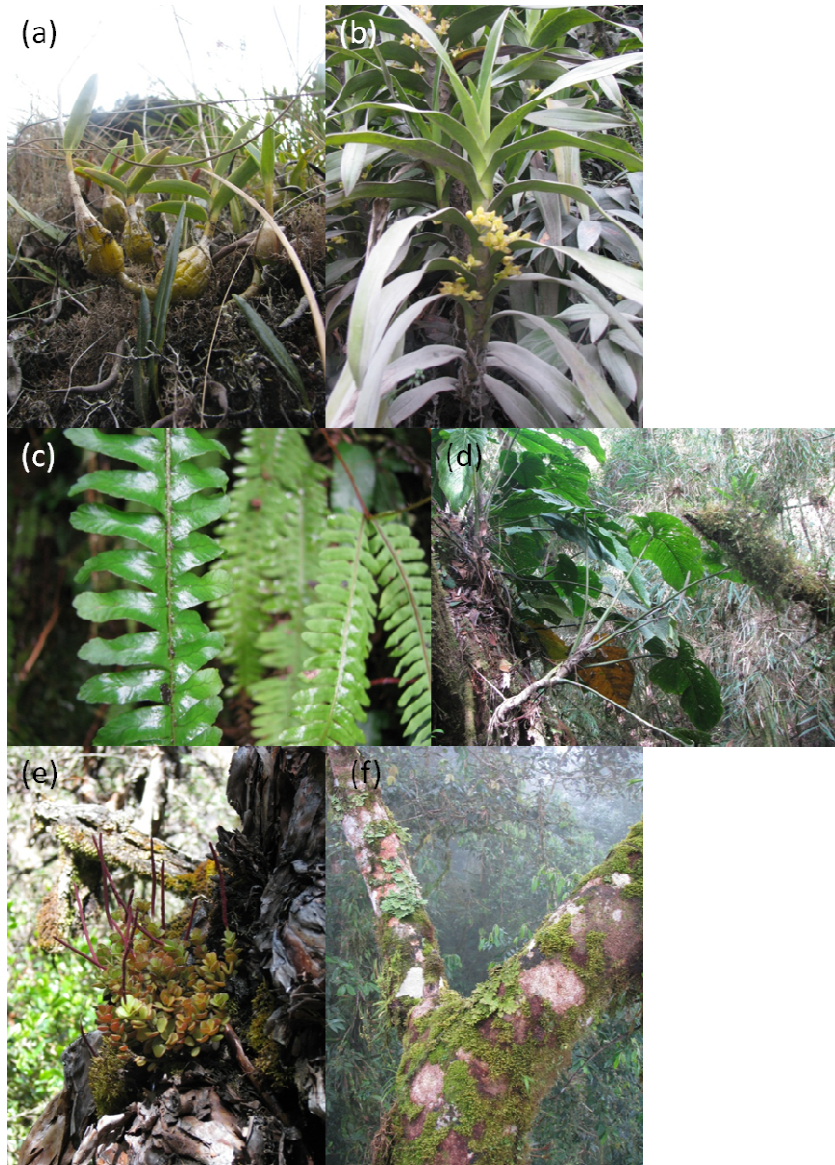


Figure 5.7. Examples of epiphytic groups found along the transect (a) orchid with leaves emerging from a simple pseudobulb, (b) orchid with leaves arranged alternately along a compound pseudobulb, (c) epiphytic ferns, (d) a large Araceae showing cordate leaves and woody stem, (e) epiphytic Piperaceae and (f) epiphytic bryophytes and lichens at 20 m height in the canopy of a mature *Ficus trigona*.

Accidental epiphytes were ignored, as they were infrequent, mostly very small and likely to have a limited life-span in the canopy. The Araceae were considered only if they were completely epiphytic. Many Araceae with large stems begin their life as epiphytes, but soon are able to develop roots in the soil, and are therefore functionally hemi-epiphytes. Araceae typically have cordate leaves (Figure 5.7d) and flowers composed of a spathe and spadex. Much of the biomass of the leaf is in the solid, succulent petiole, and the size of a petiole increases with distance from the apex of the leaf whorl, consequently, there is a strong linear relationship between leaf length (reported excluding the petiole) and dry weight. The leaves of hemi-epiphytes in other families were quantified in the same way as the aroid leaves in terms of structure and the importance of petioles in determining total biomass. Like aroids, they also send down roots which mean they are not epiphytes for most of their lives. They were present only in the plot at 1000 m, and many were terrestrially rooted. The small number of juveniles which were true epiphytes did not contribute significantly to vascular epiphyte biomass.

Table 5.3. Mean biomass of cohorts with sample size (n) and standard error of the mean (SE). The cohorts are used to convert a count of leaves in each size category to a biomass.

Group	Location	Size cohort (cm)	n	Mean biomass (g)	Standard error
Araceae	All	Leaf mass per 10cm	82	1.10	0.10
		Wood per cm	13	0.67	0.10
Other hemi-epiphytes	All	Mass per 10cm	31	0.62	0.08
Bromeliads	All	5 to 25	37	7.32	1.71
		25 to 50	18	54.70	9.89
		50 to 100	24	152.38	32.56
		Over 100	3	476.48	128.50
Ferns	Wayqecha	0 to 10	30	0.51	0.08
		10 to 25	34	1.36	0.12
		25 to 50	15	3.40	0.41
		Over 50	13	8.25	0.80
	Lowland	0 to 10	16	0.75	0.11
		10 to 25	54	1.45	0.13
		25 to 50	29	3.92	0.24

		Over 50	29	11.50	0.34
Orchids	Wayqecha	0 to 10	10	0.86	0.28
		10 to 25	43	1.10	0.22
		25 to 50	27	2.53	0.31
		Over 50	9	5.46	0.92
	Lowland	0 to 10	12	0.53	0.19
		10 to 25	8	1.93	0.66
		25 to 50	7	1.84	0.21
		Over 50	5	11.23	1.28
Piperaceae	All	Mass per 10cm	19	0.92	0.11

5.8.2 ASSESSING COHORT SIZE IN THE FIELD

As the size of individual plants was initially assessed by eye, it was important to test the accuracy of the collectors' ability to identify plant sizes. This was done by assessing plants close to the ground, then measuring the plant for comparison. It was found that all collectors were able to assign leaves accurately to the correct cohort after a short (*circa* 30 minute) initial practice period. Errors were most common at the boundary of cohorts, but these errors were not systematically biased. For the two most abundant groups, ferns and orchids, samples were collected from three sites representing the tropical montane cloud forest (Wayqecha), the tropical montane forest (San Pedro) and the tropical lowland rainforest (MLC).

5.8.3 SPLITTING MEASUREMENTS BY FOREST TYPE

A large number of samples were lost at the San Pedro site due to inadequate drying facilities. The samples which survived were therefore pooled with the tropical lowland forest data to give two sets of values, for the TCF and lowland forest (TMF and TRF).

5.8.4 ROOT BIOMASS

A special subset of plants was collected with complete roots systems, and this was used to determine the contribution of root biomass to total plant biomass for ferns, orchids and bromeliads. For ferns the root biomass included rhizomes. For orchids the pseudobulb was

included as part of the root system as its size was difficult to judge in ground-based count. Plants with roots were removed from the tree and the root systems separated out and washed to remove soil before drying. Some fine root matter was lost during the collection and washing stage, however the fine roots contributed only a small amount to overall root biomass. The rest of the data was from samples based on the leaves alone, as leaves could be sampled in a non-destructive way, leaving the plant alive. I hoped this would reduce the impact of sampling on the forest. I then used the relationship between root biomass and plant biomass from the first phase to estimate plant biomass from the leaves collected in the second phase. In the tropical lowland forest, a patchy distribution of rare orchid species might have meant that destructive sampling could have posed a serious threat to rare species. The decision was taken to use only plants at treefall sites created by recent landslides, where the plants already had a very high probability of imminent death. However the sample size for orchids was small in the lowland rainforests (Table 5.3).

For the ferns and orchids, the measured leaf biomass was adjusted upwards to include the biomass of roots. Roots contributed between 40% and 60% of individual epiphyte biomass when rhizomes and pseudobulbs are included. While this seems like a high proportion, the roots represent the most lignified part of most epiphytes, and therefore have a higher dry weight. There was no significant difference in the root biomass of orchids between cloud forest and lowland plants ($t = 0.79$, $p = 0.44$), so this data was pooled together for further analysis. Ferns showed a lower root biomass in the lowland forest than the cloud forest ($t = 2.98$, $p < 0.01$) so this data was kept separate.

5.8.5 SCALING UP FROM TREE TO PLOT

Having converted the counts of different epiphytes into a biomass value, the next stage is to use tree counts to scale up to plot level biomass. This was done using correlation between tree size and the biomass of vascular epiphytes. The estimates of tree size used were: 1) DBH; 2) DBH x

height; 3) Stem surface area index (SSAI) calculate for each tree using Chambers *et al.* (2004) with corrections for montane forest trees following (Robertson *et al.* 2010); and 4) 'Tree size' as calculated in Wolf *et al.* (2009) by combining DBH, tree height and the number of branching points. I assessed which of these variables had the highest r^2 values across all plots. Both (2) "DBH x height" and (4) 'tree size' were good predictors (data not shown). Therefore "DBH x height" was selected as the best predictor of the vascular epiphyte biomass of a single tree across all plots. All plots, except TAM3 (2750 m), showed correlation between the vascular epiphyte biomass and tree size (measured as ddb x height) (Figure 5.3). This allowed scaling from individual measurements of tree size to estimate vascular epiphyte load on trees, which can be summed over all trees to give a plot-level estimate of epiphyte biomass.

6. THE IMPORTANCE OF WATER-AVAILABILITY IN THE GEOGRAPHIC RANGES OF THE BROMELIACEAE: A STUDY ALONG AN ALTITUDINAL TRANSECT IN SOUTHERN PERU

6.1. ABSTRACT

1. Altitudinal transects are the ideal study system to look for the relationship between plant distribution and climate, and the role played by specific physiological adaptations.
2. In this study we used bromeliads along an altitudinal transect in Southern Peru to test the importance of adaptation to water availability to see if species distributions could be explained by water availability gradients.
3. A typical bromeliad with a phytotelm (water-impounding shoot) of 30 cm diameter can expect to spend 50% of days with an empty phytotelm in the LRF and TMF, but only 40% in the TCF. In the TCF, the number of days is reduced by an additional 10% if bromeliads are able to intercept fog.
4. Epiphytic bromeliads show differences in anatomy and morphology of leaves and phytotelms between different ecological zones, with plants in the tropical montane cloud forest have many, large leaves and large phytotelm to maximise water interception and storage.
5. Plants in the lowland tropical rainforest have a greater diversity of forms, and the presence of CAM photosynthesis allow species to avoid the effects of drought.

6.2. INTRODUCTION

There is concern that the eastern slopes of the Amazon, one of the most diverse ecosystems on the planet (Myers *et al.* 2000), is already being significantly altered by climate change (Feeley *et al.* 2011). Understanding the role of the environment in observed species distributions is important to understand and predict the impact the changing climate will have on ecosystems (Bellard *et al.* 2012). While many studies on the impacts of changing climate on species distributions use simple correlation between climate and existing range, realisation of hypothesised range shifts may be controlled by specific plant traits rather than simple relationship with environment (Midgley *et al.* 2006). This is supported by the fact that species' observed distribution does not always represent the full potential area that could be occupied based on physical environment alone (Gaston 2009; Soberón & Nakamura 2009). Epiphytes occupy a stress-tolerant niche *sensu* Grime (1977) and bromeliads have a large range of adaptations to this niche (Benzing 2000). However, the stressful environment is taken to mean that their distribution is therefore closely linked to their environment (Benzing 1998). Not only is it likely that they will be sensitive (and vulnerable) to climate change, a study of their distribution should reveal important information about the most important drivers of range shifts (Benzing 1998; Zotz & Bader 2009). The only significant barrier to epiphytes occupying their entire fundamental niche, the potential area a species could occupy (Gaston 2009; Soberón & Nakamura 2009), is dispersal limitation (Cascante-Marín *et al.* 2009). Altitudinal transects present strong climate gradients in a small geographic space meaning that dispersal limitation is very unlikely (Malhi *et al.* 2010).

The epiphytic niche is primarily water stressed (Laube & Zotz 2003), although there is some evidence that temperature plays an important role in epiphytic bromeliad range limits observed in the field (Gilmartin 1973). Studies have shown that water availability is important

to bromeliad population dynamics and ecology (Freiberg & Turton 2007; Kohler *et al.* 2007; Krömer, Kessler & Gradstein 2007; Laube & Zotz 2007; Reyes-Garcia *et al.* 2008; Obregon *et al.* 2011; Wester *et al.* 2011), physiology (Laube & Zotz 2003; Zotz *et al.* 2010) and distribution (Griffiths & Smith 1983; Jones, Szyska & Kessler 2011). To investigate the importance of water-availability in determining ranges we examine the Bromeliaceae, a family with about 50% of species as obligate epiphytes, found along an altitudinal gradient in primary rainforest in the Southern Andes (Malhi *et al.* 2010). The field sites occur in an “Andean superhumid zone” (Killeen *et al.* 2007) where water is generally abundant in the wider ecosystem. Water-availability and temperature vary independently along the transect (Girardin *et al.* 2010), although temperature is directly linked to altitude (Korner 2007).

The overall morphology of bromeliads, can be important in determining species ranges within and between forest types (Pittendrigh 1948; Sugden 1981; Bennett 1982) and plays an important role in the ability of plants to maintain leaf water potential (Schmidt & Zotz 2001). Phytotelm bromeliads begin to lose internal water pressure once the external water supply is lost, but can continue to photosynthesise up to 50% tissue water deficit meaning adult phytotelm bromeliads could withstand over one month without re-filling of the phytotelm (Zotz & Thomas 1999). Narrow leaf syndrome (a large number of narrow leaves) is a suite of morphological characters that maximise interception of cloud moisture and provides a way to increase water interception in areas of high cloud immersion (Martorell & Ezcurra 2007). Species may use physiological adaptations to overcome a shortage of water, including CAM photosynthesis (Pierce, Winter & Griffiths 2002; Crayn, Winter & Smith 2004).

In this chapter I look at the ranges of species along the altitudinal transect, with reference to the ecological zones of (Chapter 4). The observed ranges are compared to different morphological and physiological adaptations relating to water availability.

6.3. FIELD SITES

The field data was collected along the altitudinal transect described in Chapter 2 and the sample sites are re-illustrated here (Figure 6.1). Species were studied in forests ranging from the lowland Amazon to the high Andes. Sampling was done extensively from 16 permanent sample plots (PSPs) along the transect (Figure 6.1) and additional plotless sampling was carried out in a further ten locations between and around the PSPs. A summary of the abiotic and biotic environment for the PSPs are given in Table 6.1.

Table 6.1. A summary of the location, climate and tree species composition of the 16 permanent sample plots (PSPs) exhaustively sampled for bromeliad species.

Site	Plot	Forest type*	Altitude (m)	Latitude	Longitude	Annual mean temp. (°C)	Annual precipitation (mm)	Dominant woody species (number of stems)
Trocha Union	TU1	TCF	3380	-13.1135	-71.6071	7.7	2600	<i>Weinmannia microphylla</i> (124); <i>Miconia</i> sp. (94); <i>Symplocos quitensis</i> (65)
Trocha Union	TU2	TCF	3200	-13.1107	-71.6045	8.9	2100	<i>Weinmannia bangi</i> (129); <i>Miconia</i> sp. (78); <i>Prunus huantensis</i> (66)
Wayqecha	WAY	TCF	3025	-13.1904	-71.5871	11.1	1700	<i>Weinmannia crassifolia</i> (406); <i>Clusia cretosa</i> (124); <i>Clusia flaviflora</i> (54)
Wayqecha	ESP	TCF	2850	-13.1759	-71.5949	12.0	1700	<i>Weinmannia latifolia</i> (154); <i>Clusia poeppigiana</i> (88); <i>Prunus integrifolia</i> (55)
Trocha Union	TU3	TCF	3020	-13.1092	-71.5977	9.8	2200	<i>Clusia cretosa</i> (135); <i>Clusia trochiformis</i> (88); <i>Weinmannia</i> sp. (60)
Trocha Union	TU4	TCF	2740	-13.1068	-71.5894	11.1	3000	<i>Cyathea delgadii</i> (115); <i>Weinmannia</i> sp. (79); <i>Clusia</i> sp. (69)
Trocha Union	TU5	TCF	2520	-13.0943	-71.5744	12.4	3700	<i>Cyathea delgadii</i> (324); <i>Clusia</i> sp (78); <i>Weinmannia bangi</i> (77)
Trocha Union	TU7	TCF	2025	-13.0735	-71.5589	16.5	4200	<i>Alzatea verticillata</i> (163); <i>Cyathea lechleri</i> (74); <i>Ilex villosula</i> (69)
Trocha Union	TU8	TMF	1850	-13.0705	-71.5557	16.1	3850	<i>Cyathea lechleri</i> (127); <i>Clethra revoluta</i> (103); <i>Clusia</i> sp. (73)
San Pedro	SAN1	TMF	1750	-13.0472	-71.5425	17.1	4500	<i>Cyathaceae</i> sp. (152); <i>Tapirira</i> sp. (48); <i>Alzatea verticillata</i> (41)

San Pedro	SAN2	TMF	1500	-13.0491	-71.5368	18.1	4900	<i>Lauraceae</i> sp. (71); <i>Cyathaceae</i> sp. (64); <i>Tachigali setifera</i> (53)
Tono	TON	LRF	925	-12.9547	-71.5535	19.6	4500	<i>Perebea guianensis</i> (42); <i>Virola elongata</i> (37); <i>Lauraceae</i> sp. (34)
Pantiacolla	PAN	LRF	580	-12.6495	-71.2625	22.0	2800	<i>Pseudosenefeldera inclinata</i> (41); <i>Coussapoa parviflora</i> (32); <i>Hevea brasiliensis</i> (26)
MLC	MLC	LRF	500	-12.7889	-71.3905	25.0	4000	N/A
Tambopata	TAM3	LRF	190	-12.8303	-69.2705	25.5	4200	<i>Pourouma minor</i> (44); <i>Pseudolmedia laevigata</i> (22); <i>Bixa arborea</i> (19)
Tambopata	TAM4	LRF	174	-12.8385	-69.296	25.5	4200	<i>Iriartea deltoidea</i> (123); <i>Socratea exorrhiza</i> (58); <i>Rinorea viridifolia</i> (32)

*based on classification of bromeliad species composition in Chapter 4

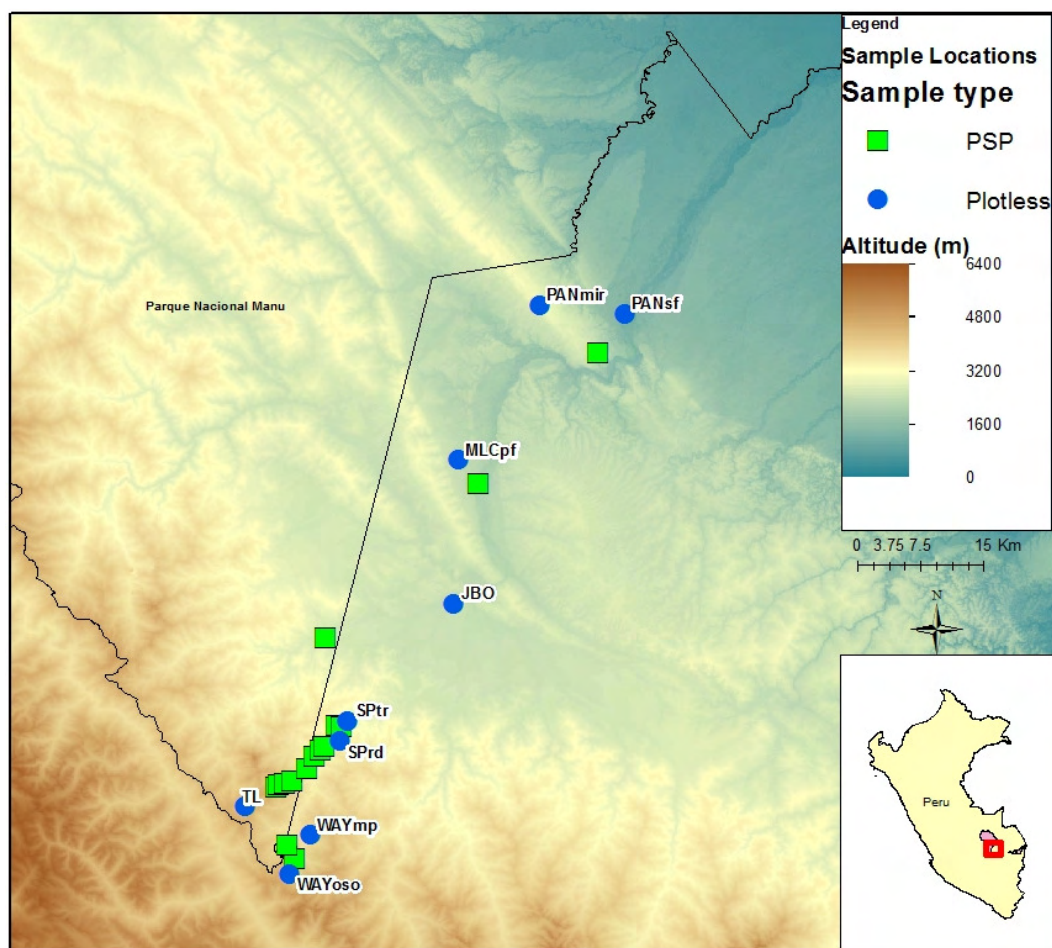


Figure 6.1. Location of Permanent Sample Plots (PSPs – names as Chapter 2) and plotless samples in the main part of the field site. The two PSPs in Tambopata are not shown on this map, they are located approximate 200 km to the east.

6.4. METHODS

The distribution of plants was recorded from May to July over 3 years of observations from 2008 to 2010. In PSPs exhaustive sampling of five 20 × 20 m subplots combined with haphazard sampling was used, and in plotless locations trees were sampled haphazardly. At each location species presence was recorded along with abundance using the subjective DAFOR scale (D = dominant, A = abundant, F = frequent, O = occasional, R =rare) in relation to the epiphyte community. Over 40 epiphyte-rich trees along the transect were searched in more detail by climbing into the canopy using the Basic Canopy Access Program double rope technique (Canopy Access Limited, Wytham, UK).

Detailed information was recorded for individual bromeliad plants that could be identified to species level (clonal aggregations were treated as a single individual). This information included height of plant from the ground, and height of the canopy, maturity, plant size and Johansson canopy zone (Johansson 1974). Distances of the plant from the ground, and to the top of the canopy were recorded using a laser rangefinder (TruPulse 200, Laser Technology Inc., Colorado, USA). All trees inside the PSPs over 10 cm DBH have an identification number and this was recorded to allow the tree ID to be checked in a database. For 77 of these plants (21 species) leaf samples were also collected and immediately dried in silica gel for carbon isotope ratio analysis. Carbon isotope analysis was carried out by Dr P. Ditchfield of the Oxford University Department of Archaeology. Carbon isotope ratios have a bimodal distribution in Bromeliaceae (Crayn, Winter & Smith 2004) so the carbon isotope ratio data from this study was used to calculate the 'carbon isotope ratio anomaly'. This was calculated as the difference between measured carbon isotope ratio and mean value for the relevant photosynthetic pathway ($C_3 = -28.78 \text{ ‰}$, CAM = -15.81 ‰) to allow inference of the effects of environment independent of the photosynthetic pathway.

Non-metric multidimensional scaling (NMDS) ordination was used to provide a summary of range of all species. The co-ordinates for each species, which quantify the differences in distribution between species, were taken from the NMDS ordination from plotless samples from Chapter 4. Analysis of similarities (ANOSIM) was used to test for clustering of species. The clusters used were the three ecological zones identified in Chapter 4. Pairwise differences in height from the ground and geographic locations were compared for bromeliads using a Mantel test with 1000 permutations and Kendall's rank correlation as the underlying correlation measure. Negative correlation between distance matrices would support the idea that bromeliads found in the same geographic locations occupy different strata. Tukey's honest significant difference post-hoc test was used to test for different groups of species based on canopy position. Significance was set to $\alpha = 0.01$ to allow for unequal group sizes.

To test the importance of water as a limiting factor we used a model developed by Zotz & Thomas (1999) to predict the number of days each year a phytotelm bromeliad would lack water in the tank. Climate data was taken from the permanent weather stations installed along the altitudinal transect (Girardin *et al.* 2010). Calculations were based on individuals of *Tillandsia complanata* Benth. of 30 cm diameter (young adult stage). A detailed breakdown of the model can be found in Section 6.9. To calculate if fog could potentially have a significant role as a water source in tropical montane cloud forest (TCF), data from a cylindrical fog-interceptor connected to an automatic tipping-bucket rain-gauge (Skye Instruments, Llandrindod Wells, Powys, UK) installed with the permanent weather station in the TCF at 3000 m (Figure 6.2) was used to calculate any increase in water availability due to fog-interception.



Figure 6.2. The cylindrical fog-interceptor installed with the permanent weather station at the Wayqecha research site.

Plant architecture of all species was recorded using digital photos which were converted to outlines in ImageJ (Abramoff, Magelhaes & Ram 2004) and areas and perimeters of the horizontal and vertical plant profiles were calculated. Water volume was measured in the field by filling the plants completely with water then allowing them to rest for 2 minutes until excess water had drained out. Volume of water retained was measured.

The presence of the narrow-leaf syndrome was tested using leaf form index (LFI) and plant form index (PFI) (Martorell & Ezcurra 2007). The leaf form index was measured as the ratio of leaf blade length to leaf blade width at one third of the distance from the base to tip (Martorell & Ezcurra 2007), a higher LFI indicates a narrower leaf. Measurements were taken on three leaves per plant, for each plant that was collected to make a herbarium specimen. Since the leaf morphology is only one aspect of the narrow-leaf syndrome, a plant form index (PFI) was also calculated, using a method similar to that described by Martorell & Ezcurra (2007). The PFI used in this study was developed combining the LFI with leaf number, leaf density (number of leaves divided by height) and longest leaf angle (angle from tip of longest leaf to

vertical line from centre). The data was combined to make the LFI using a principal components analysis (PCA) in R version 2.6.0 (R Core Development Team 2005).

6.5. RESULTS

6.5.1. SPECIES DISTRIBUTION AND ECOLOGICAL ZONES

Species ranges and abundances are shown in Table 6.2. NMDS axis 1 was strongly correlated with altitude ($r^2 = 0.685$, $p < 0.001$), whereas axis 2 was significantly correlated with precipitation ($r^2 = 0.518$, $p = 0.028$). The NDMS ordination analysis showed species to be grouped into three groups corresponding to the forest types based on climate (ANOSIM, $R = 0.97$, $p < 0.001$). The groups are here referred to as lowland rainforest (LRF), montane forest (TMF) and cloud forest (TCF) (Figure 6.3) and their affinity to existing forest classifications is discussed in Chapter 4. Further niche differentiation occurred through restriction to different heights within the canopy. For the 44 species with canopy position data, no significant correlation was found between geographic proximity of ranges and occupation of different heights within the canopy (Mantel test, $r = -0.011$, $p = 0.64$). There were also no significant groups of species at different heights within the canopy, and this was confirmed by Tukey's HSD test, showing only pairwise difference between a small number of species. However, there was a clear gradation of species heights in each forest type, with no 'unoccupied' heights (Figure 6.4). In the lowland rainforest, species with CAM photosynthesis did not occupy more exposed canopy positions across all sites ($t = -1.13$, $p = 0.26$), however when the TON plot (1000 m) was excluded species with CAM photosynthesis did occupy positions higher in the canopy ($t = 3.63$, $p = 0.0008$).

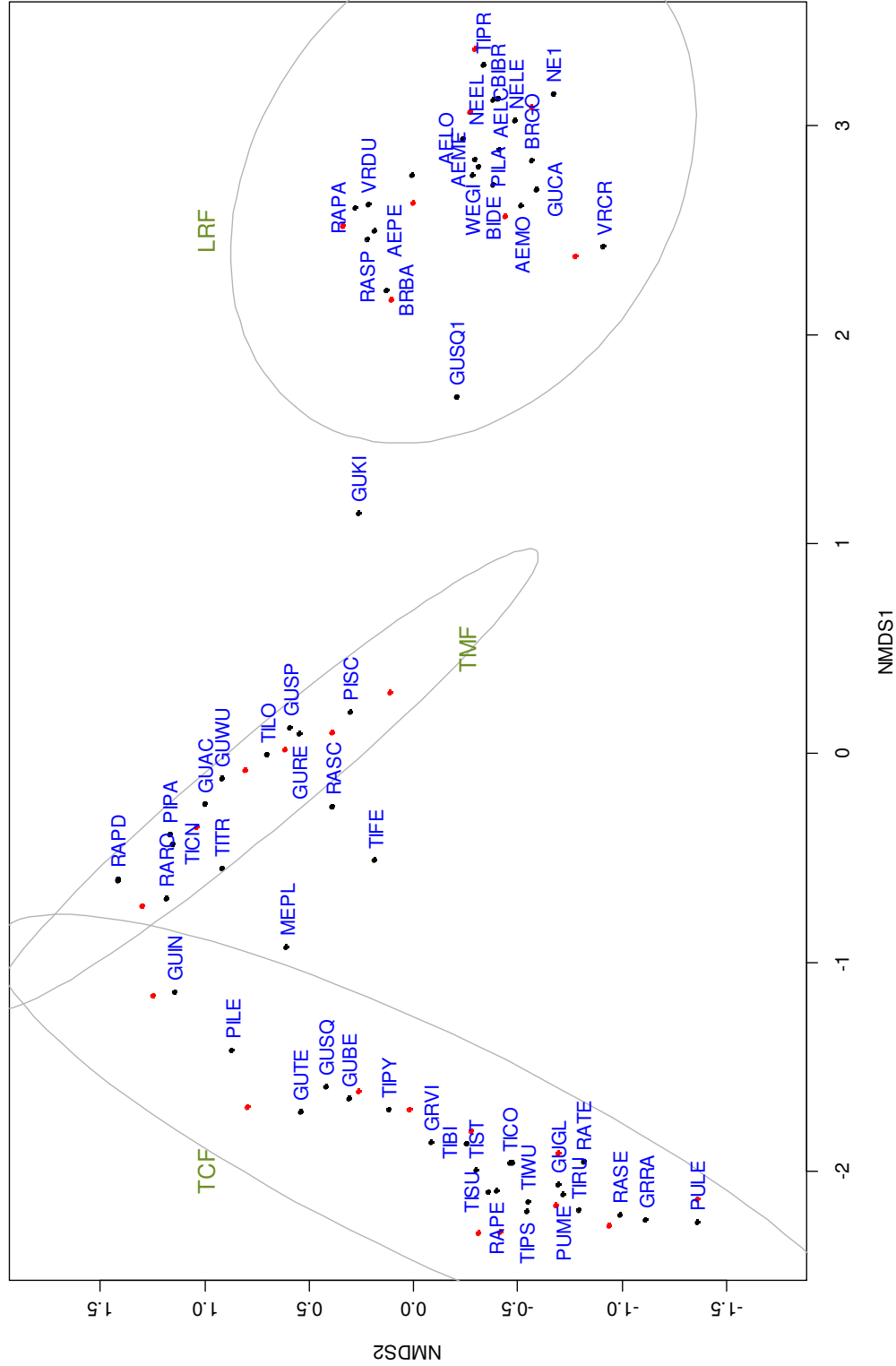


Figure 6.3. Location of species (black circles) in the ordination of plotless samples. Species names are abbreviated to four letter codes shown in Table 6.2. Red circles show the location of plotless samples in the ordination. The grey circles show ellipses fitted to 95 % confidence interval for error of each group based on average scores of each sample site.

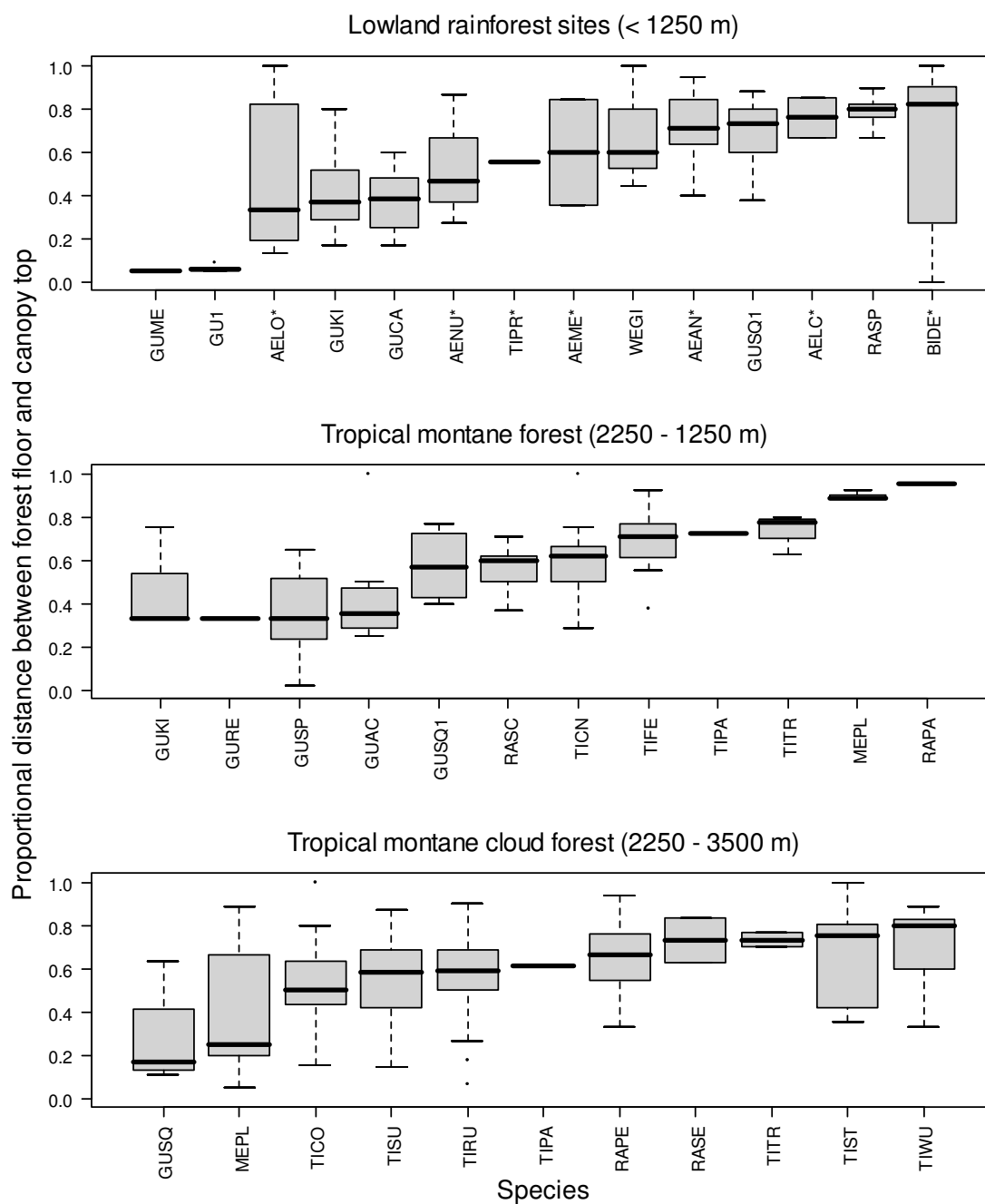


Figure 6.4. Canopy position of species split into the three forest types. The canopy position is measured as the proportion of distance between the ground and the top of the canopy. Species names are abbreviated to four letter codes shown in Table 6.2. An asterisk after the species names (*) marks species with CAM photosynthesis.

6.5.2. ADAPTATIONS TO LOW WATER AVAILABILITY: SHAPE AND SIZE

Using the modified equations of Zotz & Thomas (1999) individuals of *T. complanata* of 30 g will spend about 50% of days with an empty tank at the LRF sites and 40% of days in the TMF and

TCF sites (Figure 6.5). The tropical montane cloud forest has the shortest number of consecutive day with an empty tank with a maximum of 7 days, but for plants in the LRF and TMF the model showed up to 24 consecutive days with empty tanks in the dry season (July – September). At Wayqecha, fog interception could alleviate an additional 10% of days with an empty tank, meaning plants at Wayqecha spend an average of 30% of days with an empty tank (Figure 6.5). This effect would be bigger in small plants, and this implies that adaptations to increase fog interception could provide a significant benefit to plants.

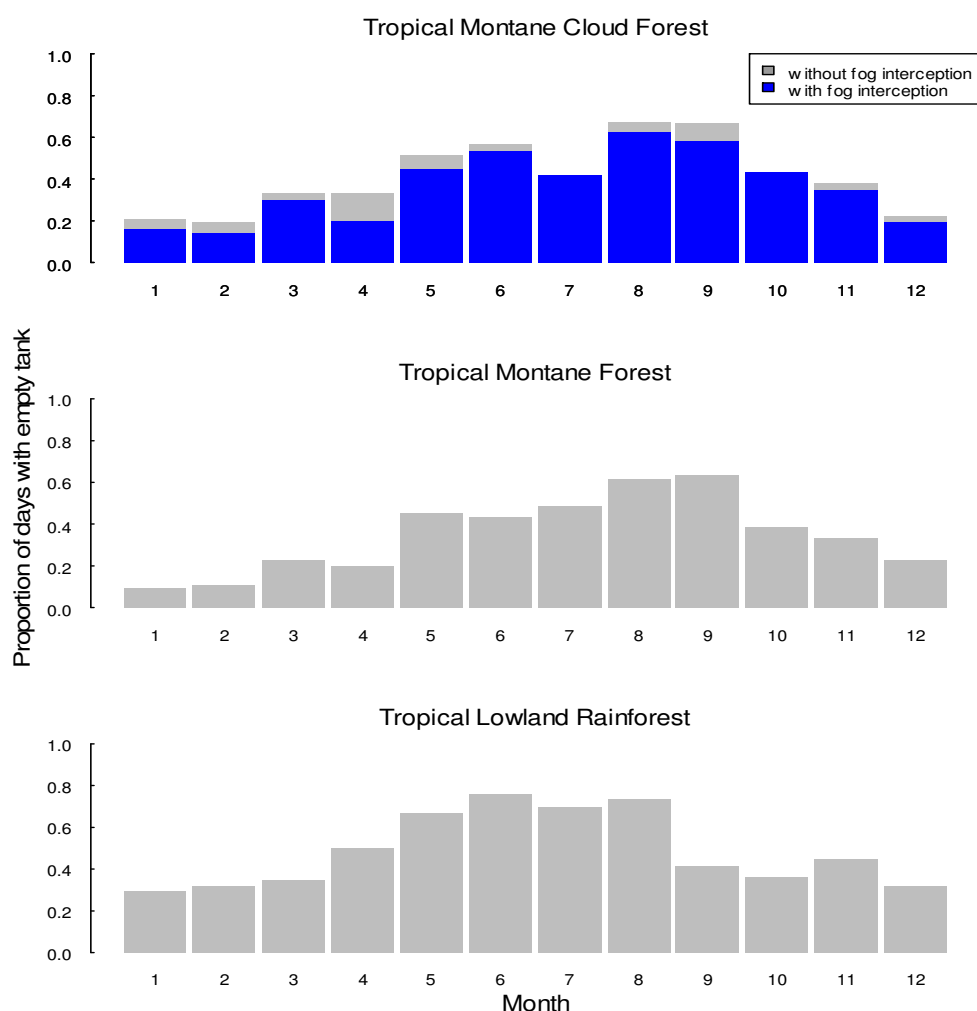


Figure 6.5. Proportion of days without water in tank for a 30 cm individual of *T. complanata* calculated using climate data from the three main forest types along the altitudinal transect. The blue bars show the results when fog interception is included.

The leaf form index (LFI) of plants in the TMF and TCF were consistent between plots, and were both lower (larger, wider leaves) and with lower variability between species when compared to the LRF (Table 6.3 and Figure 6.6). Plants in the TCF had more leaves than plants from the TMF and LRF ($t = -3.82$, $p < 0.001$) so total leaf area of plants was high in the TCF (Table 6.3). High leaf area is consistent with increased moisture interception from cloud (Martorell & Ezcurra 2007). The larger, wider leaves found in the TCF are not the most efficient for intercepting cloud water but if leaf shape may be constrained by the need for broad overlapping leaves to maximise phytotelm storage capacity (Schmidt & Zotz 2001). Large, wide leaves designed to maximise phytotelm capacity also provide the secondary benefit of higher total leaf area per plant that will increase fog interception. Species in the LRF have a more diverse range of leaf sizes. The leaves with the highest LFI belong to *Aechmea longifolia*, found only at 1000 m and below where cloud interception is unlikely to be a significant source of water. This species does not form a phytotelm, but does have CAM photosynthesis which represents an alternative way to avoid drought compared to large-water storing phytotelm. No correlation was found between the mean canopy position of species and either LFI ($t = -1.01$, $p = 0.32$) or PFI ($t = -0.25$, $p = 0.80$) suggesting that in these forests, canopy position does not depend on leaf or shoot morphology.

Table 6.3. Changes in leaf and plant shape along the elevation transect. Mean and range are for all species present at each site. Values are dimensionless unless stated.

Sites	Altitude	n	LFI		PFI		Total leaf area (cm ²)	
	(m)	(species)	mean	range	mean	range	mean	range
Trocha Union (>2500 m)	2500 - 3500	10	6.5	6.1	-1.5	19.9	1118	2464
Trocha Union (<2500 m)	1800 - 2500	14	9.6	22.7	-1.2	26.8	1224	4805
Wayqecha	2500 - 3000	11	11.9	23.8	0.5	36.5	1166	2361
San Pedro	1400 - 1750	11	11.6	23.8	0.7	36.5	1168	2284
Tono	800 - 1000	6	23.4	56.6	-6.0	61.5	1257	1610
Pantiacolla & MLC	400 - 600	6	20.7	57.5	-12.1	57.9	883	1710
Tambopata	150 - 250	4	26.0	57.5	-19.1	56.2	548	981

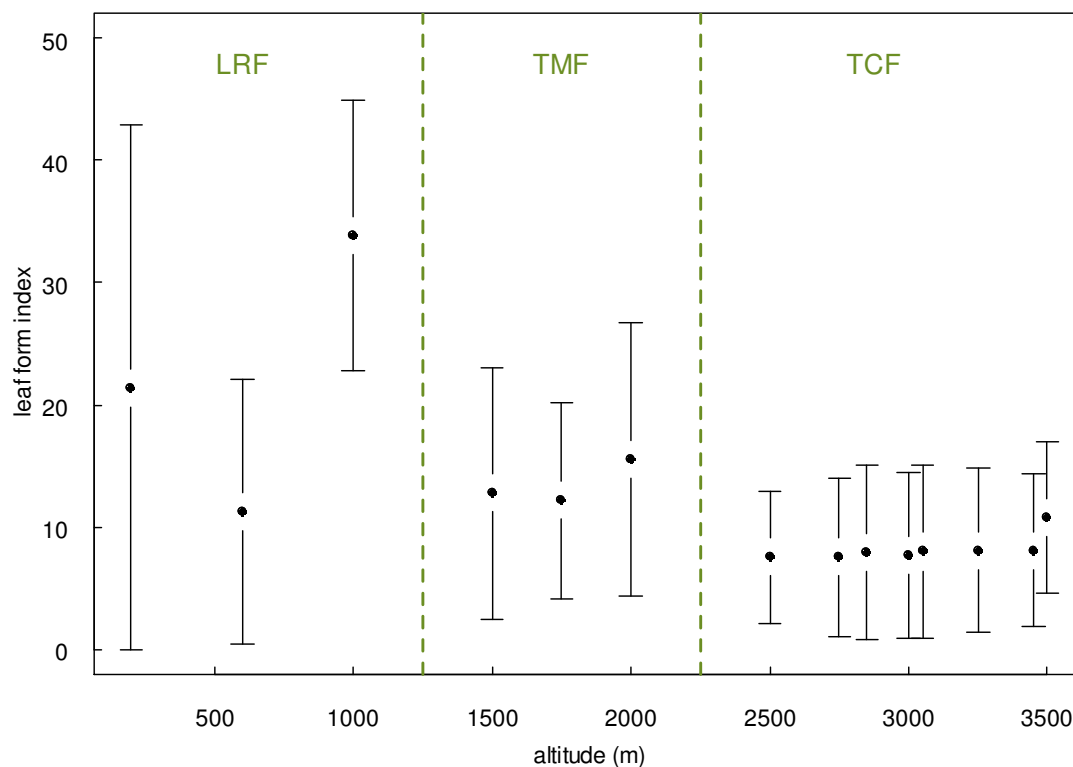


Figure 6.6. Change in leaf form index along transect, calculated as the mean and 95% CI of all species occurring at each altitude. Green lines show the altitudes of the boundaries for different ecological zones based on the analysis in Chapter 4.

For plants in the TCF and TMF the maximum volume of water contained in a tank was strongly correlated with diameter of the tank across all species ($r^2 = 0.8$, $p < 0.001$) (Figure 6.7). That all species in the TCF and TMF show the same linear relationship suggests that change in morphology with plant growth is optimised to maximise rainfall interception and water retention, as larger plants are less dependent on external water input and so better able to survive dry periods (Schmidt, Stuntz & Zotz 2001; Schmidt & Zotz 2001). In lowland sites there was no consistent relationship between plant diameter and volume across all species as a result of the greater diversity in plant form. It is likely that within species, size correlates with water-impoundment volume, but insufficient juveniles were collected for any species to test this. The

diversity of forms includes species with narrow tanks, which may be optimised to reduce evaporative losses and species with no significant phytotelm.

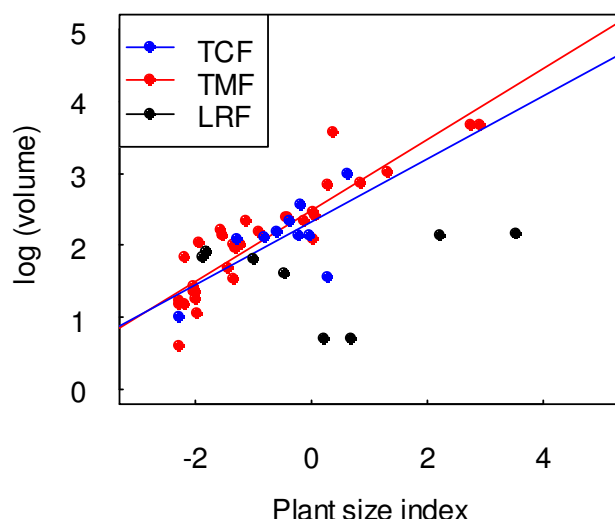


Figure 6.7. The relationship between tank volumes and tank size (measured as plant size index, a combination of diameter and depth of tank) measured in the field for twelve species in the three main forest types. Ecological zone abbreviations are: LRF - lowland rainforest; TMF - tropical montane forest; TCF - tropical montane cloud forest.

Taken together these results show that bromeliad tank design plays an important role in determining the ranges of plants. At highest altitudes, in the TCF, plant architecture seems to be more restricted, perhaps as a trade-off between water interception and storage. This leads to a number of species which have similar phytotelm morphology, particularly species in *Tillandsia* subgenus *Allardtia* (*sensu* Smith & Downs 1977) including *T. complanata* (high-altitude form – see Appendix A), *T. fendleri*, *T. rubella*, *T. stenoura*, *T. superba* and *T. wurdackii*. At lower altitude, in the LRF, there is greater variation in both plant and leaf architecture, perhaps as different species have different mechanisms to cope with increased water-stress. A higher evapotranspiration in the LRF means a large open phytotelm would lose water faster (Benzing 2000). These forms include the tall, narrow tanks found in *Billbergia* spp. and some *Aechmea* including the common *A. mertensii*. In the lowlands some species form an open loose phytotelm, which appears to have little or no water impounding capacity including *Aechmea longifolia* and to a lesser extent *Guzmania calothyrsus*. Alternatively the increase in diversity of

shoot morphology might reflect the increase in niches available in the tall-stature forests. The TMF appears to be intermediate between the TCF and LRF. In the TMF forest there are numerous large-phytotelm species that are also found in the TCF, including *Guzmania squarrosa* and *Tillandsia fendleri* but there is also an increase in the abundance of narrow-leaved species including the small *Racinaea schumanniana* and the large *Tillandsia longifolia*. The distribution of bromeliad morphologies over the three forest types is illustrated schematically in Figure 6.8.

6.5.3. ADAPTATIONS TO LOW WATER AVAILABILITY: CAM PHOTOSYNTHESIS

Of the 21 species from which samples were collected, seven species had carbon isotope ratios less negative than -20‰, indicative of CAM photosynthesis (Section 6.8). The other species all had ratios typical of C₃ plants. CAM species were abundant below 1000 m, no specimens were found above the 1000 m plot. Extensive searches from 1500 m and above showed no CAM species present. This was confirmed by examining available herbarium specimens from the locality. For this field site the highest altitude record of a species with CAM photosynthesis occurs at 1400 m (Zevallos 2008). The presence of CAM photosynthesis in the LFR is coincident with the longest dry periods for phytotelm bromeliads (Figure 6.5) as well as the warmest annual mean temperatures.

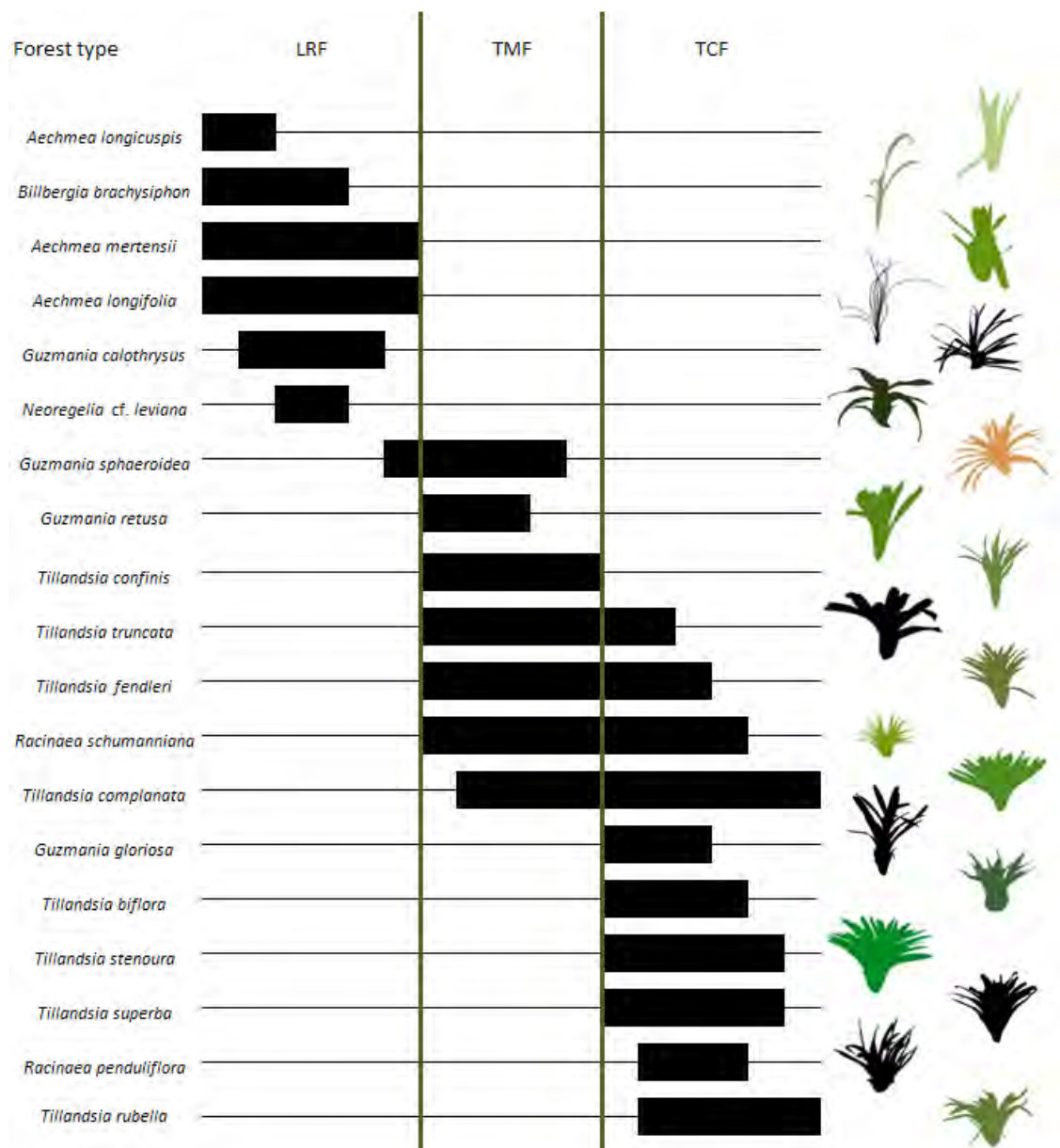


Figure 6.8. Typical profiles of 19 species shown with their altitudinal range and corresponding forest type. Plant profiles are not to scale.

6.6. DISCUSSION

Bromeliads are stress tolerance plants (Benzing 2000) and the separation of species' ranges along this altitudinal transect is expected to be the result of environmental tolerances, with direct inter-specific interactions rare. The species present separated into three discrete ecological zones, in a similar way to bromeliad species in a ridge-valley system in Colombian

cloud forest (Sugden 1981). Separation also occurs within habitats by the occupation of different parts of the canopy, although the canopy position appears vary continuously and no evidence was found for species separating into the discrete strata proposed by Johansson (1974). The variation in size and shape of epiphytic species in this transect corresponded to type III and type IV bromeliads in the physiognomic classification of Benzing (2000) with a fully developed phytotelm and roots that primarily function mechanically.

Phytotelm bromeliads are likely to spend a significant amount of time without water in their tanks, particularly in the juvenile and young adult growth stages, leading to potential water limitation of growth consistent with physiological studies (Schmidt & Zotz 2001; Laube & Zotz 2003; Zotz *et al.* 2010). The different shoot morphologies found in the three ecological zones suggest that adaptations to cope with water-stress are important in the restriction of species to the ecological zones. As epiphytic bromeliad growth is towards achieving a continuous supply of water (Schmidt, Stuntz & Zotz 2001; Schmidt & Zotz 2001) the strong relationship between size and volume across all species in the TCF and TMF suggests large phytotelm are the most efficient way of maximising water availability in the TCF. In addition large leaf areas, that maximise total plant leaf area, predicted as one aspect of the narrow leaf syndrome (Martorell & Ezcurra 2007) was present in species found in the TCF. Plants in the lowland rainforest had a greater diversity of forms, and a greater variation in anatomy; this may partly represent a greater number of niches in lowland rainforest compared to montane forest, and suggests that maximising water supply in the LRF may be more complex. The increased prevalence of phytotelm structures with narrow openings could be an adaptation to reduce water-loss through evaporation (Benzing 2000).

In the LRF the diversity of forms perhaps reflects niche differentiation, supported by the different strata occupied by species with CAM photosynthesis and species with C₃

photosynthesis typical of stratification seen at other sites (Bennett 1987; Benzing 2000; Arévalo & Betancur 2006; Flores-Palacios & Garcia-Franco 2006; Krömer, Kessler & Gradstein 2007). In the TMF, and even more so in the TCF, species have much similar shoot morphologies leading to questions about co-existence in the presence of niche overlap. While species did occupy a range of different canopy positions, possibly determined by light-availability (Pittendrigh 1948; Griffiths & Maxwell 1999), there was a significant overlap. Niche differentiation relating to biotic factors, such as pollinator may be important in separating niches (Krömer, Kessler & Herzog 2006). It could be that dispersal limitation reduces inter-specific competition in instances where species would normally occupy the same niche (Cascante-Marín *et al.* 2009). It is likely a combination of the factors discussed above lead to the co-existence of bromeliads with similar shoot morphology in the TCF and TMF.

CAM photosynthesis was present in epiphytic species below 1400 m, and terrestrial species below 1000 m. Rainfall is high in this part of Peru (Killeen *et al.* 2007), and species with CAM photosynthesis occupied more exposed niches in the forest below 1000 m, but not above that altitude. CAM photosynthesis is an important physiological adaptation for drought-avoidance (West-Eberhard, Smith & Winter 2011) and may allow species to avoid the drought stress caused by days without water in the phytotelm. The presence of CAM photosynthesis may also allow plants in the LRF to deviate from the strong cross-species relationship between size and volume found in all species in the TMF and TCF, as phytotelm storage may not be the most successful way to maximise water supply.

The relative importance of water availability, as opposed to temperature, in causing the range limits is difficult to determine without experimental manipulation, this study shows epiphytic bromeliads are well adapted to cope with water stress in their present locations using a suite of adaptations (Sugden 1981; Schmidt & Zotz 2001; Laube & Zotz 2003; Zotz, Laube &

Schmidt 2005; Kohler *et al.* 2007; Reyes-Garcia *et al.* 2008; Zotz *et al.* 2010; Obregon *et al.* 2011). While the interaction of epiphytes and water are important for understanding the response of epiphyte species to climate change, the influence of temperature is also likely to play a significant role, as it does for trees (Feeley *et al.* 2011). While temperature is predicted to keep increasing under most climate change scenarios, the effects of precipitation are less certain (O'Gorman 2012). For bromeliads this may lead to problems where regions with appropriate temperatures will have water-regimes for which the species are poorly adapted, potentially leading to local or global extinctions for species.

6.7. REFERENCES

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6.8. APPENDIX 5A: CARBON ISOTOPE RATIO DATA

Table 6.4. Specimen data for samples where carbon isotope ratios were measured

Species	Sample number	Carbon isotope ratio (‰)	Altitude (m)	Latitude	Longitude	Distance from ground ¹	Exposure ²	Johansen zone ³	Life stage ⁴	Habit ⁵	Host species ⁶
C3 species											
<i>Guzmania killipiana</i>		-31.0	1457	-13.0500	-71.5356	0.47	L	2	F	E	<i>Tapirira sp.</i>
<i>G. killipiana</i>		-30.7	1543	-13.0489	-71.5364	0.42	M	2	F	E	<i>Heisteria sp.</i>
<i>G. killipiana</i>		-29.5	1457	-13.0500	-71.5356	0.30	L	2	F	E	<i>Tapirira sp.</i>
<i>G. killipiana</i>		-26.8	1457	-13.0500	-71.5356	0.23	L	2	F	E	<i>Tapirira sp.</i>
<i>G. morreniana</i>		-29.8	2529	-13.0942	-71.5744	0.54	M	2	F	E	
<i>G. squarrosa</i>		-31.0	2686	-13.1779	-71.6074	0.10	ML	1	S	E	
<i>G. squarrosa</i>		-30.9	2742	-13.1062	-71.5891	0.43	L	2	S	E	
<i>G. squarrosa</i>		-30.8	2742	-13.1062	-71.5891	0.43	L	2	S	E	
<i>G. squarrosa</i>		-30.6	2742	-13.1062	-71.5891	0.47	L	2	S	E	
<i>G. squarrosa</i>		-28.7	2686	-13.1779	-71.6074	0.10	ML	1	S	E	
<i>G. cf. squarrosa</i>		-30.1	1526	-13.0489	-71.5371	0.66	M	4	S	E	<i>Inga sp.</i>
<i>G. cf. squarrosa</i>		-27.9	1524	-13.0487	-71.5363	0.77	H	3	S	E	<i>Coussapoa sp.</i>
<i>G. undulobracteata</i>		-32.8	2041	-13.0742	-71.5597	0.00	L	1	S	T	
<i>Mezobromelia</i>		-30.7	2742	-13.1062	-71.5891	0.27	L	2	S	E	
<i>M. pleiosticha</i>		-30.3	2742	-13.1062	-71.5891	0.19	ML	2	S	E	
<i>M. pleiosticha</i>		-30.2	2742	-13.1062	-71.5891	0.31	L	2	S	E	
<i>M. pleiosticha</i>		-27.9	2215	-13.1621	-71.5890	0.27	M	2	S	E	
<i>Racinaea penduliflora</i>		-30.5	3041	-13.1905	-71.5875	0.50	L	2	S	E	<i>Weinmannia crassifolia</i>
<i>R. penduliflora</i>		-30.4	3041	-13.1905	-71.5875	0.88	ML	2	S	E	<i>Clusia alata</i>
<i>R. penduliflora</i>		-30.3	3037	-13.1088	-71.5998	0.33	ML	2	S	E	<i>Weinmannia crassifolia</i>
<i>R. penduliflora</i>		-29.7	2739	-13.1061	-71.5891	0.78	MH	4	F	E	<i>Alchornea pearcei</i>
<i>R. penduliflora</i>		-29.6	3041	-13.1905	-71.5875	0.64	L	3	S	E	<i>Weinmannia crassifolia</i>
<i>R. penduliflora</i>		-28.2	3037	-13.1088	-71.5998	0.25	H	2	F	E	
<i>R. penduliflora</i>		-25.9	3037	-13.1088	-71.5998	0.33	H	2	S	E	
<i>Tillandsia buseri</i>		-30.3	3041	-13.1905	-71.5875	0.33	L	2	S	E	
<i>T. complanata</i>		-28.6	2820	-13.1756	-71.5951	0.89	M	4	F	E	
<i>T. complanata</i>		-28.5	3041	-13.1905	-71.5875	0.67	ML	2	F	E	<i>Bejaria aestuans</i>
<i>T. complanata</i>		-28.3	3041	-13.1905	-71.5875	0.18	L	2	S	E	<i>Clusia cretosa</i>

Species	Sample number	Carbon isotope ratio (‰)	Altitude (m)	Latitude	Longitude	Distance from ground ¹	Exposure ²	Johanssen zone ³	Life stage ⁴	Habit ⁵	Host species ⁶
<i>T. complanata</i>		-28.1	2820	-13.1756	-71.5951	0.33	L	3	F	E	
<i>T. complanata</i>		-27.9	3351	-13.1122	-71.6073	0.67	ML	3		E	<i>Weinmannia sp.</i>
<i>T. complanata</i>		-27.5	2742	-13.1062	-71.5891	0.47	L	2	S	E	
<i>T. complanata</i>		-27.4	3041	-13.1905	-71.5875	0.50	ML	2	F	E	<i>Weinmannia crassifolia</i>
<i>T. complanata</i>		-26.9	2742	-13.1062	-71.5891	0.33	L	2	F	E	
<i>T. complanata</i>		-26.2	2858	-13.1754	-71.5945	0.88	M	4	S	E	
<i>T. complanata</i>		-26.2	2742	-13.1062	-71.5891	0.40	L	3	S	E	
<i>T. complanata</i>		-25.3	3351	-13.1122	-71.6073	0.83	MH	2		E	<i>Weinmannia sp.</i>
<i>T. complanata</i>		-24.9	3351	-13.1122	-71.6073	0.83	MH	2		E	<i>Weinmannia sp.</i>
<i>T. fendleri</i>		-28.3	1489	-13.0487	-71.5363	0.76	H	4	F	E	<i>Inga heterophylla</i>
<i>T. ionochroma</i>		-25.7	3400	-13.2479	-72.1685	0.60	MH	4	F	E	
<i>T. patula</i>		-26.3	2788	-13.1730	-71.5853	0.43	H	3	S	E	
<i>T. rubella</i>		-29.6	3041	-13.1905	-71.5875	0.60	L	2	S	E	<i>Weinmannia crassifolia</i>
<i>T. rubella</i>		-29.6	3041	-13.1905	-71.5875	0.42	L	2	S	E	<i>Weinmannia crassifolia</i>
<i>T. rubella</i>		-29.1	3336	-13.1111	-71.6065	0.67	H	2	F	E	
<i>T. rubella</i>		-29.1	3260	-13.1107	-71.6041	0.33	MH	2	S	E	<i>Clusia cretosa</i>
<i>T. rubella</i>		-29.1	3336	-13.1111	-71.6065	0.67	H	2	S	E	
<i>T. rubella</i>		-29.0	3260	-13.1107	-71.6041	0.33	MH	2	S	E	<i>Axinaea sp.</i>
<i>T. rubella</i>		-28.8	3260	-13.1107	-71.6041	0.33	M	2	S	E	<i>Cyathea caracasana</i>
<i>T. rubella</i>		-28.7	3041	-13.1905	-71.5875	0.38	L	2	S	E	<i>Weinmannia crassifolia</i>
<i>T. rubella</i>		-28.3	3336	-13.1111	-71.6065	0.67	H	3	S	E	
<i>T. rubella</i>		-27.7	3260	-13.1107	-71.6041	0.33	HH	1	I	E	Fallen branch
<i>T. rubella</i>		-27.4	2896	-13.1738	-71.5881	0.25	H	3	S	E	
<i>T. rubella</i>		-27.3	3260	-13.1107	-71.6041	0.33	MH	2	S	E	<i>Miconia sp.</i>
<i>T. rubella</i>		-25.9	2863	-13.1759	-71.5849	0.25	H	2	S	E	
<i>T. stenoura</i>		-30.0	3041	-13.1905	-71.5875	0.55	ML	2	F	E	<i>Escallonia myrtilloides</i>
<i>T. stenoura</i>		-29.5	3041	-13.1905	-71.5875	0.64	LM	4	F	E	
<i>T. stenoura</i>		-28.8	2669	-13.1741	-71.5819	0.50	H	3	F	E	
<i>T. stenoura</i>		-28.3	3041	-13.1905	-71.5875	0.73	MH	3	F	E	<i>Weinmannia crassifolia</i>
<i>T. stenoura</i>		-27.0	2865	-13.1779	-71.5837	0.56	MH	4	F	E	
<i>T. superba</i>		-30.6	2742	-13.1062	-71.5891	0.47	L	3	F	E	
<i>T. superba</i>		-29.9	3041	-13.1905	-71.5875	0.67	M	4	S	E	
<i>T. superba</i>		-29.9	2742	-13.1062	-71.5891	0.40	L	3	F	E	<i>Weinmannia crassifolia</i>
<i>T. superba</i>		-29.7	2742	-13.1062	-71.5891	0.33	L	2	F	E	x

Species	Sample number	Carbon isotope ratio (‰)	Altitude (m)	Latitude	Longitude	Distance from ground ¹	Exposure ²	Johanssen zone ³	Life stage ⁴	Habit ⁵	Host species ⁶
<i>T. superba</i>		-29.7	2820	-13.1756	-71.5951	0.17	MH	2	F	E	
<i>T. superba</i>		-29.0	3041	-13.1905	-71.5875	0.67	M	4	S	E	<i>Weinmannia crassifolia</i>
<i>T. superba</i>		-28.1	3037	-13.1088	-71.5998	0.42	H	3	S	E	
<i>T. truncata</i>		-30.4	2530	-13.0935	-71.5737	0.75	M	2	S	E	
<i>T. truncata</i>		-27.4	2530	-13.0935	-71.5737	0.75	M	3	I	E	
CAM species											
<i>Aechmea longicuspis</i>		-16.2	203	-12.8368	-69.2933	0.40	H	1	S	E	garden
<i>A. longifolia</i>		-16.3	201	-12.8289	-69.2866	0.00	H	0	S	E	
<i>A. longifolia</i>		-15.6	951	-12.9596	-71.5660	0.90	H	4	F	E	<i>Tachigali polyphylla</i>
<i>A. mertensii</i>		-14.0	203	-12.8368	-69.2933	0.33	H	1	S	E	garden
<i>A. sp. A</i>		-16.8	211	-12.8299	-69.2704	0.61	L	3	S	E	<i>Acalypha triplinervia</i>
<i>A. sp. A</i>		-15.4	211	-12.8299	-69.2704	0.36	L	3	S	E	<i>Jacaranda obtusifolia</i>
<i>Billbergia cf. decora</i>		-16.6	185	-12.8423	-69.2925	0.51	LM	2	I	E	<i>Iriartea deltiodea</i>
<i>B. cf. decora</i>		-15.1	199	-12.8305	-69.2710	0.89	L	3	S	E	<i>Bertholletia excelsa</i>
<i>Neoregelia</i>		-15.8	205	-12.8333	-69.2838	0.27	H	1	S	E	
<i>Tillandsia paraensis</i>		-16.2	196	-12.8368	-69.2959	0.56	H	2	S	E	<i>Endlicheria formosa</i>

¹ Distance from ground calculated as proportion of distance from forest floor to canopy; ² exposure estimated in the field (H = high, M = medium, L = low); ³ from Johansson

(1974); ⁴ Life stages: F = flowering, I = immature, S = dispersing seed; ⁵ Habit: E = epiphyte, T = terrestrial; ⁶ Host tree identification taken from ABERG database

6.9. APPENDIX 5B: APPLICATION OF ZOTZ & THOMAS' MODEL

To estimate the number of days a 'typical' epiphytic bromeliad would have access to water stored in the phytotelm, the model from Zotz and Thomas (1999) was applied in the following way.

The plant chosen to be the 'model' was *Tillandsia complanata* Benth. as this was a common, typical species throughout most of the transect. The model equations are only reliable for individuals with a phytotelm diameter between 2 and 30 cm so these calculations were performed for plants of 30 cm phytotelm diameter. No accurate way of estimating the age of plants of this size was available but for this species 30 cm diameter represents a plant slightly smaller than typical flowering size. Zotz and Thomas (1999) present two model types relating to phytotelm morphology and *T. complanata* most closely matches the 'multi-chamber' type from the model as leaves mostly form independent stores of water.

Environmental variables were taken from climate stations adjacent to permanent research plots at three altitudes representing the three forest types (TCF – Wayqecha at 3000 m; TMF – San Pedro at 1500 m; LRF – Manu Learning Centre at 500 m). The variables temperature (daily minimum, daily maximum), precipitation (daily total), RH (daily minimum, daily maximum), windspeed (daily mean) and for Wayqecha total daily fog interception were used, and their sources are discussed in Chapter 2. The environmental variables were then used to calculate evapotranspiration and vapour pressure deficit (VPD) following the steps of Rapp (2010). Throughfall was calculated as 88% of total rainfall as discussed in Zotz & Thomas (1999).

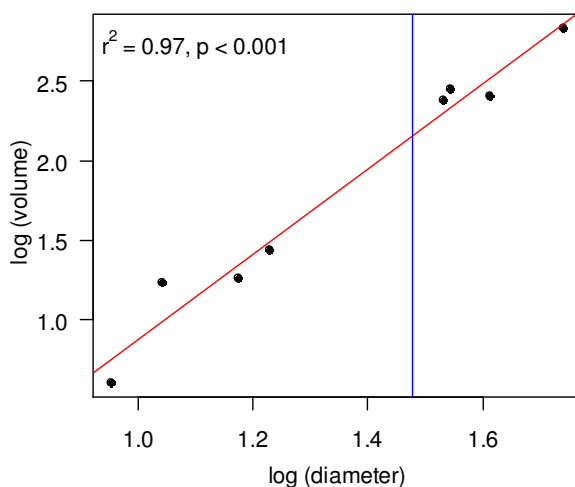


Figure 6.9. Volume - diameter relationship used to interpolate the volume of a 30 cm diameter individual of *T. complanata*. The vertical blue line shows the log of the diameter of a 30 cm individual.

To calculate the parameters of water content (C_{max}) and water surface area (S_{max}) of a filled phytotelm, along with transpiratory water loss (T) and projected rosette area (A_{proj}) volume estimates were taken from measurements made *in situ* using eight plants for which morphological characters were measured (Figure 6.9) and dry mass from 10 individuals. Conversions were carried out using the equations in *Table 1* of Zotz & Thomas (1999). The model parameters were then combined iteratively following equation (3) of Zotz & Thomas (1999) to estimate the total volume of water in the bromeliad tank on any given day. This equation is given below:

$$C_{day\ n} = C_{day\ n-1} + (FA_{proj}) - E_{tank} - T$$

where C is the tank water content, F is canopy throughfall, A_{proj} is the plant projected area, E_{tank} is evaporation from the tank and T is transpiration rate. The variable E_{tank} is calculated using the following equation:

$$E_{tank} = k S_{act} E_{pot}$$

where k is the ratio of evaporation from a phytotelm to evaporation from an equivalent area open surface, S_{act} is the actual water surface and E_{pot} is the potential evaporation.

7. ECOLOGICAL IMPORTANCE OF CAM PHOTOSYNTHESIS IN THE BROMELIACEAE

7.1 ABSTRACT

CAM photosynthesis is a carbon-concentrating mechanism found in about half of all bromeliad species and 6% of plant species globally. Despite its prevalence, few studies have shown how the presence of CAM photosynthesis influences large scale distribution patterns within a family. Digitised herbarium data and species lists for bromeliads across their distribution range were collected. A large data set of carbon isotope ratios allowed each species to be assigned as using C₃ or CAM photosynthesis. This data was used to demonstrate that terrestrial bromeliads with CAM photosynthesis occupy significantly drier sites than terrestrial bromeliads with C₃ photosynthesis. For epiphytic bromeliads, species with CAM photosynthesis occupy warmer, but not drier, sites than species with C₃ photosynthesis. This suggests species with CAM photosynthesis have an ecological advantage in higher temperature environments, and it is proposed this is due to lower photorespiration relative to C₃ species at high temperatures. This distinction is only apparent in epiphytes, which are pre-adapted to a water-stressed environment. Evidence is also presented that, in bromeliad species with C₃ photosynthesis, carbon isotope ratios become more negative with increasing rainfall and temperature, but not in CAM species. Species with carbon isotope ratios intermediate between C₃ and CAM photosynthesis occupy cooler, drier environments than species in either category. This study presents a new perspective on the ecological implications of CAM photosynthesis on broad ecological scales.

7.2 INTRODUCTION

Crassulacean Acid Metabolism (CAM) is a carbon-concentrating mechanism (CCM) present in approximately 6% of vascular plant species (Winter & Smith 1996; West-Eberhard, Smith & Winter 2011) that provides an alternative method of photosynthesis compared to the standard C₃ pathway in 90% of species. CAM photosynthesis is common in plants of arid and semi-arid ecosystems of the world, a biogeography that supports physiological studies showing the primary advantage is the increased water use efficiency (WUE) during photosynthesis (Winter & Smith 1996; Cushman 2001). There have been few comparative studies of the biogeography of CAM photosynthesis within a single family or on a continental scale.

The increasing availability of global datasets of environmental variables and of species distribution information mean that large-scale analyses are becoming increasingly common and allow for higher resolution and more extensive geographical analyses. Broad scale patterns in plant diversity (Kreft & Jetz 2007) have already been tested, and similar studies of physiology are becoming more prevalent (Olson *et al.* 2009). The factors determining plant distribution at certain scales can be very different and are often independent (Brown, Jennings & Clements 2003; Chase & Myers 2011), and broad-scale patterns complement those from local-scale studies. Therefore, a complete picture of the distribution of a species is only possible once the broad-scale biogeography is placed in the context of the local factors influencing distribution (Soberón 2007; Chase & Myers 2011).

In the Bromeliaceae, 44% of the 1873 species measured (representing approximately 60% of the family) demonstrate CAM photosynthesis (Crayn, Winter & Smith 2004). This classification is based on the strongly bimodal distribution of carbon isotope ratios, with species with an intermediate values (-20‰ to -23‰) being comparatively rare (Crayn, Winter & Smith 2004). This allows bromeliads to be classified in a binary manner as showing either

CAM or C₃ photosynthesis (C₄ photosynthesis and the associated Kranz anatomy have never been found in the Bromeliaceae.). The Bromeliaceae have a large number of physiological adaptations to stressful growing conditions, and the evolution of CAM photosynthesis is one of a suite of adaptations allowing the occupation of many and varied niches (Griffiths *et al.* 1986; Smith 1987; Benzing 2000; Givnish *et al.* 2011). CAM photosynthesis represents an important physiological adaptation, and may have been responsible for several evolutionary radiations in the family (Quezada & Gianoli 2011). However, other factors including the tank habit, absorptive foliar trichomes, special nutrient economies and reduction of root function act in different combinations to determine the potential niche of each species. Although CAM photosynthesis is only found in plants of the epiphytic growth habit in orchids (Silvera *et al.* 2009), it is found in both epiphytic and terrestrial bromeliads (Crayn, Winter & Smith 2004).

The most detailed study of bromeliad distributions in relation to their physiology was carried out over a number of years in Trinidad. Studies in the forests of Trinidad showed that the CAM species tend to occupy more exposed microclimates, mostly due to their ability to tolerate high light intensities (Pittendrigh 1948; Griffiths & Maxwell 1999) and, across the island, were more prevalent at drier sites (Griffiths & Smith 1983). These patterns are the same as those found in Mexican forests, where the proportion of CAM species decrease as both altitude and annual precipitation increase (Hietz, Wanek & Popp 1999). In the lowest-precipitation forests of Chamela, Mexico (770 mm year⁻¹ long-term average annual precipitation) only CAM species of Bromeliaceae are able to survive the climate (Reyes-Garcia *et al.* 2008). In the Atacama desert regions of Peru and Chile, CAM species in the genus *Tillandsia* dominate the drier regions, and a few C₃ species that grow in this biome are restricted to areas with heavy fog and dew deposition (Rundel & Dillon 1998). Despite the strong association with aridity, CAM species can also be present in wet biomes. Two studies looking at the presence of CAM species in the wet climate of rainforests in Costa Rica and

Panama (total annual rainfall >4000 mm) showed that CAM species are present, although not abundant, in a range of niches (not limited to apparently dry niches) despite the high annual rainfall (Carter & Martin 1994; Pierce, Winter & Griffiths 2002b). Since rainfall is only one aspect of water availability, it is not clear if these truly are 'wet' environments, and quantifying potential or actual evapotranspiration would give a clearer picture, along with microclimate data. Pierce *et al.* (2002b) showed that a greater CO₂ uptake period in *Aechmea dactylina* (CAM) compared to *Werauhia capitata* (C₃) allows for higher carbon gain. Carter and Martin (1994) speculated that night-time CO₂ uptake will allow species with CAM photosynthesis to avoid competition with other plants for CO₂ during the light period, but there is little evidence to show that CO₂ depletion during the daytime in such environments is sufficient to limit photosynthesis. The importance of historical migration and dispersal are also discussed in the context of these high rainfall forests, with Pierce *et al.* (2002b) suggesting that CAM is a recent invasion of wet rainforests and could become more prevalent over time, although phylogenetic reconstruction indicates that CAM photosynthesis has been present in the Bromeliaceae for at least the last ten million years (Givnish *et al.* 2011), so this argument seems tenuous. Re-evaluation of climate data to consider evapotranspiration, as well as rainfall, may show these forests to be drier than predicted.

Many studies at a local scale show a strong relationship between CAM photosynthesis and total annual precipitation (Griffiths & Smith 1983; Hietz, Wanek & Popp 1999), drought intensity (Graham & Andrade 2004) and humidity or fog interception (Rundel & Dillon 1998). The physiological basis of this is the reduced water loss during carbon exchange associated with nocturnal stomatal opening. CAM photosynthesis is up to 10 times more efficient in water-use per carbon fixed than C₃ photosynthesis. Lüttge (2004) cites carbon fixed per water lost (A:E) ratios of 6-30 x 10⁻³ mol CO₂ fixed : mol H₂O transpired for CAM plants compared to 0.6-1.3 x 10⁻³ mol CO₂ fixed : mol H₂O transpired for C₃ plants. The increased quantum yield of C₄

photosynthesis (relative to C_3 photosynthesis) at higher temperatures is believed to be less important in plants with CAM photosynthesis because of the higher cost of the carbon-concentrating step in CAM photosynthesis (Nobel 1991), although this not been tested empirically.

CAM photosynthesis has strong parallels to C_4 photosynthesis. A large number of biogeographical studies of C_4 photosynthesis exist, especially in the Poaceae (e.g. Teeri & Stowe 1976; Cabido *et al.* 2008; Edwards & Still 2008; Osborne & Freckleton 2009). These studies have shown that the C_4 CCM is an adaptation to high temperatures and low rainfall, but may also provide ecological benefits in environments with low nutrient availability and high salinity. The first studies in the Poaceae of North America found a remarkable positive correlation between the proportion of C_4 grass species in a flora and the growing season (July) temperature (Teeri & Stowe 1976). This was demonstrated to be a result of the decrease in quantum efficiency caused by increasing photorespiration in C_3 grasses (Ehleringer 1978). The CCM of C_4 plants prevents any increase in photorespiration, meaning at higher temperatures they achieve a higher quantum yield than C_3 species, overcoming the extra energetic cost of the initial carbon-concentrating stage.

The advantages of a CCM in warmer environments have rarely been examined in CAM species. Partly this is because the energetic cost of CAM photosynthesis is significantly higher than that of C_4 photosynthesis (Winter & Smith 1996). This means the compensation point required to equalise quantum yield is predicted to be significantly higher. Studies that have examined the effects of temperature on CAM photosynthesis have focused mainly on the biochemistry of the pathway; with Wagner and Larcher (1981), for example, showing that day-time remobilization of malate was reduced in an approximately linear way from 40 °C down to 15 °C. In the environment this effect was confirmed for plants in Papua New Guinea, with CAM

species decreasing in abundance as temperature decreased (Earnshaw *et al.* 1987). Studies of CAM photosynthesis in cultivated pineapple (*Ananas comosus*, subfamily Bromelioideae) have shown that optimum productivity is achieved with day temperatures of 30 °C and night temperatures of 15 °C (Benzing 2000), but there have been few studies of the temperature dependence of CAM activity in bromeliads in the field.

There has been recent interest in variation in carbon isotope ratios across large scales, with an emerging strong link between annual precipitation and carbon isotope ratios, and a much smaller, but disputed, degree of influence of temperature (Diefendorf *et al.* 2010; Kohn 2010; Freeman *et al.* 2011; Kohn 2011). The large distribution and isotope datasets presented here allow testing of the relationship between climate and carbon isotope ratios, although isotope samples were typically taken from only a single plant of each species (Crayn, Winter & Smith 2004). The assumption that carbon isotope ratios show little variation within a species may be reasonable for slow-growing epiphyte species (Griffiths *et al.* 1986; Smith *et al.* 1986; Griffiths *et al.* 2007), but the results will be less precise than if the isotope ratio was associated with a plant at each location.

In this study I look at the biogeography of the Bromeliaceae, with specific reference to the presence of CAM photosynthesis in both the epiphytic and terrestrial species. With a large data set of digitised herbarium specimens I use species distribution modelling to examine habitat suitability across the distribution range of the family, combined with logistic regression modelling, to try to confirm the importance of water availability in the ecological distribution of CAM photosynthesis, and to test for an effect of temperature. I then use a separate data set of species lists to see if any patterns are consistent, using linear and spatial modelling. Additionally, I delimit novel biogeographic regions based on bromeliad species composition and look for broad scale patterns in carbon isotope ratios amongst species of bromeliad.

7.3 METHOD

7.3.1 DISTRIBUTION DATA

Species distribution data was based on records published in online herbaria and published distribution maps (see Section 7.8 Appendix 2 for full citations). Records were collected covering 2054 species. Only specimens with coordinate accuracy of 5 minutes or better were used. Records were visualised in GIS software (ArcGIS Version 10.1, ESRI, Redlands, California) and those that were incorrectly georeferenced (e.g. in the ocean), and those from cultivated plants, including all records of the widely cultivated *Ananas comosus* (Pineapple), were discarded. Taxonomy was updated to match Luther (2008) using Marks (2009) to update synonyms. To test for disparity in sampling between countries the number of known species in each country was taken from the Encyclopaedia of Bromeliads (Gouda, Claessen & Gouda 2009). The data in this section represents a snapshot from November 2010, and more data is constantly becoming available online.

The accuracy of georeferencing was checked by assessing the provided coordinate precision. Over 95% of the data was reported with coordinates with a precision of 1 minute or less, so an accuracy of 1 minute was taken as the highest resolution of any analysis. Data accuracy was then tested on a random selection of 100 species in the most common genera, *Tillandsia* and *Aechmea*. For randomly selected species, the level 1 administrative zone (typically state) and country were compared for the herbarium voucher and the provided geographic coordinates. At this scale, 2 of 100 records were incorrectly placed, with disparities between the data label and map location that had no obvious explanation. Other discrepancies occurred where plants were located along borders or where geographic boundaries had changed since the time of collection, but these were taken to be accurately georeferenced if they occurred within 5 minutes of the correct state. One hundred specimens were then taken from Peru and the accuracy of their distribution assessed to the lowest political division available

(province). Here it was found that 4 % of georeferenced coordinates occurred in a different province from the one listed on the herbarium voucher, without obvious explanation for the discrepancy. This level is lower than the value found for legumes (Yesson *et al.* 2007), but is likely to result from a more stringent exclusion process in the data set before accuracy analysis was performed. It was decided that while 4 % is high, the noise thereby created should not significantly influence the results.

Bromeliad species lists were taken from published Flora and special herbarium collections from parks and reserves (Table 7.1). The Floras used in the analysis were selected using the following criteria; areas which were too large (over 5000 km², with the exception of the homogenous Yasuní National Park in Ecuador) or with too much topographic variation were excluded, as were islands, due to the complication of dispersal and colonisation issues. Areas at the latitudinal extremes of the distribution of the family were excluded as they were all species poor, and persistence is likely to be a result of specialised micro-habitats. At these latitudinal extremes of the distribution of the family, the bromeliad floras are dominated by *Tillandsia* subgenus *Diaphoranthema*, which are all species with CAM photosynthesis, in itself an interesting observation (Smith & Downs 1977; Till 1992). A total of 48 Floras were included in the final analysis (Table 7.1). Data on the photosynthetic pathway of species in the flora was taken from Crayn *et al.* (2004) and used to calculate the proportion of species in each list with CAM photosynthesis. Where no data was available for a species it was excluded from the analysis. There is the possibility that collections are incomplete, but it was assumed the incomplete records were not biased in favour of either photosynthetic pathway. This assumption was tested taking 46 randomly generated sets of 10 species from the entire family and comparing the proportion of CAM species in the Flora data set (mean ($\pm$ 1 S.D.) = 0.58 ± 0.24) to the proportion of CAM species generated at random (mean ($\pm$ 1 S.D.) = 0.55 ± 0.07). The two values do not differ significantly ($d.f. = 44, t = 0.79, p = 0.44$).

Table 7.1. Details of geographic locations with species lists for Bromeliaceae.

Country	Location	Centre point		Survey year	Area (km ²)	No. of bromeliad species		
		Lat	Long			CAM	C ₃	Unkn
Bolivia	Cordillera Mosetenes ¹	-16.2	-66.4	2004	2600	14	1	0
Brazil	Massambamba Protected Area ²	-22.9	-42.2	2008	1	6	1	0
Brazil	Una Biological Reserve ³	-15.2	-39.1	2008	70	21	9	6
Brazil	Reserva Biológica Estadual da Praia do Su ⁴	-23.2	-44.3	2006	36	12	4	0
Brazil	Ducke Reserve, Manaus ⁵	-3.0	-59.9	1999	100	9	4	1
Brazil	Ilha do Mel ⁶	-25.5	-48.4	2001	27.6	4	12	0
Brazil	Prainha Municipal Park, Rio de Janeiro ⁷	-23.0	-43.5	2006	1.3	13	3	0
Brazil	Restinga de Jurubatiba National Park ⁸	-22.3	-41.7	2000	148.6	9	1	0
Brazil	Serra dos Orgões National Park, Rio de Janeiro ⁹	-22.3	-43.3	2008	106	19	15	1
Brazil	Tijuca National Park, Rio de Janeiro ⁹	-23.0	-43.3	2008	32	31	11	4
Brazil	Itatiaia National Park ⁹	-20.3	-43.6	2008	300	16	7	2
Brazil	Monte Pascoal National Park ³	-16.9	-39.3	2008	140	11	6	2
Brazil	The Serra do Teimoso Natural Reserve ³	-15.2	-39.5	2008	2	18	3	2
Brazil	Serra da Piadade Nature Reserve ¹⁰	-19.7	-43.7	2001	19.5	8	8	2
Brazil	Parque Estadual de Ibitipoca, Minas Gerais ¹¹	-21.7	-43.8	2007	19.2	13	11	4
Brazil	The Serra Grande Forest, Serra do Condurú State Park ³	-14.4	-39.0	2008	113	8	4	1
Brazil	Itajura Municipal Park, Minas Gerais ¹²	-20.9	-42.5	2008	2	16	9	2
Colombia	Santa Maria de Chivor, Boyaca ¹³	4.9	-76.3	2008	500	4	18	0
Colombia	Meta ¹⁴	-1.0	-71.7	2000	1000	6	6	0
Colombia	Amacayacu ¹⁵	-3.4	-70.0	2005	2930	10	3	0
Colombia	Serrania de Macuira National Park ¹⁶	12.2	-71.5	1979	0.1	8	1	0
Costa Rica	La Selva Biological Station ¹⁷	10.4	-834.0	2008	15	12	18	0
Costa Rica	Palo Verde Biological Station ¹⁸	10.4	-85.4	2009	190	3	1	0
Costa Rica	Monteverde Cloud Forest ¹⁹	10.3	-84.8	1993	0.2	0	5	0
Ecuador	Bilsa Biological Station ²⁰	-1.0	-79.0	2009	30	5	16	1
Ecuador	San Francisco Biological Reserve ²¹	-34.0	-79.1	2002	10	7	66	7
Ecuador	Jatun Sacha Biological Station ²⁰	-1.1	-77.6	2009	20	12	5	1
Ecuador	Rio Palenque Science Centre ²²	-0.5	-79.3	1978	1.7	5	13	0
Ecuador	Yasuní National Park ²⁰	-1.0	-76.0	2009	9820	16	2	0
French Guiana	Saul River Basin ²³	3.7	-53.3	2000	1402	17	14	1
Guiana	Kaieteur National Park ²⁴	5.2	-59.5	2007	627	9	23	1
Guiana	Iwokrama Forest Conservation Park ²⁵	4.5	-59.0	1997	3600	4	5	0
Mexico	Sierra de Manantlán Biosphere Reserve ²⁶	19.6	-104.3	1995	1400	19	10	5
Mexico	Soconusco State ²⁷	15.3	-92.7	2006		17	11	0
Mexico	San Martin Tuxtla Volcano, Veracruz ²⁸	18.3	-94.8	2007	85	15	12	4
Mexico	La Selva Baja Caducifolia Reserve, Veracruz ²⁹	19.6	-96.8	2007	39.7	13	2	0
Mexico	Chichinautzin Biological Corridor ³⁰	19.1	-99.2	2009	53.96	11	7	1

Country	Location	Centre point		Survey year	Area (km ²)	No. of bromeliad species		
		Lat	Long			CAM	C ₃	Unkn
Mexico	Polygon 5 El Triunfo reserve ³¹	15.8	-93.1	2008	4.5	7	9	0
Peru	Cocha Cashu Biological Station ³²	-11.8	-71.6	2005	5	5	2	0
Peru	ACEER Canopy Walkway, Amazon Biosphere Reserve, Iquitos ³³	-3.3	-72.9	1997	5	13	3	0
Panama	Barro Colorado Island Nature Reserve ³⁴	9.2	-79.6	1978	15.6	8	10	0
Panama	Boca del Toro River Valley ³⁵	9.0	-82.5	2008	3202	6	13	0
Venezuela	Guaramacal National Park, Portuguesa and Trujillo States ³⁶	9.2	-70.2	2000	21.5	1	14	0
Venezuela	San Carlos de Rio Negro River Basin ³⁷	1.9	-67.1	2008	c. 1000	14	6	0

References: ¹(Kromer & Kessler 2004), ²(Rocha-Pessoa *et al.* 2008), ³(New York Botanical Gardens), ⁴(Nunes-Freitas *et al.* 2006), ⁵(Ribeiro *et al.* 1999), ⁶(Kersten & Silva 2001), ⁷(Bocayuva *et al.* 2006), ⁸(Cogliatti-Carvalho *et al.* 2001), ⁹(Rio de Janeiro Botanic Gardens 2010), ¹⁰(Marques & Filho 2008), ¹¹(Monteiro, Neto & Forzz 2007), ¹²(de Paula & Guarçoni 2007), ¹³(Betancur & O-Zethelius 2005), ¹⁴(Benavides *et al.* 2005), ¹⁵(Lleras & Cruz 2005), ¹⁶(Sugden & Robins 1979), ¹⁷(Organizacion para Estudios Tropicales 2007), ¹⁸(Organizacion para Estudios Tropicales 2010), ¹⁹(Ingram & Nadkarni 1993), ²⁰(Missouri Botanical Garden), ²¹(Bussmann 2001), ²²(Dodson & Gentry 1978), ²³(Cremers *et al.* 1996), ²⁴(Kelloff & Funk), ²⁵(Clarke, Funk & Hollowell 2001), ²⁶(Vásquez *et al.* 1995), ²⁷(Santiago *et al.* 2006), ²⁸(Krömer & Acebey 2007), ²⁹(Campos, Aranda & Hurtado 2007), ³⁰(Esparza, Serna & Ferrari 2009), ³¹(Meléndez, Farrera & Sermiento 2008), ³²(Duke University), ³³(Murray, Lowman & Wittman 1997), ³⁴(Croat 1978), ³⁵(Laube *et al.* 2008), ³⁶(Dorr, Stergios & Smith 2000), ³⁷(B. Holst, unpublished data).

7.3.2 PHOTOSYNTHETIC PATHWAY CLASSIFICATION

The photosynthetic pathway was classified based on carbon isotope ratios for 1400 species collected by Crayn, Winter and Smith (2004). Carbon isotope ratios more positive than -20‰ was classified as CAM photosynthesis, ratios more negative than -20‰ were classified as C₃ photosynthesis. Growth habit is typically conserved within genus, so each genus was classified as either epiphytic (E) or terrestrial (T), depending on the dominant growth habit of the genus described by Luther & Norton (2008). Lithophytic species were classified as epiphytes as they only use their substrate for mechanical support. As carbon isotope ratio is influenced by the environment the values the carbon isotope ratio of each species, as reported in Crayn *et al.* Crayn, Winter and Smith (2004), were placed into 1‰ groups and compared to the environmental conditions of that species (the mean of all distribution records for that species), to look for environmental patterns in carbon isotope ratios.

7.3.3 PUTATIVE DETERMINANTS AND CLIMATE DATASETS

High-resolution gridded datasets (30 arc minute precision) were used as the environmental variables in the modelling. Monthly rainfall and monthly maximum and minimum temperature, along with 19 biologically relevant derivatives of temperature and rainfall, were taken from the WorldClim database (Hijmans *et al.* 2005). In this data set temperature and precipitation seasonality are calculated as the coefficient of variation of daily precipitation averaged over the year; this meaning is used throughout this Chapter. Data on actual evapotranspiration (AET), potential evapotranspiration (PET) and annual water balance (WB) was taken from Ahn & Tateishi (1994). Data on relative humidity (RH) and the number of days with rainfall ('wetdays') was taken from New *et al.* (2002). The maximum climatological water deficit (MCWD) was calculated as the sum of the rainfall deficit when precipitation was less than 100 mm month⁻¹ as described in Aragão *et al.* (2007), summed for the longest period of consecutive months when the rainfall was below the threshold.

7.3.4 DELIMITING BIOGEOGRAPHIC REGIONS

Biogeographic regions delimited using local bromeliad composition were created using the framework set out in Kreft & Jetz (2010). Comprehensive expert range maps are not available for the Bromeliaceae, so the input data was taken to be presence or absence of species in 2° grid cells based on herbarium collection localities, which give a good balance of species numbers with geographic precision. The ecoregions were then delimited using the non-hierarchical clustering method, k-means, implemented in the PAST software (Hammer, Harper & Ryan 2001). K-means were used to produce 2 clusters, and these groups were then split further using k-means within the groups until a reasonable balance of the number of areas and size of each area was reached. The presence of widespread species from *Tillandsia* subgenus *Diaphoranthema* in grid cells with few species overall gave rise to some geographically separate

regions that clustered together, these were examined manually and removed from the data set if only species from this subgenus were present.

7.3.5 BIOCLIMATIC MODELLING

Bioclimatic modelling was carried out using maximum entropy niche modelling (MAXENT) method of climate envelope fitting, implement in the MAXENT software (Phillips & Dudik 2008). The MAXENT algorithm predicts the climate envelope by using presence-only data points, and has been shown to perform well compared to other bioclimatic niche models (Elith & Graham 2009). The models were produced using nine climate variables from the WorldClim data set (Hijmans *et al.* 2005). The herbarium data set was used to provide input points, with the records classified into groups of epiphytes (including lithophytes) and terrestrials, and then subdivided into CAM species and C₃ species. Data was partitioned randomly, with 10% of each taxon excluded from the model training process and used as test data to validate the model. The models were run for 50 iterations per species and the results averaged. The model accuracy was assessed using the receiver operator characteristic (ROC) which compares the model accuracy to a random process, with the area under the curve (AUC) statistic providing a good assessment of model accuracy.

The output of the MAXENT model was summarised by 1° grid cells. The average suitability of each grid cell was modelled using linear and quadratic models to predict habitat suitability based on annual precipitation, precipitation of the driest three months, and mean annual temperature of the grid cell for the four models. A comparison of habitat suitability was also made within the biogeographic regions delimited with the distribution data. Differences between groups within habitats was calculated using the post-hoc Tukey's Honest Significant Difference (HSD) test at $\alpha = 0.01$ to allow for unequal group sizes.

7.3.6 STATISTICAL ANALYSIS

The mean climate and climate variability of each species were calculated by taking the mean of all records occurring in separate 2.5 arc minute grid cells; species means were then summarised by group (CAM/C₃ and terrestrial/epiphyte). Different environmental variables were then analysed using a general linear model (GLM) with binomial distribution of error terms to estimate the parameters of a logistic regression model (LRM), in the R statistical software package (R Core Development Team 2005). In this way it was possible to predict if a species was more likely to be CAM or C₃ based on its environment. McFadden's rho-squared (ρ^2) was calculated to approximate the ordinary least squares (OLS) standard coefficient of determination (Terribile *et al.* 2009). This analysis was carried out separately for both the terrestrial species and the epiphytic (including lithophytic) species.

The proportion of species with CAM photosynthesis in local floras was tested for correlation with climate variables. Variables that showed non-normality were log transformed. The proportion of species with CAM photosynthesis was transformed using the arcsine-square root transformation. The analysis was performed in the S.A.M. software (Rangel, Diniz-Filho & Bini 2006). Due to the uneven spatial distribution of points the data set showed significant spatial autocorrelation. To test individual variables, correlation coefficients with corrected degrees of freedom were used to remove the effects of spatial autocorrelation using Dutilleul's method (Dutilleul 1993). The p value for the spatially corrected degrees of freedom is reported as p^* to distinguish it from the uncorrected p -values. Significance was tested against the Bonferroni-corrected significance level of $\alpha = 0.0028$, to account for the 18 variables tested.

A combined predictor model was then developed using the best-fitting variables from four categories. All variables from the four categories were put into a multi-model selection procedure in S.A.M. (Rangel, Diniz-Filho & Bini 2010). Running a single model selection procedure was too computationally intensive, so the following selection procedure was

implemented. The variables from the best-performing single-predictor model, based on Akaike's Information Criteria (AIC), from each category were then combined and the model selection procedure was run again with the combination of the best variables (Johnson & Omland 2004). The categories used were temperature, rainfall, seasonality and water-energy models and non-climate variables. The output of the model selection procedure is included in Section 7.7. The best model from these variables was analysed with and without the biogeographic regions as a proxy for the phylogenetic influence on the data. The data was modelled in four combinations. A simple GLM was used, including and excluding the biogeographic regions. The different models provide a proxy for the influence of any geographic structure due to historical constraints on the dispersal of species and genera. To account for spatial autocorrelation, data was modelled using a spatial error simultaneous autoregressive model (SAR) (Dormann *et al.* 2007). The difference in the variation between the GLM and the SAR models shows the importance of space as an explanatory variable. Spatial autocorrelation in the model residuals of all models was checked using Moran's *I* values (Dormann *et al.* 2007). The amount of variation explained by each model was compared using the deviance using the same method as Kreft and Jetz (2007).

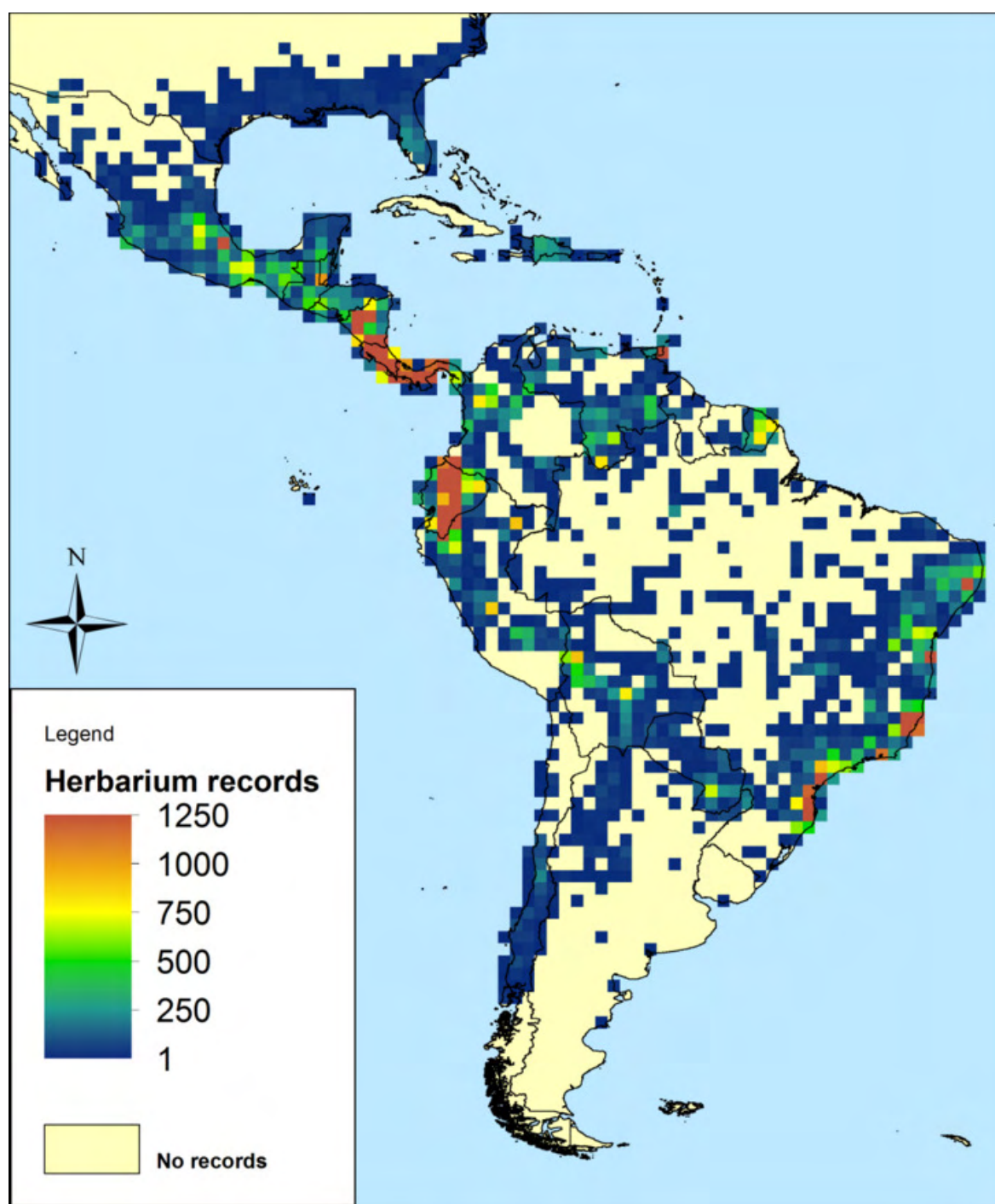


Figure 7.1. Density of herbarium records used in this study. The number of records in each 1° grid square is shown. Some species are represented by more than 1 record in each grid square.

7.4 RESULTS

A total of 31 239 georeferenced specimens of Bromeliaceae were selected for inclusion in the final analysis. The specimens were not sampled equally from all countries even when taking into account the size of the native bromeliad flora for each country (Table 7.2 and Figure 7.1). Some countries have over 100 % of species sampled because the best comparative species list at the country level are based on the *Flora Neotropica* (Gouda, Claessen & Gouda 2009) which was published in the 1970s. The records covered the entire geographic range of Bromeliaceae and including 55 of the 58 currently accepted genera (Givnish *et al.* 2011). Species with both C₃ and CAM photosynthesis were represented across their entire known geographic ranges.

Table 7.2. Number of records and species taken from online datasets compared to country area and bromeliad species from the country from (Gouda, Claessen & Gouda 2009).

Country	Number of records in data set	Number of species in data set	Country area (km ²)	Bromeliad species in national Flora	% species from national Flora in data set
Argentina	289	55	2 766 000	110	50
Belize	236	49	23 000	38	129
Bolivia	1137	267	1 099 000	219	122
Brazil	7241	696	8 515 000	1127	62
Chile	283	20	757 000	28	71
Colombia	1120	330	1 142 000	414	80
Costa Rica	4218	201	4 608 000	113	178
Ecuador	5040	540	272 000	328	165
El Salvador	181	49	21 000	36	136
French Guiana	554	54	84 000	29	186
Guatemala	225	75	109 000	116	65
Guiana	43	25	215 000	52	48
Honduras	235	82	112 000	71	115
Mexico	3029	242	1 973 000	341	71
Nicaragua	1932	104	130 000	46	226
Panama	1536	157	76 000	109	144
Paraguay	448	50	407 000	56	89
Peru	1376	314	1 285 000	404	78
Suriname	44	24	164 000	39	62
Trinidad and Tobago	273	35	5 000	59	59
United States	647	20	9 827 000	22	91
Uruguay	1	1	176 000	19	5
Venezuela	1371	264	916 000	343	77

7.4.1 BIOGEOGRAPHY

Using the methods of Kreft and Jetz (2010) eight different biogeographic regions were delimited *de novo* for the Bromeliaceae based on unique species compositions (Figure 7.2). Similarity matrices showed rapid turnover of species in short geographic space (high β -diversity) that results from actual species turnover and in part from incomplete knowledge of species distributions. The eight geographic regions were labelled as Andes and Amazon (AND; including the Andes in Peru, Ecuador, Bolivia and also the central Amazon), Northern South America (NSA; including Venezuela, French Guiana, Panama and Costa Rica), Atlantic Rainforest (ATL; South-east Brazilian and Uruguayan coasts), Caribbean (CAR; Caribbean islands, Florida and coastal areas in Central America), Chile (CHI), Guiana Shield (GUI), Mexico (MEX; including most of Central America), North America (NAM), Pleistocene Dry Arc (PDA; including the southeast of Brazil inland from the coast, with Paraguay and parts of Bolivia, from Pennington, Prado and Pendry (2000) and Pennington *et al.* (2004) who demonstrate a band of SDTF across this region in the Pleistocene leading to distinctive patterns in speciation of SDTF species). These regions correspond well with other known biogeographic regions (e.g. Udvardy 1975; Ellenberg 1981; Pennington, Prado & Pendry 2000; Olsen *et al.* 2001) and the regions published by Givnish *et al.* (2011) based on bromeliad evolution.

Table 7.3. Estimated percent contribution of climate variables to MAXENT model output calculated using the jackknife measure of variable importance.

Variable	Percent contribution to MAXENT model			
	Terrestrials		Epiphytes	
	C ₃	CAM	C ₃	CAM
Annual mean temperature	5.3	2.4	2.3	4.8
Temperature seasonality	68.0	71.4	65.2	49.5
Temperature of the warmest month	5.1	8.6	6.1	10.1
Temperature of the coldest month	0.9	0.4	0.2	19.6
Annual temperature range	13.1	6.6	14.9	1.1
Annual precipitation	0.5	0.7	0.1	0.5
Precipitation of the driest month	2.1	2.2	1.7	8.7
Precipitation of the wettest month	3.4	6.8	8.9	4
Precipitation seasonality	1.6	0.9	0.5	1.8

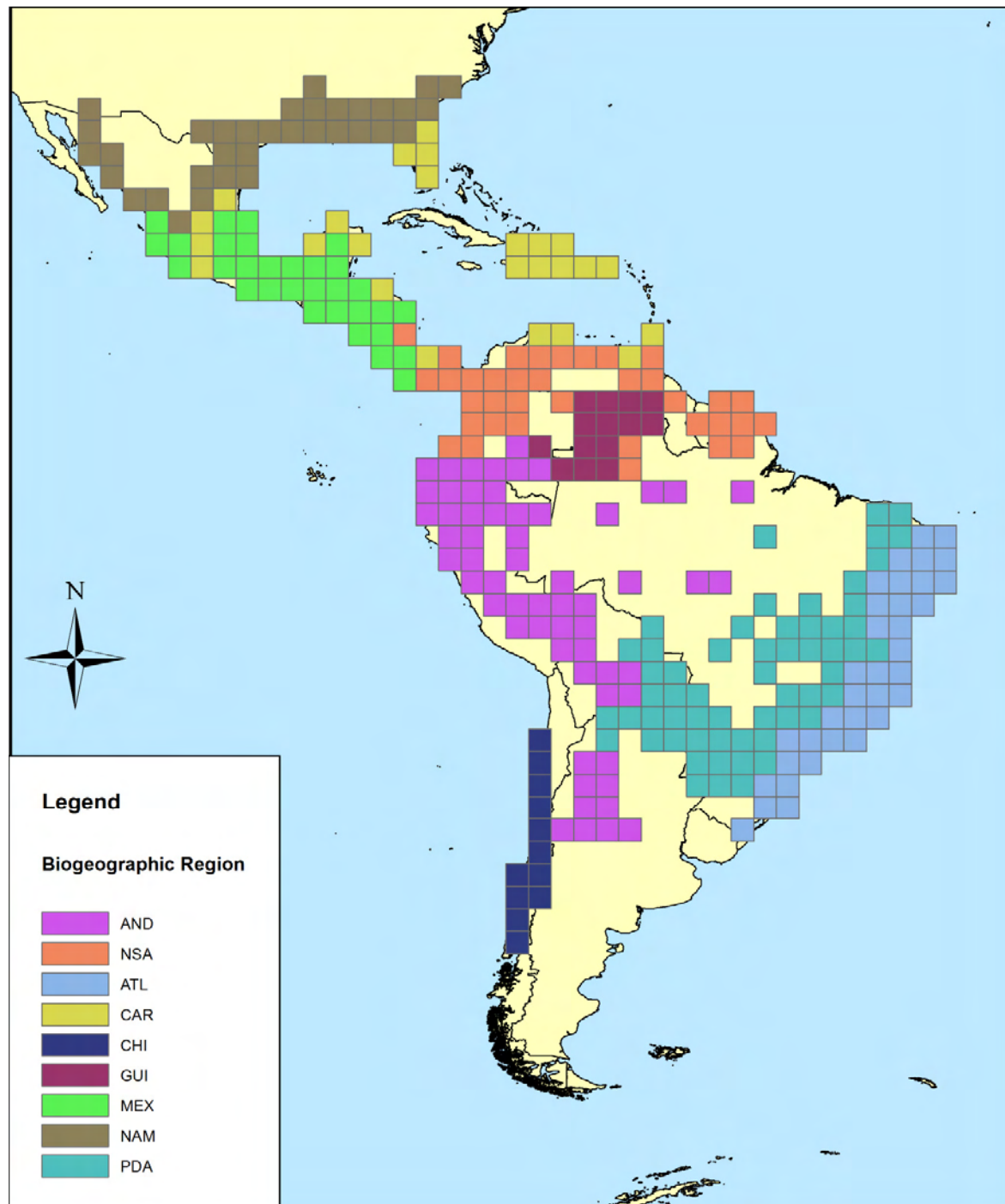


Figure 7.2. Biogeographic regions derived *de novo* from species composition for the Bromeliaceae (AND - Andes; NSA - Northern South America; ATL - Atlantic Rainforest; CAR - Caribbean; CHI - Chile; GUI - Guiana Shield; MEX - Mexico and Central America; NAM - North America; PDA - Pleistocene dry arc)

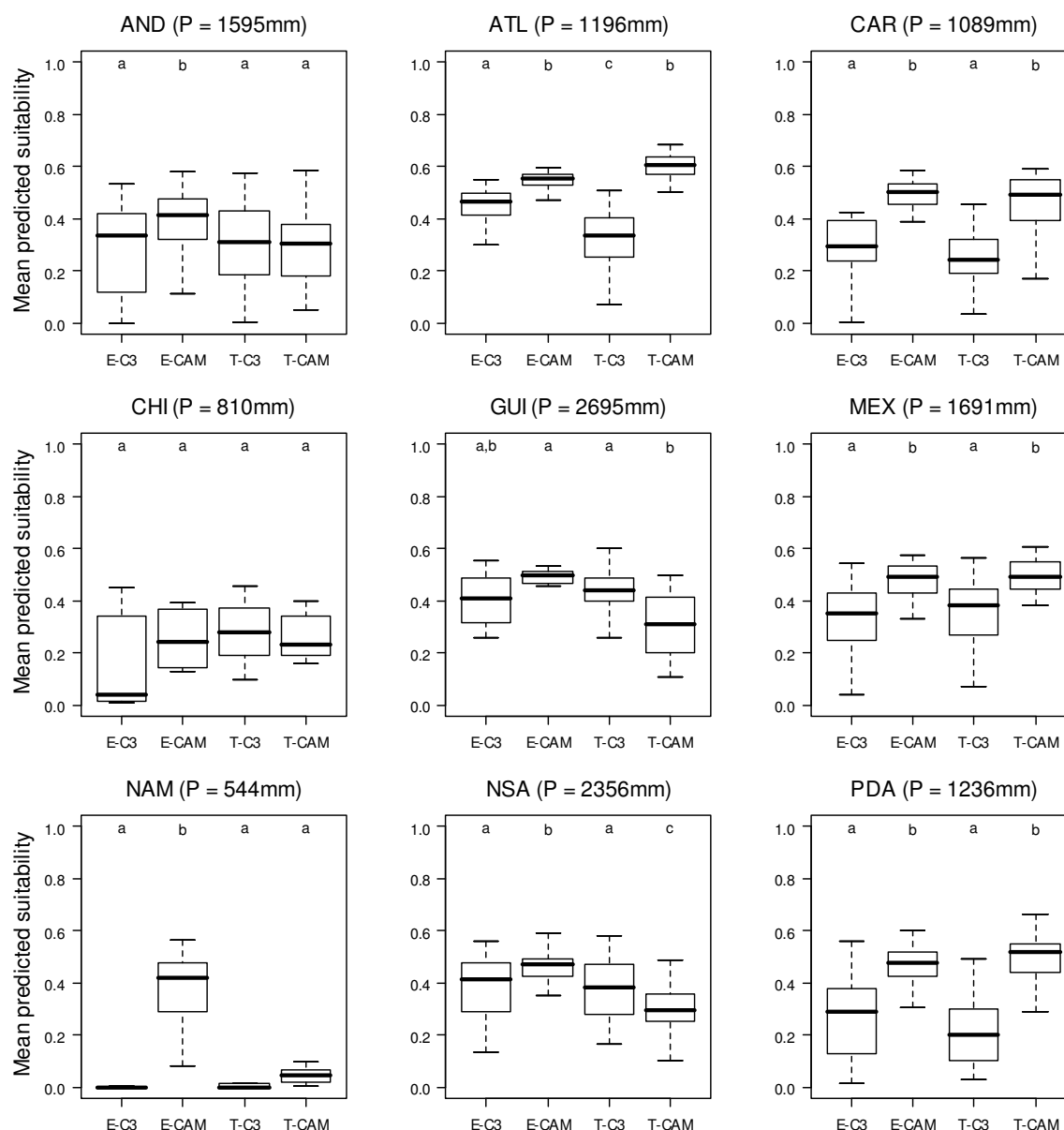


Figure 7.3. Environmental suitability predicted for bromeliads in each of the nine biogeographic regions delimited in this thesis. Suitability is taken from the corresponding MAXENT models. Letters above boxes indicates groups identified using Tukey's HSD test, significant at $p = 0.01$. Abbreviations "E" = epiphyte, "T" = terrestrial.

Environmental suitability was examined in a geographical context using the MAXENT species distribution algorithm to predict environmental suitability for the four division of the bromeliad (C₃/CAM with epiphyte/terrestrial). The species distribution models showed a good fit for all four groups (C₃ epiphytes: mean area under curve (AUC) = 0.805; C₃ terrestrials: AUC =

0.849; CAM epiphytes: AUC = 0.708; CAM terrestrials: AUC = 0.825). The jackknife measure of variable importance showed that across all species the seasonality of temperature was the most important modelling variable (values > 45%) (Table 7.3), reflecting the northerly and southerly limits to the distribution of the whole family. The models show a higher environmental suitability for epiphytic CAM species across much of the distribution range of bromeliads (Figure 7.4), and this is likely to be due to the ability of the small atmospheric *Tillandsia* to find suitable microclimate in all ecoregions. Within the ecoregions, comparison of terrestrial species with the different photosynthetic pathways is more revealing than for epiphytic species, with most of the biogeographic regions show a higher suitability for terrestrial species with CAM photosynthesis, including the driest areas, the Pleistocene dry arc (PDA), the Caribbean (CAR) and the Atlantic rainforest (ATL) (Figure 7.3). However, in the two wettest biogeographic regions, the Guiana Shield (GUI) and Northern South America (NSA) area, show a higher suitability for terrestrial C₃ species. The Chile (CHI) area is an exception to general patterns, being equally suitable for all groups, and this is likely to reflect its position on the periphery of the range of the Bromeliaceae, and the large variety of climates found within Chile. At the other periphery, the North America region (NAM) is only suitable for epiphytic CAM species.

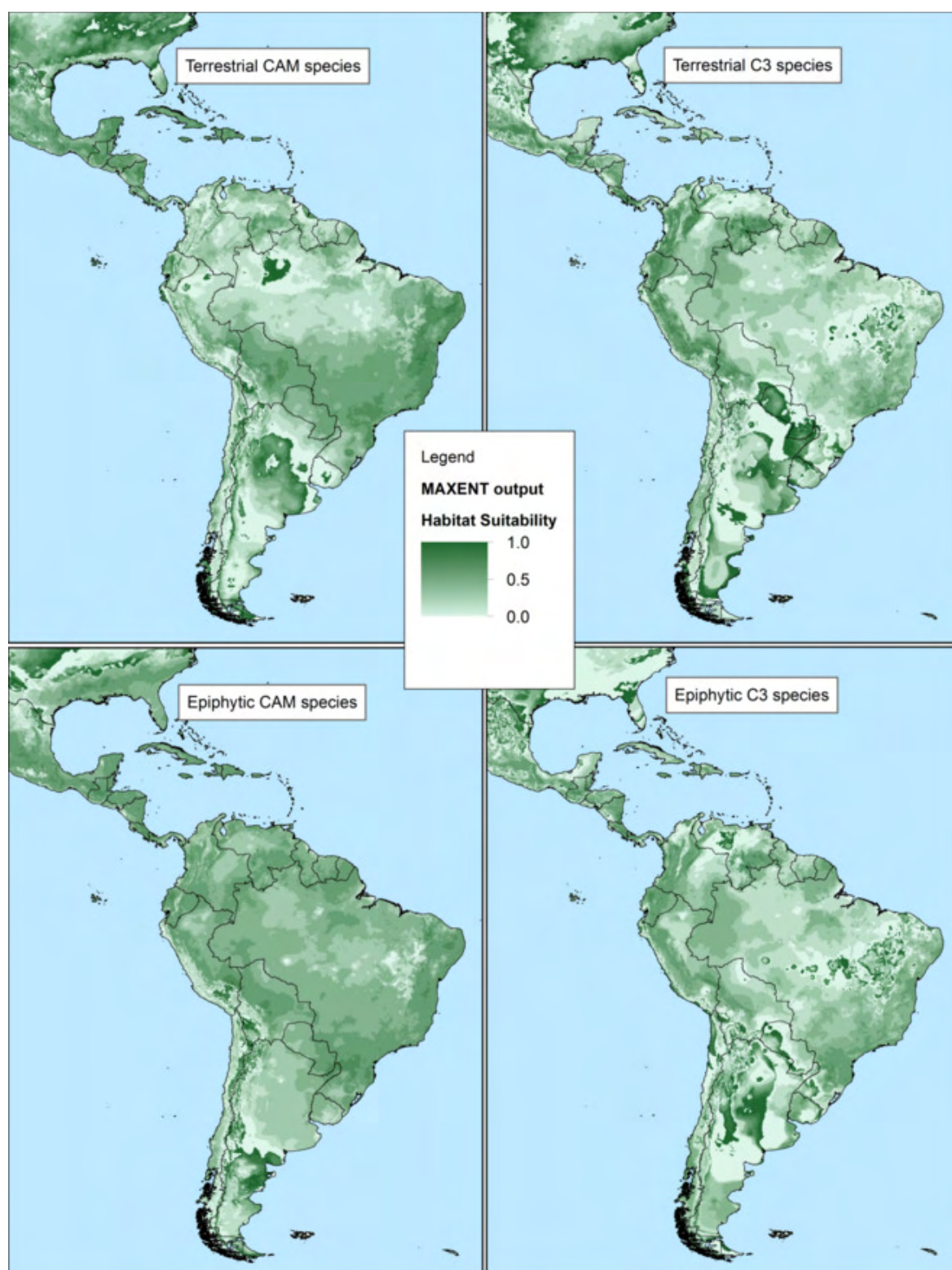


Figure 7.4. Average MAXENT prediction of habitat suitability for the four groups of bromeliads. Outputs show the mean values calculated from repeat runs of the MAXENT modelling process.

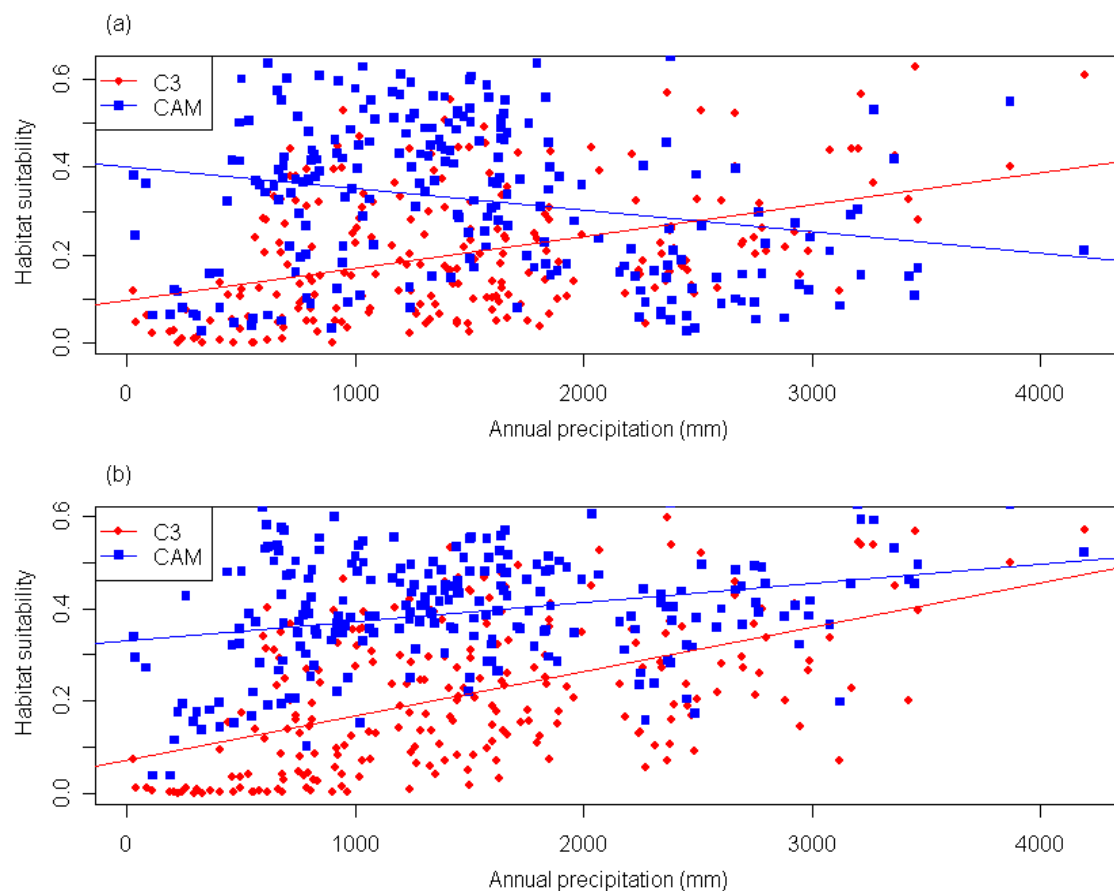


Figure 7.5. A comparison of habitat suitability over the range of annual precipitation for (a) terrestrial bromeliads and (b) epiphytic bromeliads. Lines show linear models with $p < 0.05$.

Using the species distribution models, habitat suitability for the different bromeliad groups can be compared. The relationship between mean environmental suitability of 1 degree grid cells for each group and mean annual rainfall in the same grid cell showed different patterns for C₃ and CAM species. The mean suitability increased linearly with annual precipitation in C₃ plants (epiphytes: $r^2 = 0.27$; terrestrials: $r^2 = 0.17$) (Figure 7.5). The relationship was the same for both epiphytes and terrestrials. CAM species showed a unimodal distribution, best modelled by a quadratic curve (epiphytes: $r^2 = 0.10$; terrestrials: $r^2 = 0.09$), although the linear model still showed a significant fit (Figure 7.5). Quadratic models showed terrestrial CAM species had the peak of highest habitat suitability at the lowest annual rainfall,

mean habitat suitability peaking between 1000-1500 mm annual precipitation and dropping rapidly either side. Habitat suitability of terrestrial CAM species was higher than terrestrial C₃ species up to 2400 mm annual rainfall (Figure 7.5). At higher rainfall values the habitat became more suitable for terrestrial C₃ species. The same patterns are maintained in terrestrial bromeliads with rainfall of the driest 3 months (Figure 7.6), with a strong cross-over of habitat suitability occurring at 275 mm rainfall, with drier environments than this more suitable to CAM species, and wetter environments more suitable to C₃ species. Comparing habitat suitability to annual mean temperature showed no significant relationships between temperature and habitat suitability, with the exception of habitat becoming more suitable at higher temperatures in epiphytic CAM species (Figure 7.7).

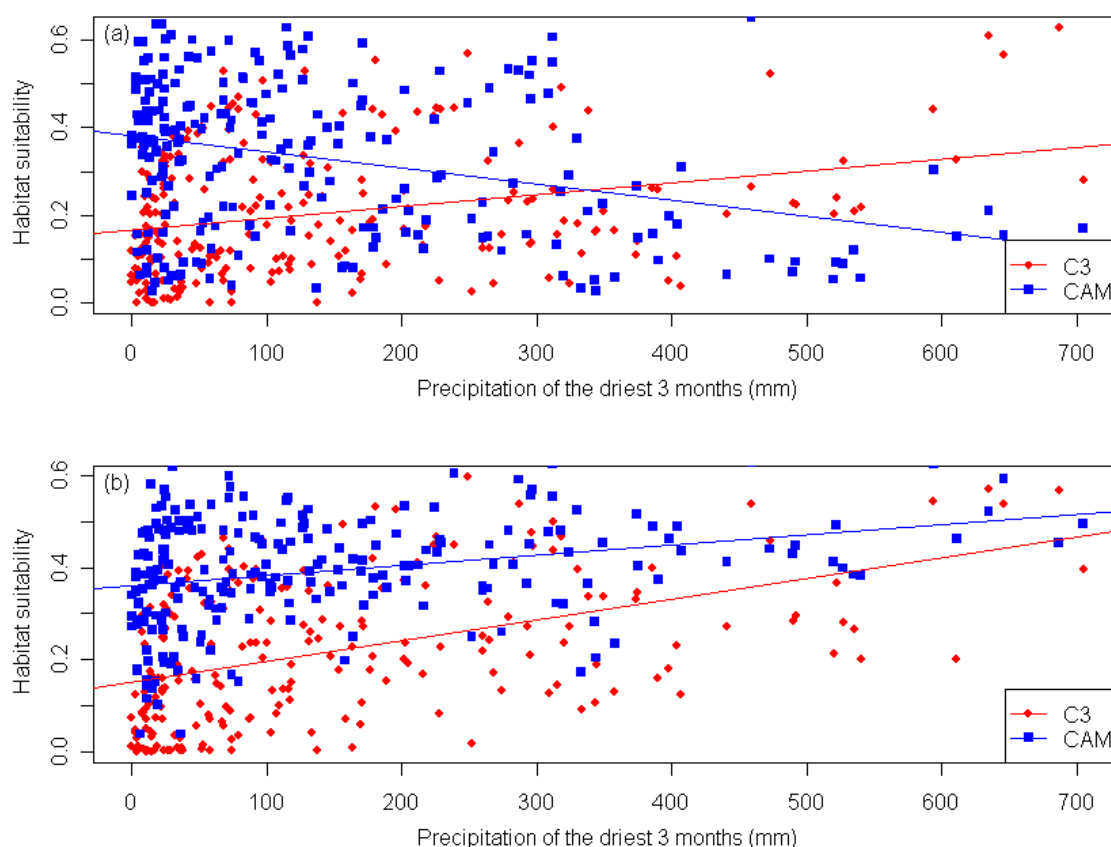


Figure 7.6. A comparison of habitat suitability over the range of precipitation of the driest 3 months for (a) terrestrial bromeliads and (b) epiphytic bromeliads. Lines show linear models with $p < 0.05$.

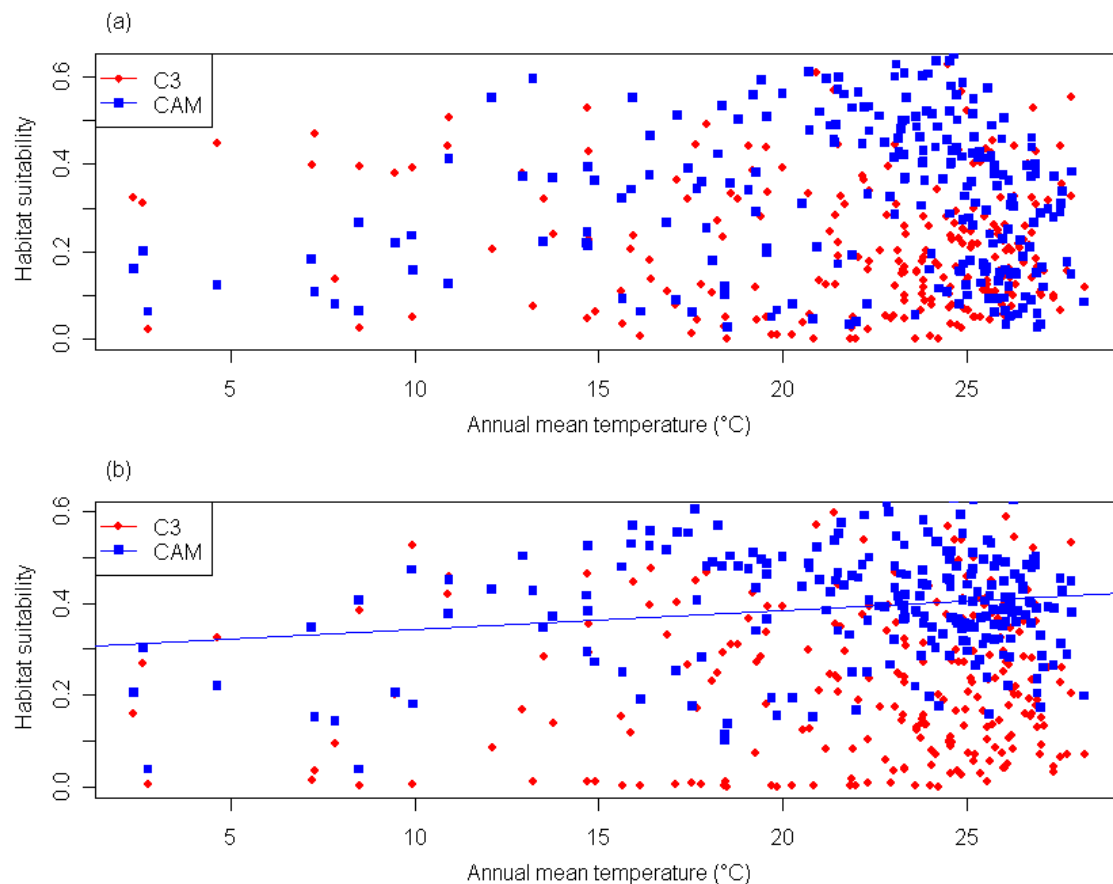


Figure 7.7. A comparison of habitat suitability over the range of annual mean temperature for (a) terrestrial bromeliads and (b) epiphytic bromeliads. Lines are linear models with $p < 0.05$.

Combining the habitat suitability scores for temperature and precipitation gives a plot of 'climate space' and shows the interaction of these two variables (Figure 7.8). These plots show that at a given temperature, the habitat is more suitable for species with CAM photosynthesis at lower precipitation values, although the distinction is clearer for terrestrial species than epiphytic species. At higher precipitation and rainfall there is a large amount of overlap for both epiphytes and terrestrials, and this may reflect the importance of other variables, such as seasonality or solar radiation.

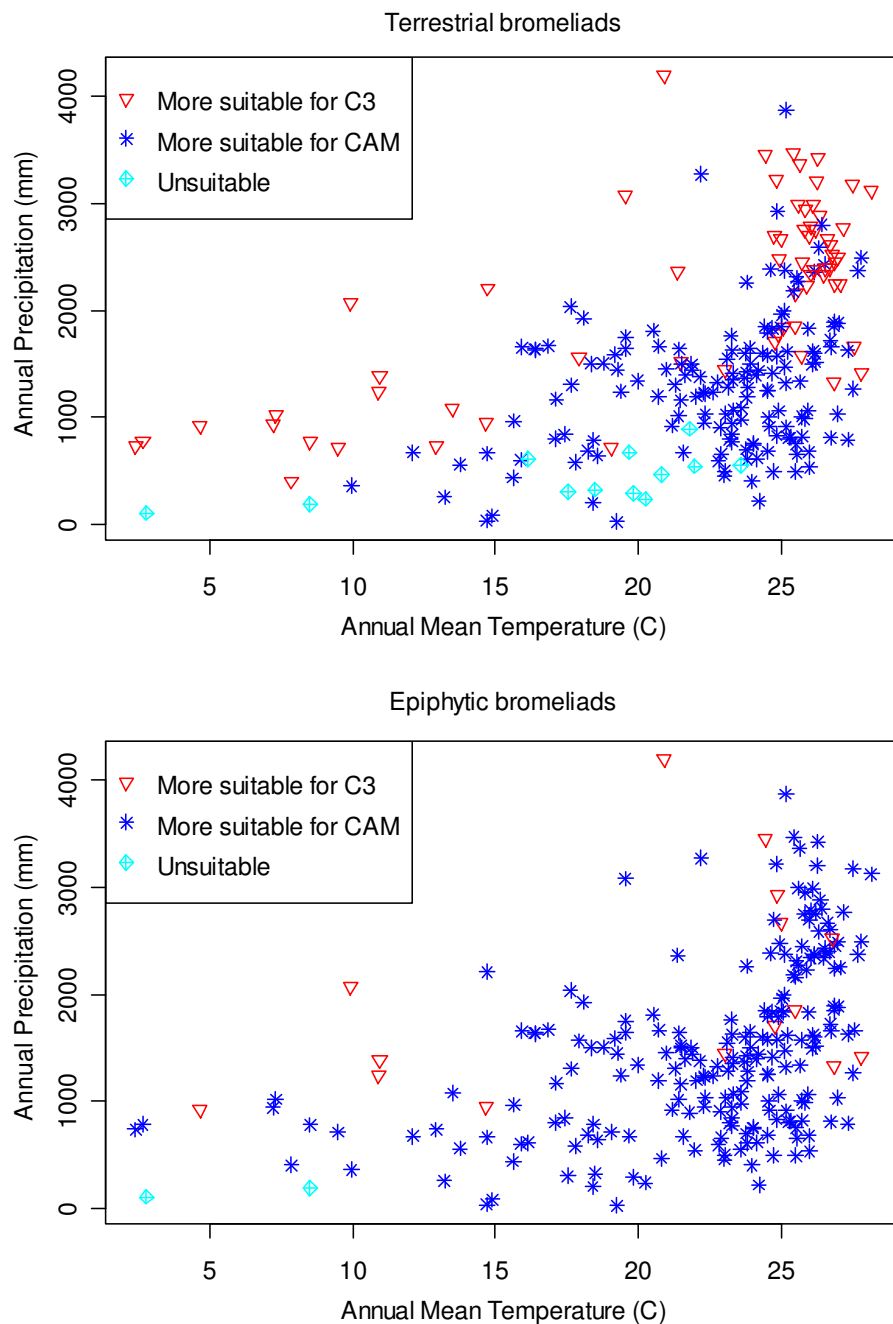


Figure 7.8. Climate space showing the photosynthetic pathway predicted to be most suitable based on the MAXENT species distribution models. Unsuitable areas are those where habitat suitability was < 0.1 for both photosynthetic pathways.

7.4.2 THE FAMILY-LEVEL DIFFERENCE BETWEEN CAM AND C_3 ENVIRONMENTS

From the species distribution modelling we expect to find differences predicted by the model in the environments of C_3 and CAM species to be found in the specimen data. The specimen data

shows terrestrial C₃ species (annual mean temperature (T) = 20.0 °C, annual precipitation (P) = 2034 mm) occupy a similar environment to epiphytic C₃ species (T = 19.3 °C, P = 2045 mm) (Table 7.4). The epiphytic CAM species are on average are found in warm and dry locations (T = 21.6 °C, P = 1625 mm) (Table 7.4). Terrestrial CAM species are found in markedly drier environments (T = 21.3 °C, P = 1213 mm) (Table 7.4). The difference between annual precipitation is more significant in terrestrials ($t = 14.9$, $p = 2.2 \times 10^{-16}$) than epiphytes ($t = 8.9$, $p = 2.2 \times 10^{-16}$). The difference in temperature is less significant in terrestrials ($t = -4.0$, $p = 6.8 \times 10^{-5}$) than epiphytes ($t = -11.2$, $p = 2.2 \times 10^{-16}$).

Table 7.4. Climate variables for the Bromeliaceae split into groups of terrestrial and epiphytic species and CAM and C₃ species. Values are mean $\pm$ standard deviation.

Variable	Terrestrial species		Epiphytic species	
	C ₃	CAM	C ₃	CAM
Number of species	514	218	626	503
Altitude (m)	1329 $\pm$ 941	848 $\pm$ 803	1342 $\pm$ 744	717 $\pm$ 666
Annual mean temperature (°C)	20.0 $\pm$ 4.8	21.3 $\pm$ 3.8	19.3 $\pm$ 3.4	21.6 $\pm$ 3.3
Temperature seasonality	94.2 $\pm$ 81.3	177.7 $\pm$ 91.3	95.4 $\pm$ 75.6	157.6 $\pm$ 92.8
Temperature of the warmest month (°C)	27.1 $\pm$ 4.7	29.6 $\pm$ 3.5	26.2 $\pm$ 3.4	29.1 $\pm$ 2.9
Temperature of the coldest month (°C)	12.7 $\pm$ 5.8	12.3 $\pm$ 5.2	12.4 $\pm$ 4.1	13.7 $\pm$ 4.8
Annual precipitation (mm)	2034 $\pm$ 915	1213 $\pm$ 558	2045 $\pm$ 821	1625 $\pm$ 769
Number of days with precipitation per year	169 $\pm$ 54	154 $\pm$ 58	182 $\pm$ 41	178 $\pm$ 58
Seasonality of precipitation	55.7 $\pm$ 23.4	73.4 $\pm$ 24.1	51.3 $\pm$ 20.1	56.0 $\pm$ 26.2
Precipitation of the wettest three months (mm)	824 $\pm$ 3334	568 $\pm$ 230	798 $\pm$ 282	656 $\pm$ 261
Precipitation of the driest three months (mm)	223 $\pm$ 167	85.7 $\pm$ 92.2	236 $\pm$ 155	191 $\pm$ 155
Maximum climatological water deficit (mm)	-212 $\pm$ 204	-420 $\pm$ 206	-191 $\pm$ 157	-264 $\pm$ 222
Actual evapotranspiration (mm)	1218 $\pm$ 319	1029 $\pm$ 251	1199 $\pm$ 197	1169 $\pm$ 263
Potential evapotranspiration (mm)	1423 $\pm$ 186	1333 $\pm$ 170	1402 $\pm$ 138	1396 $\pm$ 171
Relative humidity (%)	77.1 $\pm$ 7.3	72.4 $\pm$ 6.5	79.9 $\pm$ 5.4	77.5 $\pm$ 6.5

To confirm the extent of these climate differences, and establish which are the strongest predictors of the differences in distributions between the photosynthetic pathways we used logistic regression models (LRM) to predict if a species was more likely to use C₃ photosynthesis or CAM photosynthesis based on environmental variables. The LRM shows no

single factor is sufficiently strong to explain a statistically significant proportion of the variation in the data (Figure 7.9). For epiphytic species altitude, temperature seasonality and the maximum temperature of the warmest month are better for predicting the photosynthetic pathway. Variables based on rainfall are very poor predictors for epiphytic species, but much stronger predictors for terrestrial species. For the terrestrial species the rainfall variables (maximum climatological water deficit, temperature of the driest quarter and annual precipitation) were more useful for predicting the photosynthetic pathway (Figure 7.9). The mixed models using the combination of the three strongest single variables showed a significant ρ^2 value (terrestrial species: $\rho^2 = 0.280$, epiphytes: $\rho^2 = 0.231$), meaning a significant proportion of the species photosynthetic pathways can be determined using environmental variables.

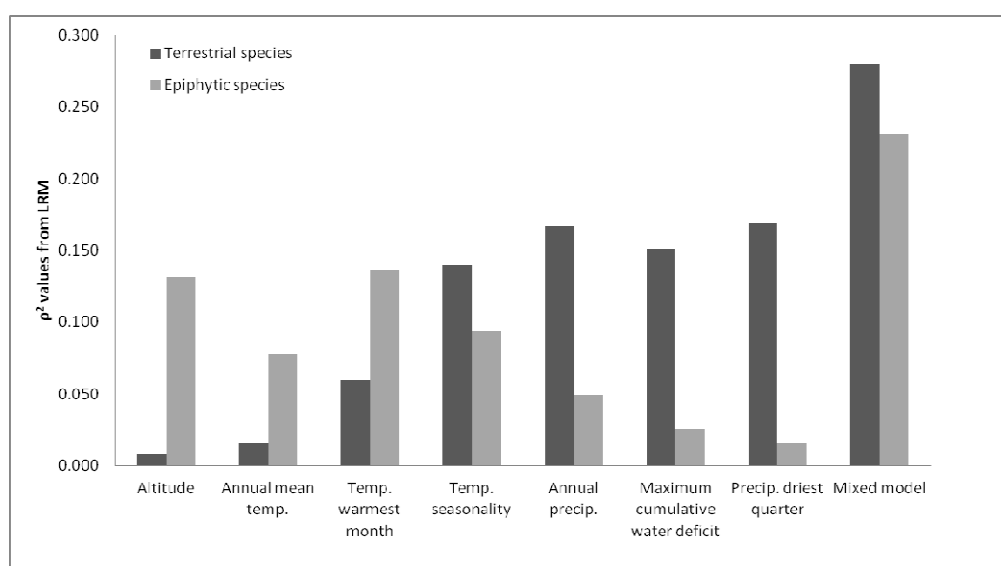


Figure 7.9. Goodness of fit values (ρ^2) for single predictors in a logistic regression model (LRM).

7.4.3 FLORAS

To test these results in an independent data set I used species lists which included bromeliads from as many locations as possible. Of the Floras which were suitable for the analysis, 44 of the 48 sites fall within the forest biomes, with two falling into tropical savannas and one in the desert biome. The Floras contain an overwhelming majority of epiphytes.

ANNUAL CLIMATE VARIABLES AS PREDICTORS OF CAM SPECIES PREVALENCE

To test whether water availability, energy availability, or a combination of the two variables was a stronger predictor, the correlation between these environmental variables and the proportion of CAM species in the Floras was compared. Water availability was approximated using annual mean rainfall and number of wet days. Energy availability was approximated with annual mean temperature and potential evapotranspiration (PET). The combined water-energy variables used were actual evapotranspiration (AET), and the water balance (WB), calculated as the sum of the difference between PET and AET. None of these variables showed correlation with the proportion of CAM species in the flora. Of the variables relating to water and energy, only the annual mean temperature showed significant correlation ($r = 0.403$, $p^* = 0.01$). Altitude, strongly co-linear with temperature over the study sites also showed a strong correlation ($r = -0.347$, $p^* = 0.04$). Neither the rainfall variables, nor the combined water-energy variables showed significant correlation at the $p^* = 0.05$ level (data not shown).

IS THERE A SPECIFIC SEASONAL EFFECT OF CLIMATE ON THE PROPORTION OF CAM SPECIES?

Annual trends are strongly co-linear with seasonal effects; however seasonal variables may be more relevant biologically. Direct monthly values were not used because the sites cross the equator, and so will have contrasting seasonality. Many of the variables have strong co-linearity. Three seasonal variables are stronger predictors of the proportion of CAM species in the Flora (maximum temp warmest month, mean temp wettest quarter, temp warmest quarter) (PPMCC, $p^* < 0.01$) forming a set of variables which characterise the temperature in the warmest part of the year (Table 7.5). Variables relating to the colder parts of the year were not correlated when the Bonferroni correction was taken into account ($0.01 < p^* < 0.05$). There was no correlation between seasonal rainfall variables and the proportion of CAM species in the flora (Table 7.6).

Table 7.5. Correlation with spatially adjusted degrees of freedom between the proportion of CAM species and seasonal environmental variables relating to temperature. * indicates significant at Bonferroni-corrected level $p = 0.0028$

Variable	Seasonal variables - Temperature					
	Temp warmest month	Temp coldest month	Temp warmest 3 months	Temp coldest 3 months	Temp of wettest 3 months	Temp of driest 3 months
Pearson	0.594	0.309	0.579	0.382	0.571	0.353
P	<.001	0.031	<.001	0.007	<.001	0.013
p^*	<.001*	0.038	<.001*	0.012	<.001*	0.018

Table 7.6 Correlation with spatially adjusted degrees of freedom between the proportion of CAM species and seasonal environmental variables relating to precipitation. * indicates significant at Bonferroni-corrected level $p = 0.0028$

Variable	Seasonal variables - Rainfall						
	Maximum cumulative water deficit	Rainfall of wettest 3 months	Rainfall of driest 3 months	Rainfall of wettest month	Rainfall of driest month	Rainfall of warmest 3 months	Rainfall of coldest 3 months
Pearson	-0.043	-0.183	0.021	-0.195	0.028	-0.006	-0.003
p	0.769	0.207	0.884	0.041	0.179	0.965	0.982
p^*	0.793	0.154	0.901	0.112	0.167	0.973	0.984

VARIATION IN THE DATA EXPLAINED BY THE COMBINED MODELS

The combined predictor models had a strong explanatory power for the data (Table 7.7). The final model contained four temperature variables (annual mean temperature, temperature of the wettest quarter, temperature of the driest quarter and temperature of the coldest quarter) and two rainfall variables (annual precipitation and precipitation of the driest month) along with topographic variability. There was significant spatial autocorrelation in the data set, and space alone was able to explain a significant proportion of the variation in the data. The spatially explicit models showed a significant increase in percentage of deviance explained from 75% to 95%. The inclusion of biogeographic regions showed little improvement in the model, suggesting there is little role of historic factors in the model. This was confirmed by the low p and z values for all the regions included in the model. The selected climate variables were all

significant in the models and without including space were able to explain over 75% of the variation in the data (Table 7.7).

Table 7.7. Output of the model predicting the proportion of species expected in a given location based on physical and environmental variables. Model parameters and performance measures are given for a general linear model fit of the data and spatially explicit model (SLM) to reduce spatial autocorrelation. Spatial autocorrelation for model residuals is characterised using Moran's I. Model performance is calculated using Akaike's Information Criteria (AIC) and % Deviance.

Variable	GLM (no regions)		GLM (regions)		SLM (no regions)		SLM (regions)	
	Coeff.	t	Coeff.	t	Coeff.	z	Coeff.	z
Annual mean temperature	5.29E-01	5.67	4.93E-01	4.71	5.14E-01	6.28	4.52E-01	6.54
Mean temp. of wettest 3 months	-1.98E-01	-4.19	-1.89E-01	-3.65	-1.89E-01	-4.56	-1.65E-01	-4.78
Mean temp. of driest 3 months	-1.05E-01	-3.66	-1.18E-01	-3.79	-9.91E-02	-3.87	-1.08E-01	-4.42
Mean temperature of Coldest Quarter	-1.82E-01	-3.65	-1.37E-01	-2.15	-1.80E-01	-4.24	-1.27E-01	-3.04
Annual precipitation	-1.69E-04	-4.28	-2.05E-04	-3.87	-1.79E-04	-5.42	-2.50E-04	-6.97
bio14	2.04E-03	3.59	2.35E-03	3.45	2.21E-03	4.67	2.94E-03	6.75
TOPOvar	6.96E-05	1.92	6.99E-05	1.87	8.43E-05	2.62	1.07E-04	3.70
BIOG-ALT	-		3.83E-02	0.43	-		5.05E-03	0.09
BIOG-CAR	-		-1.58E-01	-0.84	-		-2.84E-01	-1.91
BIOG-GUY	-		-1.05E-02	-0.07	-		-2.35E-01	-2.05
BIOG-MEX	-		8.64E-02	1.03	-		8.39E-02	1.63
% Deviance	74.58		75.89		95.91		96.47	
AIC	-43.32		-37.86		-42.08		-41.34	
Moran's I	-0.06		-0.11		-0.002		-0.058	

7.4.4 VARIATION IN CARBON ISOTOPE RATIOS

The results show different relationships between the environment and carbon isotope ratios for CAM species and C₃ species. The environmental data for each species showed a large amount of scatter so the species were binned into 1‰ groups. The C₃ species (ratios more negative than -20‰) showed more negative carbon isotope ratios with both increasing rainfall and increasing temperature (Figure 7.11). However, CAM species (ratios less negative than -20‰) showed little variation and no significant trends with respect to rainfall, and variation but no significant trends with respect to temperature (Figure 7.11). An interesting group of 'intermediate' species

emerges with carbon isotope ratios values from -20‰ to -23‰. These species form a cluster, representing the coolest, driest group of species (Figure 7.11) and occupy habitats such as the Atacama Desert, the eastern slope of the Peruvian Andes, central northern Andes, Central American mountains and the Guiana Shield Tepuis (Figure 7.10).

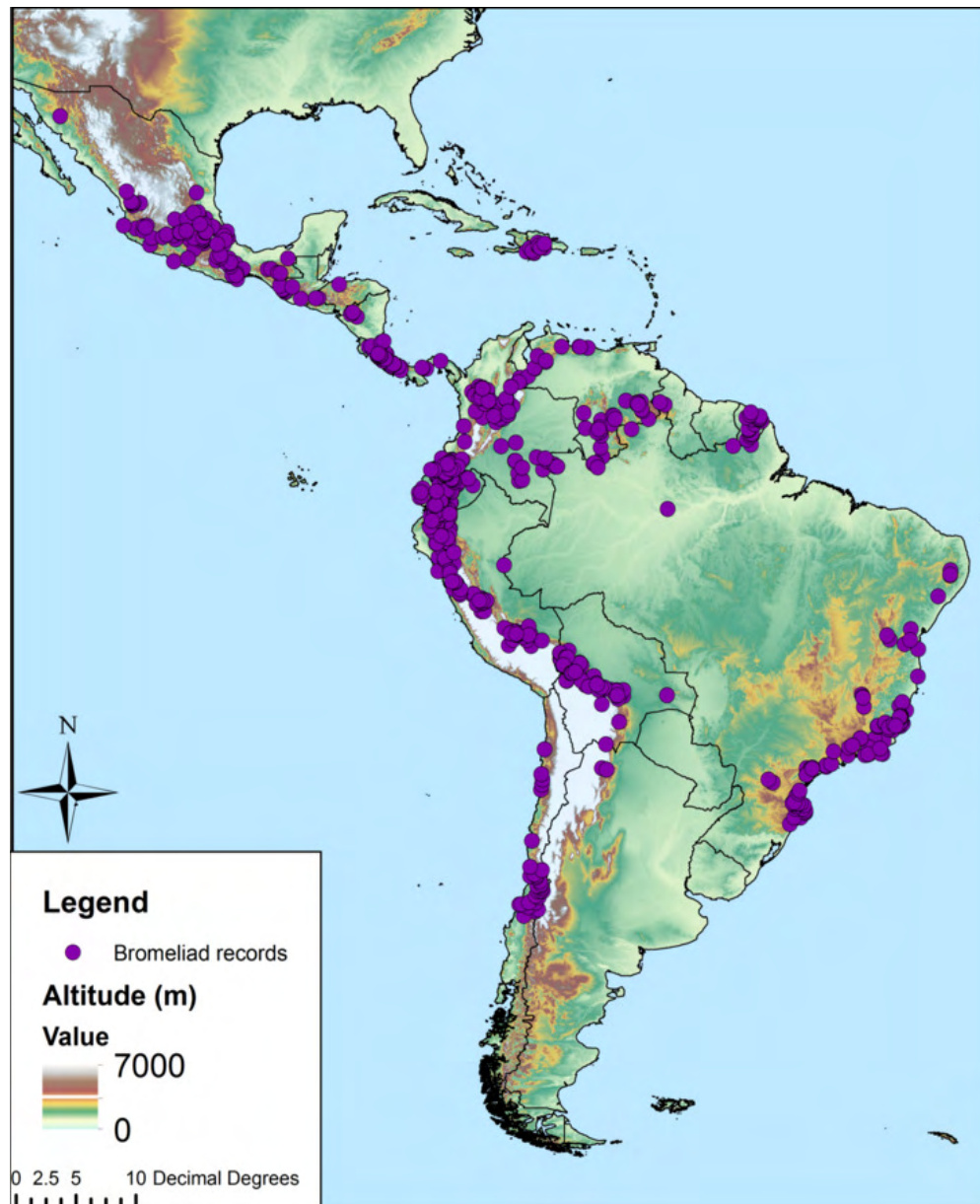


Figure 7.10. Geographic distribution of bromeliad records for species with carbon isotope ratios from -20‰ to -23‰.

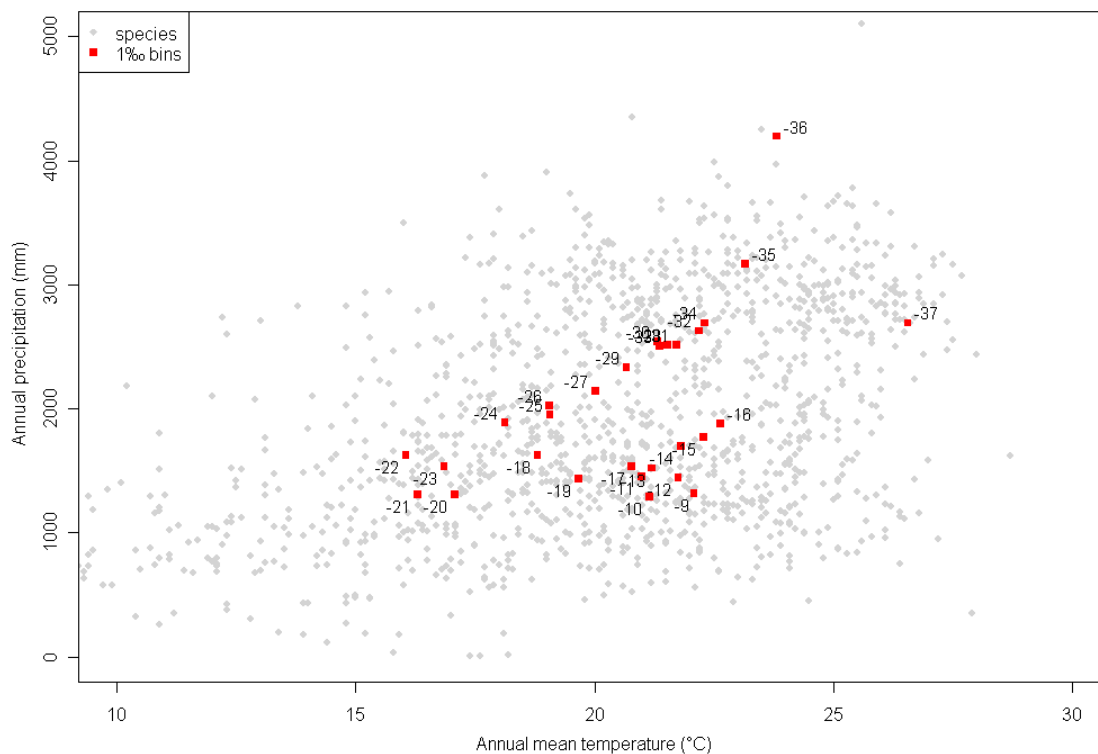


Figure 7.11. Precipitation–temperature plots for each species (grey) and species binned by 1 ‰ carbon isotope ratio (red).

7.5 DISCUSSION

7.5.1 BIOGEOGRAPHY OF CAM BROMELIADS

The biogeographical regions obtained reflect strongly the biogeographic areas of South and Central America from other studies (Udvardy 1975; Ellenberg 1981; Pennington, Prado & Pendry 2000; Olsen *et al.* 2001), and regions already discussed in bromeliad literature (Benzing 2000; Crayn, Winter & Smith 2004; Givnish *et al.* 2004; Givnish *et al.* 2011). The divisions in these are based on species composition, but strongly reflect prevailing climate and vegetation type, which are also important in influencing the distribution of bromeliad species, so the similarities between the regions discovered in this study and previous studies are expected. Evolutionary history plays an important role in species composition at any given location

(Givnish *et al.* 2011), and a more refined set of regions could be developed by including phylogeny (Riddle 2009). This is exemplified by the restriction of the earliest-diverging lineages to the Guiana Shield area, resulting in the species composition in the Guiana Shield being very different from the lowland Amazon. The lowland Amazon is classified with the Andes due to the presence of a small number of wide-ranging *Aechmea* and *Tillandsia* species, although the Andes themselves have a large number of narrow endemics. The Amazon is known to have few bromeliads (Reitz 1965), and if species abundance were taken into account it is likely the Amazon would form a distinct region. The establishment of Chile as a separate region, most likely due to its location on the edge of the distribution range of bromeliads, is supported by recent evidence in *Puya* species of a monophyletic clade of species endemic to Chile (Jabaily & Sytsma 2010). The Pleistocene Dry Arc area (based on the region discussed by Pennington, Prado and Pendry (2000) which was covered in seasonally dry tropical forest (SDTF) in the Pleistocene leading to distinctive patterns in speciation in SDTF lineages (Pennington *et al.* 2004)) encompasses the Cerrado, including the majority of the range of the *Dyckia*, *Deuterocohnia* and *Encholirium* clade of terrestrial CAM species (Crayn, Winter & Smith 2004). The Atlantic rainforest of Brazil, although recently decimated by deforestation (Ribeiro *et al.* 2009), is home to a significant number of species, particularly endemics, from the Bromelioideae, and the much wetter conditions of the coastal Atlantic forests yield different species composition to the adjacent Pleistocene dry arc region. The Andes fall predominantly into a main Andean area, although the extreme northern area, including the cordilleras of Venezuela and northern Colombia form part of the Northern South America region that extends in along the Caribbean coast of South America to French Guiana. The exact boundaries of the Andes and Northern South America areas were very mobile depending on the scale of the classification, and represent the gradual turnover of a few endemic species, combined with numerous widespread shared species. Central America divided into three regions, with the

southern part joining the Northern South America region. Mexico has a high diversity of endemic *Tillandsia* and *Hechtia*, and 'North America' is the extreme north of the distribution of the family, with a few widespread *Tillandsia* subgenus *Diaphoranthema* species. The Caribbean, Florida and some coastal areas of Mexico, and Venezuela form a separate region.

While this classification matches well with known biogeographic regions and fits well with current knowledge of bromeliad distribution patterns, the non-hierarchical clustering mechanism is not as robust as hierarchical clustering mechanisms recommended in Kreft and Jetz (2010). This was primarily due to the difference in data availability. The map of ecoregions based on bromeliad distribution could be drawn at a higher resolution and with more certainty if more detailed range maps were available for all species.

7.5.2 CAM PHOTOSYNTHESIS - AN ADAPTATION TO LOW WATER AVAILABILITY

The merits of CAM photosynthesis as an adaptation to drought have been extensively discussed in the literature (Winter & Smith 1996; Cushman 2001; Lüttge 2004). Increased water-use efficiency due to daytime stomatal closure allows plants to avoid drought stress and continue photosynthesis for longer than C_3 species under drought conditions. This physiological adaptation is apparent in the ecological niche differentiation of species. From the analysis of terrestrial species, CAM photosynthesis has higher habitat suitability than C_3 species in climate regions with less than 2300 mm annual rainfall. This differentiation based on modelled climate suitability is supported by the mean differences in climate for individual bromeliad species. The mean climate of species based on herbarium records shows that terrestrial CAM species occupy environments with 800 mm lower annual rainfall than terrestrial C_3 species, although variation between species is high. The niche differentiation based on water availability is consistent with a lower ratio of evaporation to assimilation (Lüttge 2004). For many terrestrial plants CAM photosynthesis is also part of a suite of adaptations to low water availability, including thick, water-retaining (succulent) leaves (Ogburn & Edwards 2010). Terrestrial species of the

Bromeliaceae with CAM photosynthesis show similar adaptations to drought, and can be found in some of the most arid habitats in South and Central America (Figure 7.2). Although terrestrial species possessing CAM photosynthesis are more likely to occur in drier habitats, the MAXENT models show a decrease in habitat suitability for CAM species below the peak at 1500 mm annual precipitation. The habitat suitability for terrestrial C₃ species increases linearly from almost zero at 500 mm annual precipitation, and increases linearly across the range of precipitation in this data set. The niche differentiation of terrestrial bromeliads as a result of water availability contrasts with patterns in epiphytic species, suggesting the influence of water availability is through the interaction of plants and soil water.

Contrary to both expectation, and patterns found in terrestrial species, there was little evidence of niche differentiation by photosynthetic pathway along the precipitation gradient in epiphytic bromeliad species. Although the average annual precipitation for epiphytic CAM species is 400 mm lower than for C₃ species, the variation is large and all precipitation variables are not significant as single predictors in a logistic regression model. The occurrence of some bromeliad species with CAM photosynthesis in wet biomes has been documented (Martin 1994; Pierce, Winter & Griffiths 2002b), but the evidence here suggests that if these wet forests were also hot, the occurrence of species with CAM photosynthesis need not be an aberration. The epiphytic niche is accepted as a water-stressed environment (Griffiths & Smith 1983; Smith 1987; Zotz & Hietz 2001), and the requirement to be adapted to low water availability may mean that, among epiphytic species, CAM photosynthesis alone is not a significant adaptation to low water availability, at least on the continental scale. The species distribution models show a higher environmental suitability for epiphytic CAM species than epiphytic C₃ species across the entire rainfall gradient. This is due to species in *Tillandsia* subgenus *Diaphoranthema* that are tolerant of a wide range of environmental conditions (Till 1992).

7.5.3 THE ROLE OF TEMPERATURE

From the herbarium data set differences in temperature are larger and more consistent than precipitation between epiphyte species with CAM and C_3 photosynthesis. The difference in the mean environment of the two groups of species is supported by the difference in predictive power in the LRMs (Figure 7.9). The proportion of CAM species in local Floras provides independent confirmation that temperature is more important than precipitation in determining the prevalence of (epiphytic) species with CAM photosynthesis. The importance of CAM photosynthesis at high temperatures is unexpected, despite the similarity of the CCM to C_4 photosynthesis. It is possible that CAM photosynthesis gives an ecological advantage at higher temperatures due to the quantum yield effect demonstrated for plants with C_4 photosynthesis (Ehleringer 1978). With the epiphytic Bromeliaceae this effect is apparent at the continental scale. The effect applies to the year round temperature, but is more pronounced with the seasonal temperature, supporting the idea that the effect is strongest when the temperatures are highest. Since these months represent the peak growing season, a higher proportion of the photosynthesis will occur in these months. A warmer temperature at this time would increase photorespiration in C_3 species, increasing the relative efficiency of CAM species. The strong correlation with temperature and particularly with temperatures of the hottest months strongly supports the theory of relative improvements (over C_3 photosynthesis) in quantum yield due to the carbon concentrating mechanism. This effect is evident on ecological scales in the same manner as for the comparison of C_4 and C_3 species from the Poaceae, despite the higher energetic cost of CAM compared to C_4 photosynthesis.

Temperature showed no predictive power to differentiate the distribution of terrestrial Bromeliaceae with different photosynthetic pathways (Figure 7.9). For terrestrial plants the gradient of water availability is of overwhelming importance, and masks any effects of temperature. It is also possible that the microclimate of terrestrial plants is important, with C_3

plants in the forest understory experiencing a significantly cooler daytime temperature than that experienced above the canopy.

7.5.4 COMPARISONS WITH C₄ PLANTS

The parallels between CAM and C₄ photosynthesis are strong on the basis of this analysis. The quantum yield effect described in C₄ grasses (Teeri & Stowe 1976; Ehleringer 1978) was initially thought not to apply in CAM plants because of the higher energy costs of carbon concentration in CAM photosynthesis. However the epiphytic CAM Bromeliaceae show a clear pattern of increased abundance in warmer environments, with no difference in rainfall, indicative of the better photosynthetic performance at higher temperature. Recent work on C₄ photosynthesis has highlighted the drought-adaptation value of the C₄ pathway (Cabido *et al.* 2008; Edwards & Still 2008). This parallels the traditional view of CAM, in that the carbon concentrating mechanism allows increased water-use efficiency, and improved performance under water-stressed conditions. This illustrates that the two different CCMs have more in common ecologically than previously assumed.

7.5.5 CONFOUNDING EFFECTS OF PHYLOGENY AND STRATIFICATION

Biogeographic patterns are rarely independent of phylogenetic signatures (Avice 2009; Riddle 2009), and this is likely to be the case in the bromeliads. The spatial autocorrelation, explaining about 25 % of the variation in the proportion of CAM species in the Floras (Table 7.7), will partly be due to species radiations creating regions with a high proportion of a particular clade (Benzing 2000). Phylogeny can cause a high diversity of taxa in specific geographic locations and this would be expected in the Bromeliaceae where certain areas are hotspots for different taxa, at the generic and species levels (Givnish *et al.* 2007). Including biogeographic regions in the general linear model and spatial autoregressive model allows the model to explain variation within the regions (Table 7.7), but the models did not show a significant improvement in predictive power, suggesting importance of climate variables is consistent across ecosystems.

The effect of stratification could not be included at this scale of analysis. It has been shown that many of the epiphytic species stratify within forest canopies (Pittendrigh 1948; Griffiths & Smith 1983; Arévalo & Betancur 2006; Reyes-Garcia *et al.* 2008). The forest canopy presents strong gradients of light, temperature, rainfall and humidity. Stratification of vascular epiphytes is well established (Smith, Griffiths & Luttge 1986; Benzing 2000; Graham & Andrade 2004; Arévalo & Betancur 2006; Krömer, Kessler & Gradstein 2007; Martinez-Melendez, Perez-Farrera & Flores-Palacios 2008) and species with CAM photosynthesis are expected to be found in more arid microclimates. Although this stratification effect would mask some of the large-scale environmental difference experienced by the CAM and C₃ species, we still found significant variation in the proportions of CAM and C₃ species at different sites and in different climates. It is likely that a large amount of the residual variation in the modelled abundance of species with CAM photosynthesis may be due to stratification. This issue could be addressed by combining detailed maps of forest structure with climate data relating microclimate gradients in the different forest types found across the biogeographic regions of South America, something that airborne LiDAR surveys may soon allow us to address (Asner 2009).

7.5.6 POTENTIAL BIASES ARISING FROM THE USE OF LARGE ONLINE DATA SETS

The use of large-volume online data can only be done with critical assessment. The main source of data, the Global Biodiversity Information Facility (GBIF) does not have universal coverage, of either species or geographic areas (Yesson *et al.* 2007). GBIF itself provides a basic level of quality control on records (Chapman 2005) and this paper uses some further criteria to restrict the records, there are still going to be some errors and biases in the data. Distribution bias occurs where some regions are more intensively sampled than others, a common feature of South American botany (Schulman, Toivonen & Ruokolainen 2007). Species distribution modelling is generally robust to bias in collection data, particularly where uncommon climate regions are under-represented (Loiselle *et al.* 2008), provided distributions are carefully

checked (Feeley & Silman 2010). Taxonomic bias can occur where some species are more prominent, easier to collect and as a consequence are more frequently collected, and with epiphytic species this may be a particular risk. However, analysis of this data set has shown there is no inherent bias in favour of CAM or C_3 species. Finally mis-identifications can cause errors in the extent of species ranges, and in tropical species the rate of mis-identification of species can be up to 8% (Dexter, Pennington & Cunningham 2010), and this is likely to be a significant source of noise in any analysis.

7.5.7 CARBON ISOTOPE RATIOS

Patterns of carbon isotope ratios seen in C_3 bromeliads are consistent with those found in other studies of C_3 plants, particularly with respect to a strong trend for less negative carbon isotope ratio with decreasing precipitation (Diefendorf *et al.* 2010; Kohn 2010). A relationship between mean annual temperature and carbon isotope ratio is not discussed in detail by Diefendorf *et al.* (2010) or Kohn (2010), but the present results suggest that increasing temperatures lead to more negative carbon isotope ratios. A possible mechanistic explanation may be an increase in photosynthesis (and hence gas exchange) with increased temperature. The lack of relationship between carbon isotope ratio and climate for species with CAM photosynthesis is a result of the lower overall gas exchange, and the way these plants are less reliant on environmental water availability. Of particular note is the distinct climate niche occupied by species with carbon isotope ratios intermediate between C_3 and CAM photosynthesis (Figure 7.11). C_3 /CAM intermediates are known from the bromeliads (Smith *et al.* 1985; Pierce, Winter & Griffiths 2002a; Zotz 2002) but the ecological significance of these has not been investigated in detail. The concentration of these species in relatively cool, wet environments (Figure 7.10) merits further investigation to determine how the flexible use of both photosynthetic pathways could provide an ecological benefit (Zotz 2002).

7.5.8 CONCLUDING REMARKS

CAM photosynthesis shows strong ecological niche differentiation along the water availability gradient. At a broad scale, terrestrial bromeliad species with CAM photosynthesis show a higher environmental suitability than species with C_3 photosynthesis in habitats with annual rainfall of less than 2250 mm. This trend contrasts with the pattern seen in epiphytic bromeliads. Epiphytic bromeliad species are adapted to a water-stressed niche and on broad ecological scales there is little niche differentiation along rainfall gradients; instead niche differentiation occurs along the temperature gradient. I propose this represents the ecological benefit of a CCM in terms of relative reduction of photorespiration at higher temperatures compared to C_3 species. In terms of ecology, CAM photosynthesis may be more similar to C_4 photosynthesis than has previously been assumed.

7.6 BIBLIOGRAPHY

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7.7 APPENDIX 1: OUTPUT OF MODEL SELECTION PROCEDURE

These are the outputs of the model selection procedure to select the variables to put forwards into the final model.

RUN 1: TEMPERATURE

Total of 2047 OLS models run, in 0.09 minutes

Response variable is ArcSin-SqRoot(pCAM).

Explanatory variables are:

Variable #1: Annual mean temperature

Variable #2: Daily temperature range

Variable #3: Isothermality

Variable #4: Temperature seasonality

Variable #5: Temperature of warmest month

Variable #6: Temperature of coldest month

Variable #7: Annual temperature range

Variable #8: Mean temperature of the wettest 3 months

Variable #9: Mean temperature of the driest 3 months

Variable #10: Mean temperature of the warmest 3 months

Variable #11: Mean temperature of the coldest 3 months

Results for the OLS Model Selection procedure, sorted by Akaike Information Criterion (AICc).

Model	Variables	nVars	r ²	Cond.Num.	AICc	Δ AICc	L(gi x)	AICc wi
Mod #887	1, 4, 8, 9, 11	5	0.690	99.8	-14.04	0.00	1.00	0.062
Mod #1013	1, 8, 9, 10, 11	5	0.686	78.5	-13.48	0.56	0.76	0.047
Mod #1014	1, 8, 9, 11	4	0.666	43.3	-13.23	0.81	0.67	0.041
Mod #824	1, 4, 5, 8, 9, 11	6	0.697	111.2	-12.31	1.73	0.42	0.026
Mod #951	1, 5, 8, 9, 11	5	0.678	59.5	-12.23	1.82	0.40	0.025

RUN 2: PRECIPITATION

Total of 1023 OLS models run, in 0.07 minutes

Response variable is ArcSin-SqRoot(pCAM).

Explanatory variables are:

Variable #1: Annual precipitation

Variable #2: Precipitation of the wettest month

Variable #3: Precipitation of the driest month

Variable #4: Precipitation seasonality

Variable #5: Precipitation of the wettest 3 months

Variable #6: Precipitation of the driest 3 months

Variable #7: Precipitation of the warmest 3 months

Variable #8: Precipitation of the coldest 3 months

Variable #9: Wetdays

Variable #10: MCWD

Results for the OLS Model Selection procedure, sorted by Akaike Information Criterion (AICc).

Model	Variables	nVars	r ²	Cond.Num.	AICc	Δ AICc	L(gi x)	AICc wi
Mod #368	1, 3, 6, 9	4	0.236	26.41	26.46	0.00	1.00	0.026
Mod #879	3, 6, 9	3	0.188	23.39	26.76	0.30	0.86	0.023
Mod #624	2, 3, 6, 9	4	0.226	24.12	27.12	0.66	0.72	0.019
Mod #848	3, 5, 6, 9	4	0.224	24.11	27.24	0.78	0.68	0.018
Mod #383	1, 3, 9	3	0.174	2.98	27.61	1.15	0.56	0.015

RUN 3: TOPOGRAPHY

Total of 3 OLS models run, in 0.05 minutes

Response variable is ArcSin-SqRoot(pCAM).

Explanatory variables are:

Variable #1: Maximum altitude

Variable #2: Topographic variation

Results for the OLS Model Selection procedure, sorted by Akaike Information Criterion (AICc).

Model	Variables	nVars	r ²	Cond.Num.	AICc	Δ AICc	L(gi x)	AICc wi
Mod #2	1, 2	2	0.419	3.76	8.19	0.00	1	1
Mod #1	1	1	0.154	1.00	23.89	15.70	<.001	<.001
Mod #3	2	1	0.007	1.00	31.56	23.37	<.001	<.001

RUN 4: EVAPOTRANSPIRATION

Total of 15 OLS models run, in 0.05 minutes

Response variable is ArcSin-SqRoot(pCAM).

Explanatory variables are:

Variable #1: Annual AET

Variable #2: Annual PET

Variable #3: Annual water balance

Variable #4: Relative Humidity

Results for the OLS Model Selection procedure, sorted by Akaike Information Criterion (AICc).

Model	Variables	nVars	r ²	Cond.Num.	AICc	Δ AICc	L(gi x)	AICc wi
Mod #15	4	1	0.041	1	29.871	0	1	0.257
Mod #8	1, 4	2	0.05	1.542	31.817	1.946	0.378	0.097
Mod #13	3	1	<.001	1	31.871	2.001	0.368	0.094
Mod #9	2	1	<.001	1	31.873	2.003	0.367	0.094
Mod #1	1	1	<.001	1	31.89	2.02	0.364	0.094

RUN 5: SEASONALITY

Total of 2047 OLS models run, in 0.12 minutes

Response variable is ArcSin-SqRoot(pCAM).

Explanatory variables are:

Variable #1: Annual mean temperature

Variable #2: Temperature seasonality

Variable #3: Mean temperature of the wettest 3 months

Variable #4: Mean temperature of the driest 3 months

Variable #5: Mean temperature of the coldest 3 months

Variable #6: Annual precipitation

Variable #7: Precipitation of the driest month

Variable #8: Precipitation of the driest 3 months

Variable #9: Maximum altitude

Variable #10: Topographic variation

Variable #11: Relative Humidity

Results for the OLS Model Selection procedure, sorted by Akaike Information Criterion (AICc).

Model	Variables	nVars	r ²	Cond.Num.	AICc	Δ AICc	L(gi x)	AICc wi
Mod #521	1, 3, 4, 5, 6, 7, 8, 9, 10	9	0.870	56.744	-43.32	0	1	0.234
Mod #522	1, 3, 4, 5, 6, 7, 8, 9, 10, 11	10	0.878	61.846	-42.671	0.65	0.723	0.169
Mod #528	1, 3, 4, 5, 6, 7, 9, 10	8	0.858	52.854	-42.462	0.858	0.651	0.152
Mod #10	1, 2, 3, 4, 5, 6, 7, 8, 9, 10	10	0.874	154.841	-41.237	2.084	0.353	0.082
Mod #529	1, 3, 4, 5, 6, 7, 9, 10, 11	9	0.864	57.175	-41.041	2.279	0.32	0.075

7.8 APPENDIX 2: CITATIONS FOR ONLINE DATA SOURCES

7.8.1 SPECIES LINK DATA SOURCES

Information on bromeliad distribution was taken from the following databases through the

Species Link data portal (<http://splink.cria.org.br>):

- Coleção de plantas medicinais e aromáticas
- Banco de DNA do Jardim Botânico do Rio de Janeiro
- Carpoteca
- Coleção de Fanerógamas do Herbário do Estado "Maria Eneyda P. Kaufmann Fidalgo"
- Fundación Puerto Rastrojo - Colombia

-
- Herbário da Escola Superior de Agricultura Luiz de Queiroz
 - Herbário da Universidade Estadual de Campinas
 - Herbário da Universidade Estadual de Londrina
 - Herbário Dimitri Sucre Benjamin
 - Herbário do Instituto Agronômico de Campinas
 - Herbário Dom Bento Pickel
 - Herbário Lauro Pires Xavier
 - Missouri Botanical Garden
 - Sistema de Informação do Programa Biota/Fapesp

7.8.2 GBIF DATA SOURCES

Information on bromeliad distribution was taken from the databases listed in Table 8.8 through the Global Biodiversity Information Facility (GBIF) (www.gbif.org):

Table 8.8. Data sources and links for data in the GBIF.

Database	Link
Andes to Amazon Biodiversity Program	http://secretariat.mirror.gbif.org/datasets/resource/56
Arizona State University Vascular Plant Herbarium	http://secretariat.mirror.gbif.org/datasets/resource/676
Australian National Herbarium (CANB)	http://secretariat.mirror.gbif.org/datasets/resource/47
Banco Nacional de Germoplasma Vegetal, México (BANGEV, UACH)	http://secretariat.mirror.gbif.org/datasets/resource/1599
Biodiversidad de Costa Rica	http://secretariat.mirror.gbif.org/datasets/resource/333
Biologiezentrum Linz	http://secretariat.mirror.gbif.org/datasets/resource/1104
Bishop Museum Natural History Specimen Data	http://secretariat.mirror.gbif.org/datasets/resource/54
BoGART	http://secretariat.mirror.gbif.org/datasets/resource/1087
Botanical Garden Collection	http://secretariat.mirror.gbif.org/datasets/resource/64
Botanical Garden Joensuu	http://secretariat.mirror.gbif.org/datasets/resource/1385

Botanical Museum, Denmark. Database of registrations of red listed plants	http://secretariat.mirror.gbif.org/datasets/resource/716
Botanical Society of the British Isles - Vascular Plants Database	http://secretariat.mirror.gbif.org/datasets/resource/839
Botanischer Garten Bochum	http://secretariat.mirror.gbif.org/datasets/resource/1366
Botanischer Garten Bonn	http://secretariat.mirror.gbif.org/datasets/resource/1374
Botanischer Garten Darmstadt	http://secretariat.mirror.gbif.org/datasets/resource/1361
Botanischer Garten der Christian-Albrechts-Universität zu Kiel	http://secretariat.mirror.gbif.org/datasets/resource/1378
Botanischer Garten Frankfurt	http://secretariat.mirror.gbif.org/datasets/resource/1372
Botanischer Garten Freiburg	http://secretariat.mirror.gbif.org/datasets/resource/1368
Botanischer Garten Gießen	http://secretariat.mirror.gbif.org/datasets/resource/1362
Botanischer Garten Graz	http://secretariat.mirror.gbif.org/datasets/resource/1390
Botanischer Garten Jena	http://secretariat.mirror.gbif.org/datasets/resource/1381
Botanischer Garten Marburg	http://secretariat.mirror.gbif.org/datasets/resource/1364
Botanischer Garten Munster	http://secretariat.mirror.gbif.org/datasets/resource/1383
Botanischer Garten Osnabruck	http://secretariat.mirror.gbif.org/datasets/resource/1382
Botanischer Garten Regensburg	http://secretariat.mirror.gbif.org/datasets/resource/1387
Botanischer Garten Rostock	http://secretariat.mirror.gbif.org/datasets/resource/1369
Botanischer Garten Saarbrücken	http://secretariat.mirror.gbif.org/datasets/resource/1376
Botanischer Garten TU Dresden	http://secretariat.mirror.gbif.org/datasets/resource/1363
Botanischer Garten Ulm	http://secretariat.mirror.gbif.org/datasets/resource/1359
California State University, Chico	http://secretariat.mirror.gbif.org/datasets/resource/737
Canadian Museum of Nature Herbarium	http://secretariat.mirror.gbif.org/datasets/resource/123
Database Schema for UC Davis [Herbarium Labels]	http://secretariat.mirror.gbif.org/datasets/resource/734
Fairchild Tropical Botanic Garden Virtual Herbarium Darwin Core format	http://secretariat.mirror.gbif.org/datasets/resource/202
Forstbotanischer Garten Tharandt	http://secretariat.mirror.gbif.org/datasets/resource/1370
Fruit and seed collection database	http://secretariat.mirror.gbif.org/datasets/resource/1093
Gothenburg Herbarium - Types (GBIF:IH:GB:Herbarium)	http://secretariat.mirror.gbif.org/datasets/resource/1766

Gruga-Park Essen	http://secretariat.mirror.gbif.org/datasets/resource/1384
Harvard University Herbaria	http://secretariat.mirror.gbif.org/datasets/resource/1827
HerbarImages	http://secretariat.mirror.gbif.org/datasets/resource/1095
Herbario de la Universidad de Sevilla, SEV-Historico	http://secretariat.mirror.gbif.org/datasets/resource/284
Herbario del Instituto de Ecología, A.C., México (IE-BAJIO)	http://secretariat.mirror.gbif.org/datasets/resource/1595
Herbario del Instituto de Ecología, A.C., México (IE-XAL)	http://secretariat.mirror.gbif.org/datasets/resource/1597
Herbario Los Tuxtlas	http://secretariat.mirror.gbif.org/datasets/resource/785
Herbario UNAP	http://secretariat.mirror.gbif.org/datasets/resource/223
Herbarium (UNA)	http://secretariat.mirror.gbif.org/datasets/resource/775
Herbarium des Staatlichen Museums für Naturkunde Görlitz (GLM)	http://secretariat.mirror.gbif.org/datasets/resource/1105
Herbarium of Oskarshamn (OHN)	http://secretariat.mirror.gbif.org/datasets/resource/1024
Herbarium specimen from "BIEL", Germany	http://secretariat.mirror.gbif.org/datasets/resource/1857
Herbarium specimen from the Estacion Scientifica San Francisco, Southern Ecuador	http://secretariat.mirror.gbif.org/datasets/resource/1614
Herbarium Specimens of Museum of Nature and Human Activities, Hyogo Pref., Japan	http://secretariat.mirror.gbif.org/datasets/resource/589
Herbarium Universitat Ulm	http://secretariat.mirror.gbif.org/datasets/resource/1224
Herbarium WU	http://secretariat.mirror.gbif.org/datasets/resource/1496
Herbier de la Guyane	http://secretariat.mirror.gbif.org/datasets/resource/1436
Herbier de Nouvelle-Caledonie	http://secretariat.mirror.gbif.org/datasets/resource/1990
Herrenhauser Garten Hannover (Berggarten)	http://secretariat.mirror.gbif.org/datasets/resource/1394
IIAPPoa	http://secretariat.mirror.gbif.org/datasets/resource/656
Ilha Solteira, Herbario	http://secretariat.mirror.gbif.org/datasets/resource/1266
Institut Botanic de Barcelona, BC	http://secretariat.mirror.gbif.org/datasets/resource/299
Institut Botanic de Barcelona, BC-Histórico	http://secretariat.mirror.gbif.org/datasets/resource/1523
Instituto de Botanica	http://secretariat.mirror.gbif.org/datasets/resource/1252
Instituto de Pesquisas Cientificas e Tecnologicas do Estado do Amapa	http://secretariat.mirror.gbif.org/datasets/resource/1246
Internation Botanical Collections (S)	http://secretariat.mirror.gbif.org/datasets/resource/1983

Jardín Botánico de Córdoba: Herbarium COA	http://secretariat.mirror.gbif.org/datasets/resource/247
MEXU/Colección Histórica	http://secretariat.mirror.gbif.org/datasets/resource/1984
MEXU/Plantas Vasculares	http://secretariat.mirror.gbif.org/datasets/resource/780
Missouri Botanical Garden	http://secretariat.mirror.gbif.org/datasets/resource/621
Museo Ecuatoriano de Ciencias Naturales	http://secretariat.mirror.gbif.org/datasets/resource/1268
Museo Nacional de Costa Rica	http://secretariat.mirror.gbif.org/datasets/resource/1269
Museu Botanico Municipal	http://secretariat.mirror.gbif.org/datasets/resource/1239
Nationaal Herbarium Nederland	http://secretariat.mirror.gbif.org/datasets/resource/1211
Nationaal Herbarium Nederland - Leiden Branch	http://secretariat.mirror.gbif.org/datasets/resource/1085
NatureServe Network Species Occurrence Data	http://secretariat.mirror.gbif.org/datasets/resource/607
Neuer Botanischer Garten Gottingen	http://secretariat.mirror.gbif.org/datasets/resource/1373
New Zealand National Plant Herbarium (CHR)	http://secretariat.mirror.gbif.org/datasets/resource/474
NSW herbarium collection	http://secretariat.mirror.gbif.org/datasets/resource/968
Okologisch Botanischer Garten Bayreuth	http://secretariat.mirror.gbif.org/datasets/resource/1360
Orto Botanico di Pisa	http://secretariat.mirror.gbif.org/datasets/resource/1386
Paleobiology Database	http://secretariat.mirror.gbif.org/datasets/resource/563
Palmengarten Frankfurt	http://secretariat.mirror.gbif.org/datasets/resource/1395
Phanerogamie	http://secretariat.mirror.gbif.org/datasets/resource/1506
Plants from Costa Rica; Helmut Dalitz	http://secretariat.mirror.gbif.org/datasets/resource/1853
Plants from Costa Rica; Juergen Homeier	http://secretariat.mirror.gbif.org/datasets/resource/1612
Plants from RBAMB, Costa Rica; Helmut Dalitz	http://secretariat.mirror.gbif.org/datasets/resource/1609
Plants from Southern Ecuador; Ben Hell	http://secretariat.mirror.gbif.org/datasets/resource/1621
Plants from Southern Ecuador; Daniel Piechowski	http://secretariat.mirror.gbif.org/datasets/resource/1638
Plants from Southern Ecuador; Florian Werner	http://secretariat.mirror.gbif.org/datasets/resource/1617
Plants from Southern Ecuador; Helmut Dalitz	http://secretariat.mirror.gbif.org/datasets/resource/1629
Plants from Southern Ecuador; Juergen Homeier	http://secretariat.mirror.gbif.org/datasets/resource/1613
Plants from Southern Ecuador; Ulf Soltau	http://secretariat.mirror.gbif.org/datasets/resource/1623
Private collection of Asta Napp-Zinn	http://secretariat.mirror.gbif.org/datasets/resource/1637
Real Jardin Botanico (Madrid), Vascular Plant Herbarium (MA)	http://secretariat.mirror.gbif.org/datasets/resource/240

Royal Botanic Gardens, Kew	http://secretariat.mirror.gbif.org/datasets/resource/629
Royal Museum of Central Africa - Metafro-Infosys - Prelude	http://secretariat.mirror.gbif.org/datasets/resource/96
Royal Museum of Central Africa - Metafro-Infosys - Xylarium	http://secretariat.mirror.gbif.org/datasets/resource/95
SANT herbarium vascular plant collection	http://secretariat.mirror.gbif.org/datasets/resource/222
SERNEC - University of North Carolina at Chapel Hill - Plants	http://secretariat.mirror.gbif.org/datasets/resource/895
Staatliches Museum für Naturkunde Stuttgart, Herbarium	http://secretariat.mirror.gbif.org/datasets/resource/1100
SysTax	http://secretariat.mirror.gbif.org/datasets/resource/1875
The AAU Herbarium Database	http://secretariat.mirror.gbif.org/datasets/resource/224
The Danish Royal Veterinary and Agricultural University's Arboretum	http://secretariat.mirror.gbif.org/datasets/resource/702
The Deaver Herbarium, Northern Arizona University	http://secretariat.mirror.gbif.org/datasets/resource/678
Type herbarium, Gottingen (GOET)	http://secretariat.mirror.gbif.org/datasets/resource/1494
UCD Botanical Conservatory	http://secretariat.mirror.gbif.org/datasets/resource/739
United States National Plant Germplasm System Collection	http://secretariat.mirror.gbif.org/datasets/resource/1429
Universidad de Costa Rica	http://secretariat.mirror.gbif.org/datasets/resource/1184
Universidad Nacional de Loja	http://secretariat.mirror.gbif.org/datasets/resource/1284
Universidad Politécnica de Madrid, Dpto. Biología Vegetal, Banco de Germoplasma	http://secretariat.mirror.gbif.org/datasets/resource/1521
Universidade de Brasilia	http://secretariat.mirror.gbif.org/datasets/resource/1272
Universidade Federal de Mato Grosso	http://secretariat.mirror.gbif.org/datasets/resource/1254
Universidade Federal do Rio Grande do Sul	http://secretariat.mirror.gbif.org/datasets/resource/1280
University of California Botanical Garden DiGIR provider	http://secretariat.mirror.gbif.org/datasets/resource/1412
USDA PLANTS Database	http://secretariat.mirror.gbif.org/datasets/resource/1066
USU-UTC Specimen Database	http://secretariat.mirror.gbif.org/datasets/resource/1508
UTCP	http://secretariat.mirror.gbif.org/datasets/resource/1540
Vascular Plant Type Specimens	http://secretariat.mirror.gbif.org/datasets/resource/731

8. DISCUSSION

8.1 ALTITUDINAL PATTERNS OF BROMELIAD ECOLOGY

The eastern slope of the Andes is dominated by the climate gradients resulting from the rapid spatial changes in altitude (Malhi *et al.* 2010). While most environmental factors vary continuously along the gradient, the combination of factors can lead to distinctive landscape-scale ecological zones forming *sensu* Grubb and Whitmore (1966). While it has been long established that the tree flora form these distinct zones in the eastern Andes, in this thesis I have shown the vascular epiphytes also form distinctive ecological zones in the eastern Andes, and have been able to define these zones from empirical data. Here these forested ecological zones are referred to as lowland rainforest (LRF), tropical montane forest (TMF) and tropical montane cloud forest (TCF) (Chapter 4). The boundaries of these forest types are within the range of equivalent zone boundaries reported by Grubb and Whitmore (1966). The estimated range limits for the ecological zones in this study occur around 1000 m for the LRF – TMF boundary and 2250 m for the TMF – TCF boundary (Figure 8.1). The three ecological zones were found to support distinct epiphyte ecologies (Figure 8.1) and bromeliad species' ranges were generally limited to one of these three climate zones, although some species do exist across these divisions (Chapter 6).

The three ecological zones of bromeliads delimited here are likely be determined largely by climate, and particularly precipitation in the same way the tree species are divided into ecological zones (Grubb *et al.* 1963; Grubb & Whitmore 1966; Grubb & Whitmore 1967). These boundaries are similar to the boundaries of ecological zones of tree species and there might be a relationship between forest structure in different ecological zones, and the vascular epiphytes, meaning ecological zones for epiphytes are partly determined by ecological zones of trees. Some studies have found an extra ecological zone in the eastern Andes including Ibisch's

classification based on epiphyte diversity which includes a 'sub-Andean rainforest' (Ibisch *et al.* 1996). Other distinct ecological zones of epiphytes have been shown for Colombian cloud forests where moisture from the prevailing wind was the most important factor in defining ecological zones (Sugden 1981). Ecological zones across Costa Rica show unique bromeliad flora, and this is anecdotally related to rainfall of the zones (Burt-Utley & Utley 1980). One study examining communities at this scale failed to find distinct communities in east-Andean Peruvian cryptograms (Kessler 2000), although the study found ecological zones based on cryptogram species in other Neotropical forests. The ecological zones of epiphytes found in this study are discussed in more detail below.

8.1.1 LOWLAND RAINFOREST

The LRF has the highest annual mean temperature, with the tallest trees and highest tree diversity. However, in the LRF the bromeliad biomass and diversity is lowest. This matches the results of other studies which show that most parts of lowland Amazonia support very few epiphytes (Gentry & Dodson 1987; Kessler 2002). At this site the few species that are present include the most diverse array of forms, as well as all the species with CAM photosynthesis. The LRF had a higher proportion of bromeliad species with narrow tubular shoot design (*e.g.* *Billbergia* spp.), and species with long, narrow leaves (*e.g.* *Aechmea longifolia*, *Guzmania calothyrsus*). In the LRF there is also stratification of bromeliads, with species with CAM photosynthesis occupying higher canopy sites than species with C₃ photosynthesis. The high biomass and diversity of the tree flora means that in these forests vascular epiphytes make very little contribution to any ecosystem function.

While most sites and plots were consistently shown to be part of one particular ecological zone, the PSP at Tono appeared intermediate between LRF and TMF. Ultimately it was classified with the LRF based primarily on the plotless sampling of bromeliads. However a PSP not included in the study suggests this forest has a distinct woody species composition

(Huamantupa-Chuquimaco 2010) and might represent a distinct ecological zones that would correspond to the 'sub-Andean rainforest' zone delimited by Ibisch *et al.* (1996). This could be confirmed by more intensive sampling around this altitude.

8.1.2 TROPICAL MONTANE FOREST

At other sites the peak of epiphyte diversity (Gentry & Dodson 1987; Hietz & Hietz-Seifert 1995; Ibisch *et al.* 1996; Kessler 2002; Krömer *et al.* 2005; Cardelús, Colwell & Watkins 2006) and biomass (Hietz & Hietz-Seifert 1995; Hölscher *et al.* 2004; Nadkarni *et al.* 2004; Kohler *et al.* 2007) are reported from altitudes corresponding to the TMF ecological zone (between 1000 m and 2250 m). In this transect the TMF had the highest α -diversity of bromeliads, although not the highest species richness. This probably reflects the fact that those sites with a higher abundance (and biomass) of bromeliads are dominated by a small number of species and this reduces α -diversity. The biomass of vascular epiphytes in the TMF along this transect was similar to biomass in the TCF, but less variable, and did not reach the very high values found in some parts of the TCF. Included as part of the TMF are the PSPs at the Trocha Union site below 2500 m (TU7 and TU8). These plots occur above the cloud base that define the lower limit of the TCF based on tree species composition. Species composition for bromeliads showed these plots to be more similar to the TMF plots at lower altitude. In addition the vascular epiphyte biomass was significantly lower in these two plots. This leads to a suggestion that these plots may be in recovery following disturbance from landslides, especially as these PSPs have a high slope. The disturbance would create drier, more open conditions that might lead to recolonisation by bromeliad species from lower altitudes, and a lag in the recovery of epiphyte biomass as forest structure recovers. Unfortunately data is currently unavailable to confirm this hypothesis, but landslides are a well known feature of the eastern Andes (Kessler 1999).

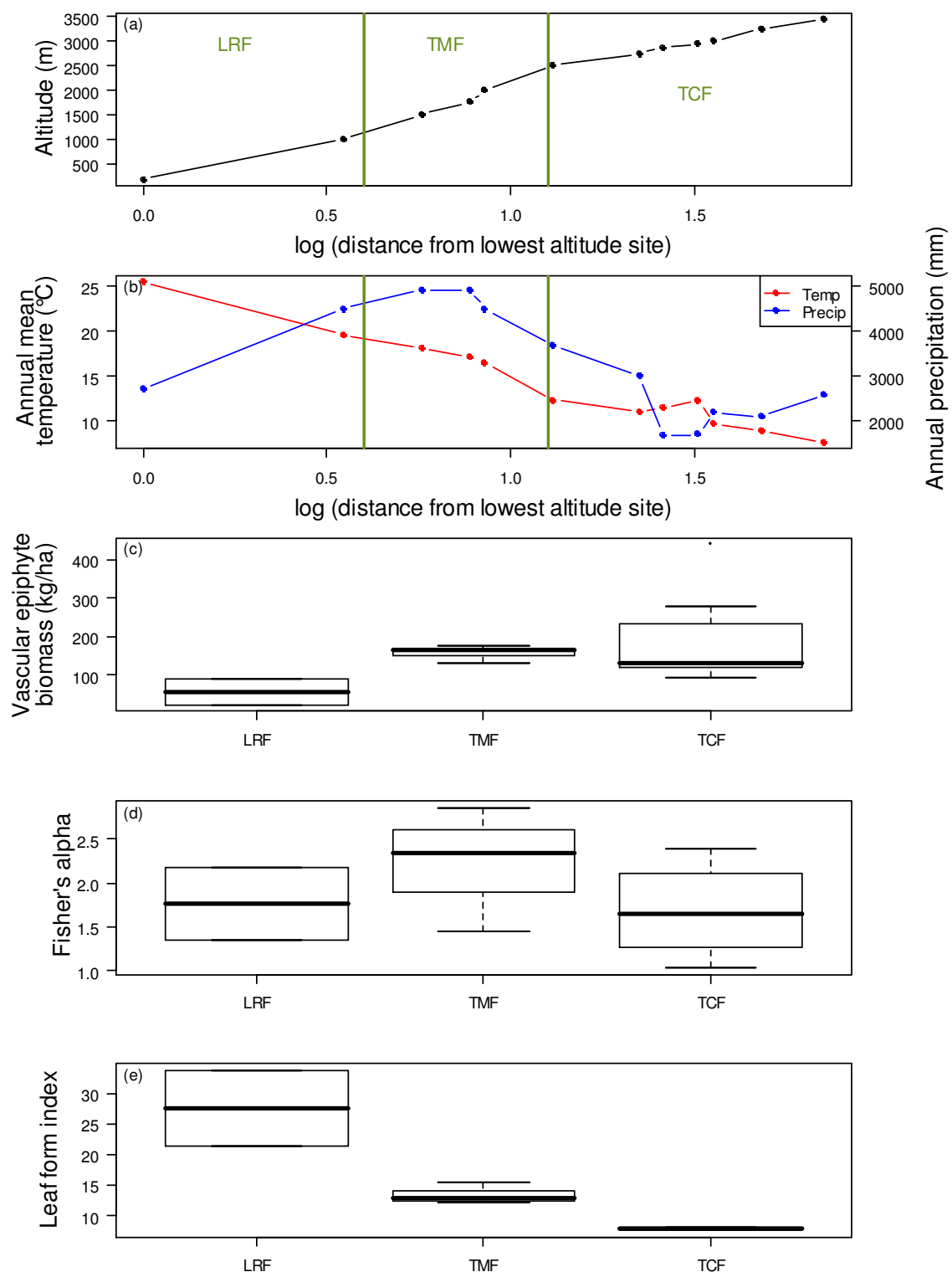


Figure 8.1. Summary of altitudinal trends for vascular epiphytes and the associated climate. Individual plots show: (b) Climate data is based on values for 12 PSPs reported in chapter 3; (c) Vascular epiphyte biomass data (from Chapter 5) averaged over plots for each ecological zone; (d) Fisher's alpha (from Chapter 4) averaged by ecological zone and (e) Leaf form index (Chapter 6) average of species found within each ecological zone.

8.1.3 TROPICAL MONTANE CLOUD FOREST

The TCF is a unique ecological zone characterised by prolonged cloud immersion leading to very low potential evapotranspiration. This forest has the highest biomass of vascular epiphytes (Figure 8.1), as well as the highest species richness of bromeliads (Chapter 4). The low evapotranspiration created by a high level of cloud immersion creates a forest rich in epiphytic bryophytes (Horwath 2011) as well as vascular epiphytes. This forest also had the lowest variation in plant form, with species all having a phytotelm apparently optimised to maximise leaf surface and water storage.

The high biomass and diversity of vascular epiphytes, and particularly bromeliads in the TCF are one reason why they are considered to be one of the most important aspects of this ecosystem (Myers *et al.* 2000). Phytotelm bromeliads in the TCF are optimised to store water (Chapter 6) and this in turn creates the ‘aerial lakes’ that are important for both wildlife (Richardson *et al.* 2000; Wittman 2000; Armbruster, Hutchinson & Cotgreave 2002; Jabiol *et al.* 2009; da Silva, Carvalho & Bittencourt-Silva 2011) and the cycling of greenhouse gasses (Martinson *et al.* 2010).

One PSP in the cloud forest, TU2, has exceptionally high vascular epiphyte biomass. It is proposed that a recent landslide on the edge of this PSP may have lead to the rapid vegetative proliferation of bromeliads, particularly *Tillandsia rubella*, in this plot.

8.2 DIVERSITY AND ABUNDANCE OF BROMELIADS IN COMPARISON TO THE WIDER ECOSYSTEM

The investigation of bromeliad diversity and vascular epiphyte biomass quantified the contribution that vascular epiphytes can make to the overall forest processes. In addition, the quantitative data can be used to compare the sites used in this study to sites elsewhere in South America. The pattern of diversity of bromeliads along this altitudinal gradient did not match the

diversity of tree species (Chapter 4) suggesting the drivers of epiphyte diversity are different to the tree flora. This is expected as tree diversity is strongly influenced by biotic factors (Bamfylde *et al.* 2005; Levine & HilleRisLambers 2009; Mangan *et al.* 2010), whereas epiphytes, in a stress-tolerant niche *sensu* Grime (1977) are more tightly linked to climate (Benzing 1998). The difference between the pattern of biomass along the altitudinal gradient of vascular epiphytes and of woody species (Chapter 5) is likely to arise for the same reasons. This supports the hypothesis that epiphytes are tightly linked to climate (Benzing 1998), and therefore are likely to be more sensitive to changes in the pattern of rainfall resulting from global climate change (O'Gorman 2012).

The overall diversity of bromeliads along this transect (Chapter 4) was lower than diversity found elsewhere in South America (Gentry & Dodson 1987; Hietz & Hietz-Seifert 1995; Ibach *et al.* 1996; Kessler 2002; Krömer *et al.* 2005), however the same is true of the diversity of trees when compared to other locations (Pitman *et al.* 2002). The vascular epiphyte biomass (Chapter 5) was also significantly lower than values reported from comparable altitudes in other studies (Hietz & Hietz-Seifert 1995; Hölscher *et al.* 2004; Nadkarni *et al.* 2004; Kohler *et al.* 2007). Two factors commonly cited to limit both biomass and diversity of vascular epiphytes are water-availability and seasonality (of both water and temperature) (e.g. Gentry & Dodson 1987; Zotz 2005b; Gehrig-Downie *et al.* 2011), but these field sites, between 12°S and 14°S of the equator, and located in an Andean superhumid zone (Killeen *et al.* 2007) are not likely to be too severely stressed by either of these factors. An alternative explanation may be the disturbances resulting from landslides that are frequent occurrences above 1000 m for all sites along this transect (K. Clarke, unpublished data). Both diversity and biomass of vascular epiphytes are slow to recover following disturbance (Dunn 2000; Barthlott *et al.* 2001; Hietz, Buchberger & Winkler 2006).

The patchy spatial distribution of vascular epiphytes is an important consideration for any study of the ecology of these plants (Nieder *et al.* 2000; Wolf 2005; Wolf, Gradstein & Nadkarni 2009), and is especially important in the context of permanent sample plots. In Chapter 4 I have shown that the total diversity recorded in each 1 ha PSP is lower than the diversity expected from the number of species predicted to be present by overlapping altitudinal ranges. While differences in microclimate, and host tree structure may partially account for absences, the patchy distribution, a consequence of dispersal limitation (Cascante-Marín *et al.* 2009), is likely to be the largest source of recorded absences from within the 1 ha plots. This is particularly a problem for rare species, and all species are generally rare towards their altitudinal limits (Sexton *et al.* 2009).

8.3 CAM PHOTOSYNTHESIS

CAM photosynthesis is an important adaptation in the Bromeliaceae, but is prevalent across the plant kingdom. Although the benefits of CAM photosynthesis as a carbon concentrating mechanism were well understood (Lüttge 2004; Andrade *et al.* 2007), a broad scale comparison of the ecological impact of the benefits had previously been absent from the literature. The importance of CAM photosynthesis in semi-arid environments is well known (Cushman 2001). Families such as Cactaceae, Agavaceae and Crassulaceae which are prevalent, species rich and conspicuous plants of semi-arid environments include only species with CAM photosynthesis (Teeri, Stowe & Murawski 1978; Nobel 1988). In contrast the Bromeliaceae, with approximately 50% CAM species provides an ideal family to compare the ecology of the two photosynthetic pathways.

In the altitudinal transect, bromeliads with CAM photosynthesis were only present below 1400 m (Chapter 6), in the sites which had the longest periods where phytotelm bromeliads would be without water. However, to fully understand the importance of CAM photosynthesis a

wider scale of investigation was used. At the continental scale I have shown that terrestrial bromeliads CAM photosynthesis is an adaptation to arid environments (Chapter 7). In epiphytic bromeliads, already adapted to a water-stressed niche, the data indicates that CAM bromeliads are more prevalent in warmer environments. There are two hypotheses for this result that could not be tested in the scope of this work. This could result from microclimate gradients, and associated micrositeing of species with CAM photosynthesis into the driest sites (*e.g.* Reyes-Garcia *et al.* 2008). Alternatively this could be a result of increased quantum yield efficiencies at higher temperatures in CAM plants, as seen in C_4 plants (Ehleringer 1978).

The input data used in this study, coming from large online datasets, results in loss of accuracy in the model due to noise in the data. Testing and refining the model using field data will allow more accurate predictions. Comparing data on the distribution of species with CAM photosynthesis from the PSPs in this study (Chapter 6) and the predicted habitat suitability based on the distribution models from Chapter 7 we can see that while most of the PSPs with exclusively C_3 species occur in climate conditions predicted to be more suitable for C_3 species, the two plots which include some species with CAM photosynthesis occur in climate conditions which do not appear most suitable for either photosynthetic pathway (Figure 8.2). The species distribution models could be improved with more accurate baseline data on the distribution of the Bromeliaceae. However, these predicted habitat suitability models should be tested against field data from a wider area and refined to provide a useful tool for predicting the occurrence of species with CAM photosynthesis.

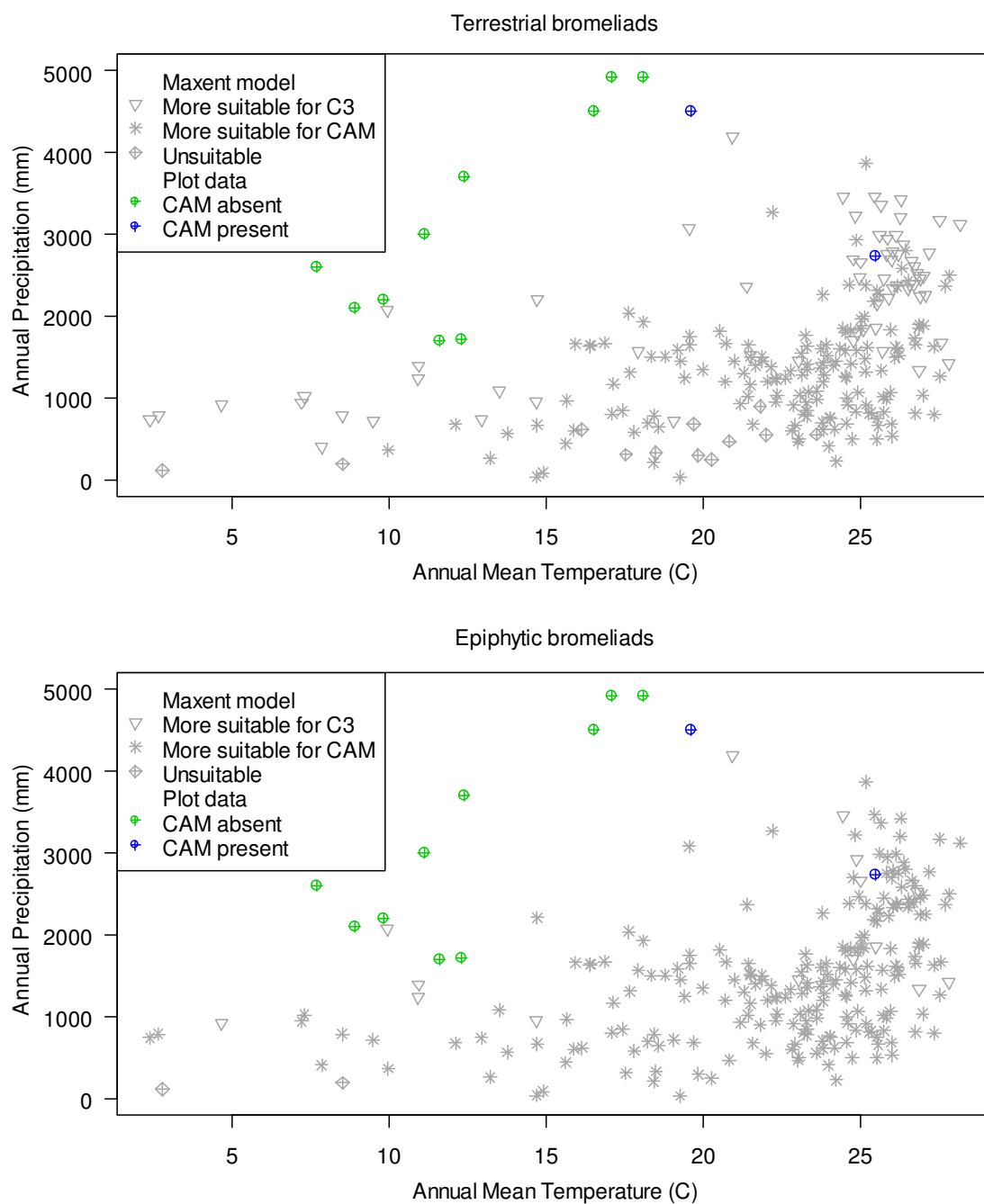


Figure 8.2. Data from the PSPs in this transect (coloured symbols) superimposed on the output of the CAM/C3 habitat suitability models. Separate plots are shown for models based on epiphytic species and terrestrial species due to the different patterns observed in these models. The habitat suitability data is illustrated in colour in Chapter 7.

8.4 FURTHER WORK

While this study has established underlying distribution patterns in the Bromeliaceae found along this montane transect, there large potential to develop this knowledge to provide data on the demography of populations. The demography of populations will indicate how species ranges are changing, if species have viable population numbers (Zotz 2005a; Feeley & Silman 2010).

While the taxonomy was resolved using morphological characters, many plants found in the Kosnipata Valley show some degree of hybridisation. Molecular DNA work would help to establish taxa, and allow plants to be identified with more certainty (Dexter, Pennington & Cunningham 2010). Many 'taxa' within the Bromeliaceae are not well defined, and the family is undergoing constant revision, even at the generic level (Horres *et al.* 2000; Crayn, Winter & Smith 2004; Givnish *et al.* 2004; Barfuss *et al.* 2005; Givnish *et al.* 2007; Schulte & Zizka 2008). Large sets of molecular phylogenetic data would also allow for geographic studies and to include phylogenetic relatedness in any discussion of ecological niches (Morlon *et al.* 2011), as it is likely the species found in montane forests show a high degree of phylogenetic niche conservatism (Peterson 2011).

The measurement of gas exchange from vascular epiphytes will complete the picture of whole forest carbon cycling, but vascular epiphytes are known to have low transpiration rates, possibly as a result of the 'water-stressed' niche they occupy (Benzing 2000). However, new research shows bromeliads will have a much more significant impact on methane cycling (Martinson *et al.* 2010). Detailed studies of methane gas exchange will allow the impact of bromeliads on climate change to be fully understood.

Finally, quantifying the true importance of bromeliads to the montane forest ecosystem can only really be achieved through study of the biota of the tanks, and species involved in the food

web centred around the tanks, which can be exceptionally diverse (Richardson *et al.* 2000; Wittman 2000; Jabiol *et al.* 2009; da Silva, Carvalho & Bittencourt-Silva 2011). Some work is already underway at one of the sites in this study to quantify and identify species of invertebrates using the tank (D. Hidaglo, pers. comm.).

8.5 CONCLUDING REMARKS

I have shown that bromeliads form distinct ecological zones in the eastern Andes, and that these zones are largely driven by climate, and the species' adaptations to these climates. The conservation of bromeliads and vascular epiphytes in general should be considered essential in Manu National Park and elsewhere. More studies of diversity, range limits and ecology are necessary to understand the impact of climate change on the individual species and the implications of this for the ecosystem. Here I have shown that bromeliad diversity and biomass do not follow simple altitudinal patterns but instead have distinct ecological zones, and that close links between ecological zones of the forest and the epiphytes are a prominent feature of these ecosystems. The complexity of epiphyte distribution is one of the main reason these species are so fascinating to study, and why they can reveal important ecological information.

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APPENDIX A: CHECKLIST OF THE BROMELIACEAE OF THE KOSÑIPATA VALLEY AND ADJACENT AREAS WITH NOTES ON IDENTIFICATION

A1. INTRODUCTION

This appendix deals with the identification of species found along the altitudinal transect as part of this study. The section includes a brief introduction, a dichotomous key and an illustrated, annotated checklist of the species. The checklist includes details of the species' distinctive characteristics, notes on habitat and altitudinal range, as well as details of specimens collected as part of this work.

NOTES ON NAMES AND TERMS

The nomenclature used here follows Luther (2008), and is strongly based on the Flora Neotropica monograph (Smith & Downs 1974; Smith & Downs 1977; Smith & Downs 1979) except for *Tillandsia patula*, one of a group of grey-leaved *Tillandsia* which were included in the genus *Vriesea* in the Flora Neotropica but later restored to *Tillandsia* (Grant 1994).

The terminology of bromeliad anatomy was largely determined by Smith & Downs (1974) and largely follows taxonomic convention. However, some terms have been incorrectly used in the bromeliad literature, and here I will follow the suggestions of Scharf and Gouda (2008) for referring to anatomy, especially with regards the terms describing inflorescence branching. Here I use the terms 'once-branched' and 'twice-branched' whereas previous descriptions would describe inflorescence branching as 'pinnate' or 'twice-pinnate'.

When Smith & Downs (1974; 1977; 1979) produced their monographs, the genera and species were assigned numbers, with similar species being given similar numbers. By ordering

species in this way it is easier to compare a plant of interest with similar species. These numbers are retained in the authoritative binomial list (Luther 2008). The order of species described in this chapter adheres to this structure, except unidentified species, where their descriptions are left until the end of the genus.

EXPANDING AN EXISTING KEY

A dichotomous key is based on the one provided by Zevallos (2008). It was modified using advice on developing keys which are intended to be widely accessible (Lawrence & Hawthorne 2006). Since the key developed by Zevallos (2008) covers a similar, overlapping geographic area, this key was translated and expanded as part of this work. The questions from the original key are clearly noted on the expanded version presented here.

A2. SPECIES LIST

This alphabetic list summarises the species described below. The numbers to the left of the species name are those used in the official list of bromeliad binomials (Luther 2008) and give the order for the species descriptions.

- | | | | |
|----------|---|-----------|--|
| 40-61 | <i>Aechmea angustifolia</i> | 8-253 | <i>Pitcairnia</i> cf. <i>scandens</i> |
| 40-41 | <i>Aechmea longicuspis</i> | 8-70 | <i>Pitcairnia lanuginosa</i> |
| 40-23.2 | <i>Aechmea longifolia</i> | 8-90 | <i>Pitcairnia lechleri</i> |
| 40-35 | <i>Aechmea mertensii</i> | 8-63 | <i>Pitcairnia paniculata</i> |
| 40-117.1 | <i>Aechmea moorei</i> | | |
| 40-82 | <i>Aechmea penduliflora</i> | 1-123 | <i>Puya leptostachya</i> |
| | | 1-120 | <i>Puya membranacea</i> |
| 42-40 | <i>Billbergia</i> cf. <i>brachysiphon</i> | | |
| 42-42 | <i>Billbergia decora</i> | 14.1-34 | <i>Racinaea pallidoflavens</i> |
| | | 14.1-55 | <i>Racinaea parviflora</i> |
| 31-8 | <i>Bromelia</i> cf. <i>balansae</i> | 14.1-42.1 | <i>Racinaea penduliflora</i> |
| 31-17 | <i>Bromelia</i> cf. <i>goeldiana</i> | 14.1-23 | <i>Racinaea pendulispica</i> |
| | | 14.1-51 | <i>Racinaea ropalocarpa</i> |
| 29-4.1 | <i>Greigia raporum</i> | 14.1-46 | <i>Racinaea schumanniana</i> |
| 29-15.2 | <i>Greigia vilcabambae</i> | 14.1-2 | <i>Racinaea seemannii</i> |
| | | 14.1-15b | <i>Racinaea spiculosa</i> var. <i>ustulata</i> |
| | | 14.1-44b | <i>Racinaea tetrantha</i> var. <i>aurantiaca</i> |
| 16-61.1 | <i>Guzmania acutispica</i> | | |
| 16-63.2 | <i>Guzmania atrocastanea</i> | 14-78 | <i>Tillandsia biflora</i> |
| 16-80.1 | <i>Guzmania besseae</i> | 14-43 | <i>Tillandsia complanata</i> |
| 16-85 | <i>Guzmania calothyrsus</i> | 14-13 | <i>Tillandsia confinis</i> |
| 16-63.1 | <i>Guzmania cuzcoensis</i> | 14-1 | <i>Tillandsia fendleri</i> |
| 16-69.2 | <i>Guzmania inkaterrae</i> | 14-114 | <i>Tillandsia longifolia</i> |
| 16-109 | <i>Guzmania gloriosa</i> | 14-321 | <i>Tillandsia paraensis</i> |
| 16-59 | <i>Guzmania killipiana</i> | 14-75 | <i>Tillandsia</i> cf. <i>pastensis</i> |
| 16-86 | <i>Guzmania melinonis</i> | 15-277 | <i>Tillandsia patula</i> |
| 16-78 | <i>Guzmania retusa</i> | 14-9 | <i>Tillandsia pyramidata</i> |
| 16-18 | <i>Guzmania roezlii</i> | 14-34 | <i>Tillandsia rubella</i> |
| 16-39 | <i>Guzmania sphaeroidea</i> | 14-15a | <i>Tillandsia stenoura</i> |
| 16-105 | <i>Guzmania squarrosa</i> | 14-15c | <i>Tillandsia stenoura</i> var. <i>mauroi</i> |
| 16-105a | <i>Guzmania</i> aff. <i>squarrosa</i> | 14-18 | <i>Tillandsia superba</i> |
| 16-51.4 | <i>Guzmania undulato-bracteata</i> | 14-55 | <i>Tillandsia truncata</i> var. <i>major</i> |
| 16-110 | <i>Guzmania</i> aff. <i>variegata</i> | 14-12 | <i>Tillandsia wurdackii</i> |
| 16-31 | <i>Guzmania weberbaueri</i> | 14-A | <i>Tillandsia</i> sp. A |
| 16-A | <i>Guzmania</i> sp. A | | |
| 17-1.1 | <i>Mezobromelia pleiosticha</i> | 15-7 | <i>Vriesea</i> cf. <i>chrysostachys</i> |
| | | 15-11 | <i>Vriesea dubia</i> |
| 26-2 | <i>Neoregelia eleutheropetala</i> | | |
| 26-4 | <i>Neoregelia</i> cf. <i>leviana</i> | 15.2-3 | <i>Werauhia</i> cf. <i>gigantea</i> |
| 26-A | <i>Neoregelia</i> sp.1 | | |

A3. SPECIES DESCRIPTIONS

The following descriptions include field characters to distinguish subfamilies, genera and species from amongst the others found in this valley. They are unlikely to be reliable when compared to species from other geographic locations. The descriptions are based on field work as part of this study. For each species the description includes notes on the species ID where applicable, a list of distinguishing field characters, the distribution and altitude range from this study only and finally some notes on the habitats from this study. Where new specimens were collected as part of this study they are listed at the end of the species information.

SUBFAMILY PUYOIDEAE

DISTINGUISHING FIELD CHARACTERS: Puyoideae can be distinguished by the presence of leaf spines (not found in Tillandsioideae), exclusively terrestrial habit (some Bromelioideae are epiphytic), winged seeds, densely flowered, lanate inflorescences (Pitcairnioideae are typically laxly flowered).

GENERA PRESENT: *Puya*.

1: GENUS *PUYA*

120. *PUYA MEMBRANACEA* L.B. SMITH

DISTINGUISHING FIELD CHARACTERS: This species is distinctive when in flower because of the green flowers on a large woolly inflorescence. Around Acanajo it is distinctive as stem and dead leaves raise the rosette above the ground, whereas *P. leptostachya* retains a basal rosette at ground level.

LOCAL DISTRIBUTION: Puna grassland, Wayqecha; PLOTS: none.

ALTITUDE RANGE: 2400 – 4000 m

HABITAT: Puna grassland, often on rocky outcrops and steeper slopes. This species suffers from selective grazing, particularly following fire when the spiny leaves have been removed and the stem is exposed. Consequently it is only found in isolated patches, particularly on terrain where grazing animals cannot easily gain access. The species is also found in small patches of grassland where forest has been cleared below the treeline, the raised rosette giving the plant some chance of competing with other vegetation.

This species tends to be found in discrete populations often of a large number of individuals

123. *PUYA LEPTOSTACHYA* L.B. SMITH

DISTINGUISHING FIELD CHARACTERS: In flower this species is easily distinguished by the blue flowers in a dense woolly inflorescence. Vegetatively the species is characterized by the “low-to-ground” morphology.

LOCAL DISTRIBUTION: Puna grassland; PLOTS: none.

HABITAT: Puna grassland above the treeline. This species is found scattered throughout the Puna grassland and is an occasional or rare species in this habitat.

ALTITUDE RANGE: 3300 – 4000 m

SUBFAMILY PITCAIRNIOIDEAE

DISTINGUISHING FIELD CHARACTERS: Pitcairnioideae can be distinguished by the presence of leaf spines (not found in Tillandsioideae), exclusively terrestrial habit (some Bromelioideae are epiphytic), winged seeds, typically red petals (except *P. lanuginosa*).

GENERA PRESENT: *Pitcairnia*

8: GENUS *PITCAIRNIA*

63. *PITCAIRNIA PANICULATA* (RUIZ & PAVÓN) RUIZ & PAVÓN (FIGURE A1)

DISTINGUISHING FIELD CHARACTERS: When flowering the large lax brown inflorescence with red flowers is distinctive. Vegetatively the basal rosette of pseudopetioled leaves distinguishes it from climbing species of *Pitcairnia*.

LOCAL DISTRIBUTION: San Pedro and roadside up to Trocha Union; PLOTS: none;

ALTITUDE RANGE: 1700 – 2200 m

HABITAT: Exposed rocky surfaces in open areas, particularly along the road sides.

SPECIMENS: SJH034 (-13 04.299, -71 33.993).

70. *PITCAIRNIA LANUGINOSA* RUIZ & PAVÓN

DISTINGUISHING FIELD CHARACTERS: This species is easily identified by the long pale yellow petals with brown spots. Vegetatively the species is difficult to separate from *P. paniculata*.

ALTITUDE RANGE: 800 – 1400 m

90. *PITCAIRNIA LECHLERI* BAKER (FIGURE A2)

DISTINGUISHING FIELD CHARACTERS: This species is easily identified by the growth form, having a slender trunk with modified leaves forming a spiny covering, with a single dense rosette of leaves at the top of the stem. The inflorescence is twice-branches with the red flowers pendulous at anthesis.

LOCAL DISTRIBUTION: Wayqecha below 2500 m and Trocha Union between plots 4 and 5;

PLOTS: none.

ALTITUDE RANGE: 1800 - 3000 m

HABITAT: Upper montane scrub and in understory of open patches of forest and at forest edges. Where present this plant can be locally frequent.

SPECIMENS: SJH069 (-13.1652, -71.5896)

253. *PITCAIRNIA* CF. *SCANDENS* ULE (FIGURE A3)

ID NOTES: This species was not seen in flower, but the vegetative characters match closely with *P. scandens*. Flowering specimens will be needed to confirm this ID.

DISTINGUISHING FIELD CHARACTERS: Vegetatively this plant is distinguished by its climbing habit (unique except for *Pitcairnia* cf. *nigra*) and is distinctive compare to *P. nigra* by the larger leaves (up to 50 cm) and second inflorescence.

LOCAL DISTRIBUTION: San Pedro; PLOTS: SP2.

HABITAT: Tropical montane forest, climbing on trees in closed canopy forest.

SUBFAMILY TILLANDSIOIDEAE

DISTINGUISHING FIELD CHARACTERS: Tillandsioideae are easily identified by their absence of spines on the leaves and the plumose seeds.

GENERA PRESENT: *Guzmania*, *Mezobromelia*, *Racinaea*, *Tillandsia*, *Vriesea*, *Werauhia*.

14: GENUS *TILLANDSIA*

DISTINGUISHING FIELD CHARACTERS: *Tillandsia* can be distinguished from other Tillandsioideae by the distichous arrangement of the flowers on the simple inflorescence or inflorescence branches (polystichous in *Guzmania* and *Mezobromelia*), an absence of petal appendages (present in *Vriesea*), and symmetric sepals (asymmetric in *Racinaea*).

1. *TILLANDSIA FENDLERI* GRISEBACH (FIGURE A4)

DISTINGUISHING FIELD CHARACTERS: *T. fendleri* is the largest of the purple-flowered *Tillandsia*.

Vegetatively it is difficult to distinguish apart from its rosette size (1 – 2 m) and leaf number (40 – 50 per individual in large specimens). Flowering specimens are distinguished by the twice-branched inflorescence with many-flowered (c. 20) green spikes at anthesis (turning red later) and the foliaceous primary bracts (especially in the lower parts).

LOCAL DISTRIBUTION: San Pedro lower research plot; PLOTS: SP2.

ALTITUDE RANGE: 1250 – 1750 m

HABITAT: This species is most often found in the upper parts of mature trees in tropical montane forest, although may also be found in isolated trees. The species can be locally abundant where it occurs, and is a popular ornamental plant in the Urubamba valley.

SPECIMENS: SJH015 (-13.0492, -71.5368).

9. *TILLANDSIA PYRAMIDATA* ANDRÉ (FIGURE A5)

DISTINGUISHING FIELD CHARACTERS: This species is difficult to separate vegetatively, although the rosette is typically wider and shorter than other *Tillandsioideae* giving a ‘squashed’ look. In flower the species is superficially similar to *T. fendleri* but can be distinguished by the red spikes at anthesis.

LOCAL DISTRIBUTION: Wayqecha Trocha Oso and Trocha Mariposa down to the river, Pillahuata; PLOTS: none.

ALTITUDE RANGE: 2000 – 2500 m

HABITAT: Large trees in open areas of tropical montane cloud forest. This species is very often found in large localized populations, apparently from localized seed dispersal.

12. *TILLANDSIA WURDACKII* L.B. SMITH (FIGURE A6)

DISTINGUISHING FIELD CHARACTERS: This species is difficult to separate using vegetative characters from other *Tillandsia* of intermediate in size. In flower the species is separated by the clustering of spikes towards the top of the inflorescence and the distinctive red and green appearance of the spikes.

LOCAL DISTRIBUTION: Roadside around Way, Upper TU down to plot 3; PLOTS: TU3, WAY.

ALTITUDE RANGE: 2750 - 3400 m

HABITAT: Tropical montane cloud forest including more open areas of forest and isolated roadside trees.

SPECIMENS: SJH009 (-13.1112, -71.6065), SJH061 (-13.1089, -71.6000).

13. *TILLANDSIA CONFINIS* L.B. SMITH (FIGURE A7)

DISTINGUISHING FIELD CHARACTERS: Another species difficult to distinguish vegetatively, being similar to *T. wurdackii* although slightly smaller and more often found as large clonal aggregations creating large colonies. In flower it is distinguished by the smaller inflorescence compared to *T. wurdackii*.

LOCAL DISTRIBUTION: Lower reaches of Wayqecha San Pedro between plots, TU7 and downwards, roadside from Trocha to SP; PLOTS: TU7.

ALTITUDE RANGE: 1100 – 2400 m

HABITAT: Tropical montane cloud forest, often locally abundant in exposed sites, such as dead trees or trees close to clearings.

SPECIMENS: SJH014 (-13.0699, -71.5560), SJH079 (-13.0471, -71.5024), SJH103 (-13.0742, -71.5597).

15. *TILLANDSIA STENOURA* HARMS (FIGURE A8)

DISTINGUISHING FIELD CHARACTERS: This is another large *Tillandsia* with rosettes 1-2 m wide but can be distinguished from *T. fendleri* by the more colourful leaves with large irregular purple-coloured patches. In flower the inflorescence is very long 1-2 m, and the branches are laxer than *T. fendleri* and much greener in appearance. The var. *stenoura* is distinguished by the patent spikes at anthesis.

LOCAL DISTRIBUTION: Wayqecha all trails and forest and dry scrub, Trocha Union 4; PLOTS: WAY, TU4.

ALTITUDE RANGE: 2000 – 3400 m

HABITAT: Tropical montane cloud forest and open secondary montane vegetation in very similar habitats to *T. stenoura* var. *mauroi*.

SPECIMENS: SJH010 (-13.1058, -71.5889), SJH091 (-13.1892, -71.5847), SJH094 (-13.1776, -71.6074).

15C. *TILLANDSIA STENOURA* HARMS VAR. *MAUROI* GILMARTIN (FIGURE A9)

DISTINGUISHING FIELD CHARACTERS: The species can be separated from var. *stenoura* only by the erect spikes.

LOCAL DISTRIBUTION: Wayqecha - throughout.

ALTITUDE RANGE: 2900 - 3000 m.

HABITAT: Tropical montane cloud forest and secondary montane vegetation.

SPECIMENS: SJH073 (-13.1840, -71.5865).

18. *TILLANDSIA SUPERBA* MEZ & SODIRO (FIGURE A10)

DISTINGUISHING FIELD CHARACTERS: This large species (much bigger than *T. confinis*) is similar to *T. stenoura* and *T. fendleri* and can be distinguished from the former by the intense red colouration of the inflorescence and the latter by the shorter spikes (8 – 10 flowers).

LOCAL DISTRIBUTION: Pillahuata, Wayqecha both plots and all trails, Trocha Union plot 3 and 4; PLOTS: TU3, TU4, WAY, ESP.

ALTITUDE RANGE: 2500 – 3400 m

HABITAT: Mature tropical montane cloud forest.

SPECIMENS: SJH002 (-13.1907, -71.5875), SJH063 (-13 10.772, -71 34.914).

34. *TILLANDSIA RUBELLA* BAKER (FIGURE A11)

DISTINGUISHING FIELD CHARACTERS: This species is typical of mid-sized Tillandsioideae but can be easily distinguished by the pink colouration in the inflorescence (except *T. biflora* which is smaller with red margins to the pale green leaves). It can be distinguished from *T. ionochroma* by the spreading spikes at anthesis (giving conical inflorescence shape).

LOCAL DISTRIBUTION: Trocha Union from tree line to TU3 and Wayqecha all areas; PLOTS: TU2, TU3, WAY, ESP.

ALTITUDE RANGE: 2600 – 3500 m

HABITAT: A common species of primary and secondary tropical montane cloud forest, often locally abundant.

SPECIMENS: SJH001 (-13.1905, -71.5837), SJH008 (-13.0925, -71.7047)

43. *TILLANDSIA COMPLANATA* BENTHAM (FIGURE A12)

ID NOTES: This is the description of the form found above 1750 m, by far the most common in Kosnipata. There is another form found at lower altitude, without red lines on the more lepidote leaves, more pointy leaf tips, and green floral bracts.

DISTINGUISHING FIELD CHARACTERS: Vegetatively this species can be distinguished by the red stripes running along the leaves. In flower this is the only *Tillandsia* with lateral inflorescences and no terminal inflorescence.

LOCAL DISTRIBUTION: 'Upland form': Wayqecha forest and dry scrub, Trocha Union from tree line down to plot 4; PLOTS: WAY, ESP, TU1, TU2, TU3, TU4, TU5. 'Lowland form': San Pedro trails and intermediate forest; PLOTS: none.

ALTITUDE RANGE: 1500 – 3500 m

HABITAT: Isolated or forest trees of any size, abundant throughout its range.

SPECIMENS: 'Upland form': SJH004 (-13.1905, -71.5875). 'Lowland form': SJH035 (-13 02.869, -71 32.289);

55. *TILLANDSIA TRUNCATA* L.B. SMITH VAR. *MAJOR* H. LUTHER (FIGURE A13)

ID NOTES: There are two distinct groups of this species, one with more intense red colouration in the stem and bracts, and lacking sterile bracts at the base of the inflorescence, the other with spikes appearing yellow and several sterile bracts at the base of each spike. It

is likely these two groups represent discrete forms of this same species (J. Manzanares, pers. comm.).

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from other Tillandsioideae (except *G. aff. variegata*) by the truncate leaves. In flower it can be distinguished by the laxly flowered spikes without overlapping floral bracts.

LOCAL DISTRIBUTION: Roadside around San Pedro, Trocha Union plot 5 and below, San Pedro between plots; **PLOTS:** TU5, TU7, SP1.

ALTITUDE RANGE: 1100 – 2750 m

HABITAT: Forest and isolated trees in tropical montane forest.

SPECIMENS: SJH099 (-13.0935, -71.57337)

75. *TILLANDSIA* CF. *PASTENSIS* ANDRÉ (FIGURE A14)

DISTINGUISHING FIELD CHARACTERS: This large species has a lax inflorescence with spikes completely enclosed in the red primary bracts.

LOCAL DISTRIBUTION: Wayqecha dry scrub and open secondary forest; **PLOTS:** None.

ALTITUDE RANGE: 2500 - 3200 m

HABITAT: Tropical montane cloud forest.

SPECIMENS: SJH005 (-13.1905, -71.5875), SJH089 (-13.1767, -71.5845).

78. *TILLANDSIA BIFLORA* RUIZ & PAVÓN

DISTINGUISHING FIELD CHARACTERS: Vegetatively this species can be distinguished by the small size (20 – 30 cm) and pale green leaves with purple to red margins. In flower the species can be distinguished by the dense inflorescence with spikes containing a pair of flowers.

LOCAL DISTRIBUTION: Wayqecha mature trees, especially areas of a high density of *Alnus* spp.

ALTITUDE RANGE: 2200 – 2700 m

HABITAT: Tropical montane cloud forest, particularly mature *Alnus* forest in more sheltered valleys

SPECIMENS: SJH070 (-13.1687, -71.5919)

114. *TILLANDSIA LONGIFOLIA* BAKER (FIGURE A15)

DISTINGUISHING FIELD CHARACTERS: This species is easily identified vegetatively by the narrow linear to narrowly triangular leaves, with cinereous appearance. The three-times-branched inflorescence distinguishes the species from other *Tillandsia* spp. except *T. towarensis* but the narrow green spikes are distinctive in *T. longifolia*.

LOCAL DISTRIBUTION: San Pedro upwards from plot 2, Rocotal; PLOTS: SP1.

ALTITUDE RANGE: 1400 – 2100 m

HABITAT: Mature trees in tropical montane forest.

227. *TILLANDSIA PATULA* MEZ (FIGURE A17)

DISTINGUISHING FIELD CHARACTERS: Vegetatively this species can be separated from other *Tillandsia* spp. by the rounded tank and having leaves cinereous on both sides. The inflorescence is pendulous with long narrow pink spikes. The long green petals are also distinct.

LOCAL DISTRIBUTION: Trocha union plot 7, Wayqecha IX and dry forest; PLOTS: WAY, TU7.

ALTITUDE RANGE: 2500 – 3200 m

HABITAT: Forest and isolated trees in tropical montane cloud forest.

SPECIMENS: SJH013 (-13.0699, -71.5560), SJH061 (-13.1886, -71.5847).

321. *TILLANDSIA PARAENSIS* MEZ (FIGURE A16)

DISTINGUISHING FIELD CHARACTERS: Vegetatively this species can be distinguished by the inflated leaf sheaths and narrow, slightly succulent leaf blades. In flower it is distinguished by the simple inflorescence with red floral bracts at anthesis.

LOCAL DISTRIBUTION: Tambopata plot 4; PLOTS: TAM4.

ALTITUDE RANGE: 180 – 200 m

HABITAT: Mature lowland tropical rainforest.

SPECIMENS: SJH096 (-12.8388, -69.2966)

A. *TILLANDSIA* SPECIES A (FIGURE A18)

ID NOTES: This taxon has a variable morphology. It is hypothesized that the taxon represents numerous independent hybridizations between *T. complanata* and *T. stenoura* (E. Gouda, pers. comm.). One major distinction of groups within the taxon is plants with the terminal inflorescence either simple or once-branched. Other distinctions include branching of the lateral inflorescence and the number of flowers per inflorescence branch.

LOCAL DISTRIBUTION: Trocha Union between plots 4 and 7, Wayqecha; Roadside at Esperanza;

PLOTS: none.

ALTITUDE RANGE: 2000 – 3000 m.

HABITAT: Mature and secondary tropical montane cloud forest, rarely on isolated trees beside roads and rivers.

SPECIMENS: SJH032 (-13.0996 -71.5806), SJH092 (-13.1773, -71.5983), SJH095 (-13.1779, -71.5837).

14.1: GENUS *RACINAEA*

DISTINGUISHING FIELD CHARACTERS: *Racinaea* can be distinguished from other genera by the distichous arrangement of flowers (polystichous in *Guzmania* and *Mezobromelia*), which are often small (< 1 cm), laxly arranged (but not secund as in *Werauhia*), white or yellow petals (typically more colourful in *Tillandsia* and *Vriesea*) and asymmetric sepals (symmetric in *Tillandsia* and *Vriesea*).

2. *RACINAEA SEEMANNII* (BAKER) M.A. SPENCER & L.B. SMITH (FIGURE A19)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished by the rounded shoot morphology, appearing dark due to colouration of the leaf sheaths. In flower the simple, or rarely with two or three spikes, inflorescences appear pink with white flowers.

LOCAL DISTRIBUTION: Wayqecha IX and road up to tree line, road to Tres Cruces and Trocha Unión down to plot 2; PLOTS: WAY, TU1, TU2.

ALTITUDE RANGE: 2800 – 3600 m

HABITAT: Tropical montane cloud forest sometimes forming dense groups of ramets.

SPECIMENS: SJH072 (-13.1834, -71.6022), SJH006 (-13.1905, -71.5875), SJH065 (-13.1753, -71.5849), SJH030 (-13.1076, -71.5952), SJH026 (-13.1121, -71.6075)

15B. *RACINAEA SPICULOSA* (GRISEBACH) M.A. SPENCER & L.B. SMITH

VAR. *USTULATA* (REITZ) M.A. SPENCER & L.B. SMITH (FIGURE A20)

DISTINGUISHING FIELD CHARACTERS: This species is most easily distinguished by the lateral brown bands on the green leaves. In flower the once-branched inflorescence with the spikes (not flowers) second is characteristic.

LOCAL DISTRIBUTION: Tono and transition forest; PLOTS: Tono Alto.

ALTITUDE RANGE: 600 – 1000 m

HABITAT: Tropical montane forest, typically a mid-canopy species.

SPECIMENS: SJH011 (-12.9586, -71.5656).

23. *RACINAEA PENDULISPICA* (MEZ) M.A. SPENCER & L.B. SMITH

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished by the once-branched inflorescence with red to pink floral bracts. The inflorescence has significantly more spike than the pink-bracted *R. seemannii*.

LOCAL DISTRIBUTION: Rocotal

ALTITUDE RANGE: 1800 – 1900 m.

34. *RACINAEA PALLIDOFLAVENS* (MEZ) M.A. SPENCER & L.B. SMITH (FIGURE A21)

DISTINGUISHING FIELD CHARACTERS: This distinctive species can be identified vegetatively by the narrowing of the phytotelm above the base as well as the appearance of the leaves of being in two opposite rows. The upward curving inflorescence spikes are also diagnostic.

LOCAL DISTRIBUTION: Trocha Union around plot 7; PLOTS: TU7.

ALTITUDE RANGE: 1900 – 2100 m

HABITAT: Rare in upper canopy of tropical montane cloud forest.

SPECIMENS: SJH011 (-13.0699, -71.5560).

42.1. *RACINAEA PENDULIFLORA* GOUDA & MANZANARES (FIGURE A22)

DISTINGUISHING FIELD CHARACTERS: This species is similar vegetatively to the grey-leaved *T. patula* but in *R. penduliflora* the phytotelm structure is more open. The inflorescence is lax and all the flowers face downwards.

LOCAL DISTRIBUTION: Wayqecha and Esperanza dry and wet forests, Trocha Union from plot 2 down to plot 4; PLOTS: TU2, TU3, TU4, WAY, ESP.

ALTITUDE RANGE: 2250 - 3250 m

HABITAT: Forest and isolated trees in tropical montane cloud forest.

SPECIMENS: SJH003 (-13.1905, -71.5873), SJH060 (-13.1089, -71.6000)

44B. *RACINAEA TETRANTHA* (RUIZ & PAVÓN) M.A. SPENCER & L.B. SMITH

VAR. *AURANTIACA* (GRISEBACH) M.A. SPENCER & L.B. SMITH (FIGURE A23)

DISTINGUISHING FIELD CHARACTERS: This species is similar to *R. penduliflora* in both habit and habitat but can be distinguished by the more glabrous green leaves and bright yellow inflorescence.

LOCAL DISTRIBUTION: Wayqecha dry forests; PLOTS: none.

ALTITUDE RANGE: 2700 – 3000 m

HABITAT: Secondary cloud forest.

46. *RACINAEA SCHUMANNIANA* (WITTMACK) J.R. GRANT (FIGURE A24)

DISTINGUISHING FIELD CHARACTERS: This small species can be distinguished from the similar sized *Racinaea* spp. by the narrowly triangular to linear, flat leaves and the branching inflorescence with six-flowered spikes.

LOCAL DISTRIBUTION: San Pedro both plots, Trocha Union including TU7 up to TU3, Wayqecha from river up through dry forest; PLOTS: SP2, SP1, TU7.

ALTITUDE RANGE: 1250 – 3200 m

HABITAT: Tropical montane cloud forest, often locally abundant on trunks and in lower part of canopy.

SPECIMENS: SJH067 (-13.1631, -71.5898), SJH021 (-13 02.950, -71 32.206), SJH030 (-13.0818, -71.5682), SJH080 (-13.0471, -71.5403)

51. *RACINAEA ROPALOCARPA* (ANDRÉ) M.A. SPENCER & L.B. SMITH (FIGURE A25)

DISTINGUISHING FIELD CHARACTERS: This small species can be distinguished from the other small *Racinaea* spp. by the crispate leaves. The green inflorescence is once-branched with 10 flowered spikes.

LOCAL DISTRIBUTION: Wayqecha by the river, Trocha Union plot 7 and San Pedro between plots; PLOTS: TU7.

ALTITUDE RANGE: 1700 – 2300 m

HABITAT: Mature tropical montane cloud forest.

SPECIMENS: SJH100 (-13.0724, -71.5597)

**55. *RACINAEA PARVIFLORA* (RUIZ & PAVÓN) M.A. SPENCER & L.B. SMITH
(FIGURE A26)**

DISTINGUISHING FIELD CHARACTERS: This species is easily distinguished by the narrow phytotelm made of inflated leaf sheaths. The leaf blades are very narrow and linear. The inflorescence is once branched with the spikes laxly 8 – 10 flowered.

LOCAL DISTRIBUTION: Pillcopata area transition forest.

ALTITUDE RANGE: 600 – 900 m

HABITAT: Forest in the montane-lowland transition zone.

15: GENUS *VRIESEA*

DISTINGUISHING FIELD CHARACTERS: *Vriesea* is distinguished from *Tillandsia* and *Racinaea* by the presence of petal appendages. In the absence of flowers, *Vriesea* is difficult to separate.

7. *VRIESEA* CF. *CHRYSOSTACHYS* E. MORREN (FIGURE A27)

ID NOTES: Only a single individual of this species was found, with a senesced inflorescence, and although it resembles *V. chrysostachys* it is not possible to be certain in the absence of fresh flowers.

DISTINGUISHING FIELD CHARACTERS: This species is distinguished by the long many-flowered distichous inflorescence with overlapping floral bracts.

LOCAL DISTRIBUTION: The Mirador at Pantiacolla

ALTITUDE RANGE: 900 – 1000 m

HABITAT: Growing at the base of a shrubby tree on a steep slope in elfin forest.

SPECIMENS: SJH056 (-12 38.182, -71 16.463)

11. *VRIESEA DUBIA* (L.B. SMITH) L.B. SMITH (FIGURE A28)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from *V. chrysostachys* by the branched, red inflorescence

LOCAL DISTRIBUTION: Transition forest around Atalaya

ALTITUDE RANGE: 600 – 800 m

HABITAT: Forest in the montane-lowland transition zone between Atalaya and Pillcopata.

15.2: GENUS *WERAUHIA*

DISTINGUISHING FIELD CHARACTERS: *Werauhia* can be easily identified in the field from the large, lax, secund flowers, typically white in colour.

3. *WERAUHIA* CF. *GIGANTEA* (MARTIUS EX SCHULTES F.) J.R. GRANT (FIGURE A29)

DISTINGUISHING FIELD CHARACTERS: As for the genus, the large, lax, secund flowers are diagnostic. This species is difficult to identify from vegetative characters, but is the most common large tillandsioid species in disturbed areas below 600 m.

LOCAL DISTRIBUTION: Atalaya village, MLC, Pantiacolla and trail to Tono Research Plot

ALTITUDE RANGE: 400 – 1000 m.

HABITAT: Open and exposed areas of tropical rainforest and isolated trees.

16: GENUS *GUZMANIA*

DISTINGUISHING FIELD CHARACTERS: *Guzmania* can be separated from other genera in the Tillandsioideae by the polystichous arrangement of the flowers on the simple or compound inflorescence, and from *Mezobromelia* by the absence of petal appendages.

18. *GUZMANIA ROEZLII* (E. MORREN) MEZ (FIGURE A30)

DISTINGUISHING FIELD CHARACTERS: This species is easily distinguished in flower by 3-5 long laxly flowered inflorescence branches (most *Guzmania* with densely flowered branches) and white flowers.

LOCAL DISTRIBUTION: MLC, Jardín Botánico des Orquídeas in Pillcopata

ALTITUDE RANGE: 500 – 800 m

HABITAT: Forest in the montane-lowland transition zone between Atalaya and Pillcopata.

31. *GUZMANIA WEBERBAUERI* MEZ (FIGURE A32)

DISTINGUISHING FIELD CHARACTERS: This species is distinguished vegetatively by the terrestrial habit, large phytotelm (1.5 – 2 m) and pattern of dark green cross-veins on the pale green leaf. In flower the rounded red spikes with yellow flowers are distinctive.

LOCAL DISTRIBUTION: San Pedro garden and upwards to Trocha Union plot 7 and downwards along roadside and river banks; PLOTS: none.

ALTITUDE RANGE: 1300 – 2000 m

HABITAT: Forest understory and open areas, rarely epiphytic towards the base of trees.

SPECIMENS: SJH033 (-13.0716, -71.5579)

39. *GUZMANIA SPHAEROIDEA* (ANDRÉ) ANDRÉ EX MEZ (FIGURE A33)

DISTINGUISHING FIELD CHARACTERS: Vegetatively this species is characterised by having a few discoloured (typically yellow) leaves amongst the otherwise normal leaves. In flower the short-stalked, rounded spikes distinguish the species from *G. acutispica* (cylindrical spikes).

LOCAL DISTRIBUTION: San Pedro plots and trail, Tono entrance trail; PLOTS: SP1, SP2.

ALTITUDE RANGE: 1400 – 1900 m

HABITAT: Tropical montane forest.

SPECIMENS: SJH078 (-13.0473, -71.5422)

51.4. *GUZMANIA UNDULATOBRACTEATA* (RAUH) RAUH (FIGURE A34)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished by the terrestrial habit and the red stripes at the base of leaf blades. The inflorescence is distinctive due to the large, once-branched, lax flowered inflorescence.

LOCAL DISTRIBUTION: Trocha Union plot 5 and downwards to plot 7, beside the road to San Pedro; PLOTS: TU7.

ALTITUDE RANGE: 1800 – 2000 m

HABITAT: Tropical montane cloud forest, at the base of trees and often climbing slightly on thickened stolon.

SPECIMENS: SJH078 (-13.0742, -71.5597)

59. *GUZMANIA KILLIPIANA* L.B. SMITH (FIGURE A35)

DISTINGUISHING FIELD CHARACTERS: This species is difficult to identify vegetatively, with size (c. 1 m) and epiphytic habit providing clues. In flower the red-stripes on the green inflorescence and long-stalked rounded spikes are distinctive.

LOCAL DISTRIBUTION: San Pedro plot 2 and riparian areas, Tono; PLOTS: SP2, TONO.

ALTITUDE RANGE: 800 – 1700 m

HABITAT: Mature tropical montane forest and riparian zones.

SPECIMENS: SJH023 (-13.0492, -71.5368), SJH039 (-12.8925, -71.5656), SJH075 (-12.9533 - 71.5493), SJH104 (-13.0500 - 71.5356)

61.1. *GUZMANIA ACUTISPICA* E. GROSS (FIGURE A36)

DISTINGUISHING FIELD CHARACTERS: In flower the short-stalked spikes and entirely green inflorescence distinguish this species from *G. killipiana*. The regular branching of spikes distinguishes this species from *G. atrocastanea*.

LOCAL DISTRIBUTION: Trocha Union plot 7, San Pedro between plots; PLOTS: TU7.

ALTITUDE RANGE: 1600 – 2100 m.

HABITAT: Tropical montane cloud forest.

SPECIMENS: SJH037 (-13.0460, -71.5443), Specimen SJH078 (-13 02.762, -71 32.658), SJH101 (-13.0742, -71.5597).

63.1. *GUZMANIA CUZCOENSIS* L.B. SMITH (FIGURE A37)

ID NOTES: *Guzmania cuzcoensis* is well known from the state of Cuzco. One plant was seen in the Kosnipata valley which bears a strong resemblance to this species, in a location from which collection was not possible, only a single photo was available for examination.

LOCAL DISTRIBUTION: Trocha union between plots 4 and 5; PLOTS: None.

ALTITUDE RANGE: 2500 - 2600 m

HABITAT: Tropical montane cloud forest.

63.2. *GUZMANIA ATROCASTANEA* H. LUTHER (FIGURE A38)

DISTINGUISHING FIELD CHARACTERS: The peduncle bract colouring (brown in the lower part and brown-striped in the upper part) and short-stalked spikes lax in the lower part of the peduncle becoming clustered at the top of the peduncle distinguish this species.

LOCAL DISTRIBUTION: Wayqecha Trocha Mariposa by the river

ALTITUDE RANGE: 2250 – 2350 m

HABITAT: Riparian zone in secondary montane vegetation.

SPECIMEN: SJH066 (-13.1619, -71.5901).

69.2. *GUZMANIA INKATERRAE* GOUDA (FIGURE A39)

DISTINGUISHING FIELD CHARACTERS: The dense cluster of 10 to 15 red spikes at the top of the inflorescence distinguishes this species from other *Guzmania*.

LOCAL DISTRIBUTION: Trocha Union plot 5, Rocotal; PLOTS: TU5.

ALTITUDE RANGE: 1700 – 2600 m (1500 – 2050 m).

HABITAT: Tropical montane cloud forest.

SPECIMENS: SJH098 (-13.0942, -71.5744), ITZ089 (-13.1028, -71.5659).

78. *GUZMANIA RETUSA* L.B. SMITH (FIGURE A40)

DISTINGUISHING FIELD CHARACTERS: The truncate leaves with dense purple spots distinguish this species vegetatively. In flower the unbranched cylindrical inflorescence distinguishes this from other species.

LOCAL DISTRIBUTION: Trail between San Pedro research plots; PLOTS: SP1, SP2.

ALTITUDE RANGE: 1500 – 1800 m

HABITAT: Abundant throughout canopy of tropical montane forest.

SPECIMENS: SJH038 (-13.0473, -71.5423), SJH071 (-13.0472, -71.5421)

80.1. *GUZMANIA BESSEAE* H. LUTHER (FIGURE A41)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished by the unbranched, dense, rounded, red inflorescence.

LOCAL DISTRIBUTION: Rocotal, Wayqecha by the river along Trocha Mariposa.

ALTITUDE RANGE: 1900 – 2300 m

HABITAT: Riparian zone of the cloud forest.

SPECIMENS: SJH071 (-13.1626, -71.5890)

85. *GUZMANIA CALOTHYRSUS* MEZ (FIGURE A42)

DISTINGUISHING FIELD CHARACTERS: The unbranched inflorescence with non-overlapping floral bracts distinguishes this species.

LOCAL DISTRIBUTION: Tono trail to research plots, all trails at Pantiacolla, MLC; PLOTS: MLC.

ALTITUDE RANGE: 400 – 900 m

HABITAT: Lowland tropical rainforest in the lower canopy and around trunks, always in deep shade.

SPECIMENS: SJH051 (-12.9581, -71.5625)

86. *GUZMANIA MELINONIS* REGEL (FIGURE A43)

DISTINGUISHING FIELD CHARACTERS: The parallel-sided strap-like leaves are indicative of this species and the few-flowered red inflorescence is characteristic.

LOCAL DISTRIBUTION: Tono and the transition forest around Pillcopata; PLOTS: Tono.

ALTITUDE RANGE: 700 - 1000 m

HABITAT: Understory of mature tropical montane forest.

SPECIMENS: SJH048 (-12.9586, -71.5655)

105. *GUZMANIA* AFF. *SQUARROSA* (MEZ & SODIRO) L.B. SMITH & PITTENDRIGH (FIGURE A44)

ID NOTES: These plants belong in the *Guzmania squarrosa* complex, but while several new species from this complex have been described from Ecuador, none have been described from Peru. These plants are likely to represent a new taxon, but this cannot be determined without any fertile material as petals are the key distinguishing character.

DISTINGUISHING FIELD CHARACTERS: This large species can be distinguished by the 5 – 8 cm yellow band in the primary bracts.

LOCAL DISTRIBUTION: San Pedro plot 2 and roadside and the riparian areas around the lodges in San Pedro, Tono trail and research plot, Pantiacolla plot and higher trails around the upper parts of the site; PLOTS: SP2, Tono, Pantiacolla.

ALTITUDE RANGE: 500 – 1750 m

HABITAT: Tropical montane forest and isolated trees.

SPECIMEN: SJH081 (-13.0941, -71.5369).

**105. *GUZMANIA SQUARROSA* (MEZ & SODIRO) L.B. SMITH & PITTENDRIGH
(FIGURE A45)**

DISTINGUISHING FIELD CHARACTERS: This species can be identified by the dense purple spots on vegetative parts and the long (> 50 cm) lower primary bracts.

LOCAL DISTRIBUTION: Trocha Union around plot 4 and below (but not in plot 5), Wayqecha Trocha Trogon and Rocotal; PLOTS: TU4.

ALTITUDE RANGE: 2000 – 2800 m

HABITAT: Understory plant of mature tropical montane cloud forest.

SPECIMENS: SJH078 (-13.1776, -71.6074)

109. *GUZMANIA GLORIOSA* (ANDRÉ) ANDRÉ EX MEZ (FIGURE A46)

DISTINGUISHING FIELD CHARACTERS: This large species can be distinguished by the red band at the tips of the primary bracts.

LOCAL DISTRIBUTION: Wayqecha trail to canopy towers and forest around canopy towers, Trocha Trogon, and Trocha Oso in lower parts. PLOTS: none.

ALTITUDE RANGE: 2400 – 3000 m

HABITAT: Lower canopy of mature tropical montane cloud forest.

SPECIMENS: SJH071 (-13.1832, -71.5841)

110. *GUZMANIA* AFF. *VARIEGATA* L.B. SMITH (FIGURE A31)

DISTINGUISHING FIELD CHARACTERS: This species can be identified by the truncate leaves with uniform deep red undersides. The white flowers distinguish this species from *Mezobromelia pleiosticha*.

LOCAL DISTRIBUTION: Trocha Union between plots 4 and 5; **PLOTS:** none.

ALTITUDE RANGE: 2500 – 2700 m.

HABITAT: Tropical montane cloud forest.

A. *GUZMANIA* SP. A (FIGURE A47)

ID NOTES: This is likely to represent a new species (E. Gouda, pers. comm.), collected once before from Quincemil.

DISTINGUISHING FIELD CHARACTERS: The linear often purple-tinted leaves and near-ground level habit distinguish this species vegetatively and the yellow inflorescence distinguished this species in flower.

LOCAL DISTRIBUTION: Area around Tono plot; **PLOTS:** Tono.

HABITAT: Tropical montane forest away from riparian areas; shaded epiphytic habitats around tree bases and lower trunk, although never terrestrial, and locally frequent.

ECOLOGY: Producing frequent asexual clones.

ALTITUDE RANGE: 900 – 1000 m.

SPECIMENS: SJH047 (-12.9590, -71.5657), SJH076 (-12.9533, -71.5493).

17: GENUS *MEZOBROMELIA*

DISTINGUISHING FIELD CHARACTERS: *Mezobromelia* can be distinguished from other Tillandsioideae (except *Guzmania*) by the polystichous arrangement of flowers, and from *Guzmania* by the presence of petal appendages.

1.1. *MEZOBROMELIA PLEIOSTICHA* (GRISEBACH) J. UTLEY & H. LUTHER (FIGURE A48)

DISTINGUISHING FIELD CHARACTERS: The only species in this genus present in the study area, this large phytotelm species can be distinguished by the red inflorescence with yellow flowers

LOCAL DISTRIBUTION: Wayqecha just below river, Trocha Union plot 4, San Pedro plot 2 and road up to junction with Trocha Union. PLOTS: SP2, TU4, TU5.

ALTITUDE RANGE: 1500 – 2750 m

HABITAT: Mature trees in tropical montane forest and tropical montane cloud forest and mature trees in more open forest along the roadside.

SPECIMENS: SJH088 (-13.1621, -71.5890)

SUBFAMILY BROMELIOIDEAE

DISTINGUISHING FIELD CHARACTERS: Bromelioideae can be identified by their spiny leaves (Tillandsioideae lack spines), sometimes epiphytic habit (Pitcairnioideae are almost never epiphytic) and baccate fruit.

Genera present: *Aechmea*, *Billbergia*, *Bromelia*, *Neoregelia*.

Ananas comosus (pineapple) is also common in the lowland parts of the study area (below 600 m), but is cultivated, and not a native plant in this region so it is not dealt with in this thesis. It is superficially similar to species of *Bromelia* but domestication has reduced the spines so they are almost non-existent, and the fruit is also distinctive in comparison.

26: GENUS *NEOREGELIA*

DISTINGUISHING FIELD CHARACTERS: *Neoregelia* is easily identified by the inflorescence sunken in the centre of the leaf rosette ('nidularioid' inflorescence). This character is not present in any other genera in the study area (it is present in the genus *Nidularium*)

2. *NEOREGELIA ELEUTHEROPETALA* (ULE) L.B. SMITH (FIGURE A49)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from the other

Neoregelia by its larger size, with the longest leaves of mature plants exceeding 50 cm. The central leaves develop a distinctive red triangle around the inflorescence at anthesis.

LOCAL DISTRIBUTION: Transition forest around Pillcopata, Pantiacolla Monk Saki trail and Tambopata main trail; PLOTS: none.

ALTITUDE RANGE: 180 – 800 m

HABITAT: Open and exposed areas in understory of lowland tropical rainforest.

4. *NEOREGELIA* CF. *LEVIANA* L.B. SMITH (FIGURE A51)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from the other

Neoregelia spp. by the triangular leaf blades with very inflated, pigmented sheaths forming a wide tank.

LOCAL DISTRIBUTION: MLC open areas of Melastomataceae forest; PLOTS: none.

ALTITUDE RANGE: 400 – 600 m.

HABITAT: Open and exposed areas in secondary tropical rainforest close to ponds and lakes.

A. *NEOREGELIA* SP.1 (FIGURE A50)

ID NOTES: Only a single individual of this species was found without flowers, so it was not possible to work out which of the narrow-leaved *Neoregelia* this species represents.

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from the other

Neoregelia species by the narrow (< 2 cm wide), linear leaves.

LOCAL DISTRIBUTION: MLC - Melastomataceae forest

ALTITUDE RANGE: 500 m

HABITAT: Melastomataceae forest, close to a small stream.

29: GENUS *GREIGIA*

DISTINGUISHING FIELD CHARACTERS: *Greigia* is easily identified by the lateral inflorescences (not found in other bromelioid genera in the field site) and high altitude terrestrial habit.

4.1. *GREIGIA RAPORUM* H. LUTHER (FIGURE A52)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from *G. vilcabambae* by the unarmed, brown primary bracts. Vegetatively this species can be distinguished by the cinereous underside of the leaves (glabrous in *G. vilcabambae*)

LOCAL DISTRIBUTION: Around tree line in the Puna and Trocha Union down to plot 1; PLOTS: TU1.

ALTITUDE RANGE: 2800 – 3800 m.

HABITAT: Understory of isolated patches of trees and upper tropical montane cloud forest, forming locally dense patches.

SPECIMENS: SJH062 (-13.1111, -71.6066).

15.2 *GREIGIA VILCABAMBAE* H. LUTHER (FIGURE A53)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from *G. raporum* by the spiny, green primary bracts. Vegetatively this species can be distinguished by the glabrous underside of the leaves (cinereous in *G. vilcabambae*).

LOCAL DISTRIBUTION: Wayqecha and Trocha Union from tree line down to plot 5; PLOTS: ESP, TU5, SP1.

ALTITUDE RANGE: 2000 – 3250 m.

HABITAT: Understory of tropical montane cloud forest, often forming a dense canopy covering the forest floor.

SPECIMENS: SJH064 (-13.1756, -71.5791).

29: GENUS *BROMELIA*

DISTINGUISHING FIELD CHARACTERS: *Bromelia* is a genus of terrestrial species easily separated from the other spiny terrestrial species based on geographic range, being a genus of lowland rainforest.

8. *BROMELIA* CF. *BALANSAE* MEZ (FIGURE A54)

ID NOTES: The identification of a specimen from the Tono site as *B. balansae* is tentative, and based primarily on leaf length. The leaves collected from the immature specimen measured over 6m, and were not necessarily the longest, merely 3 representative samples. *B. balansae* is the only species known to have leaves up to 7m in length. Only one example of this plant was found, sheltered under the spiny roots of a stilt palm. It did not flower during the three years the plant was investigated. Another specimen from a similar geographic location, with flower, but without leaf detail, provides further support to this tentative identification (C. Vargas 016881, CUZ).

LOCAL DISTRIBUTION: Tono

HABITAT: Tropical lowland forest, only one plant found under the spiny roots of palm tree.

SPECIMEN: SJH049 (-12.9572, -71.5602).

17. *BROMELIA* CF. *GOELDIANA* L.B. SMITH (FIGURE A54)

ID NOTES: Only one small colony of these plants was found, and all plants were without flower. While a definite identification is not possible with the material available, *B. goeldiana* has previously been collected from the area.

LOCAL DISTRIBUTION: Pantiacolla; PLOTS: None.

ALTITUDE RANGE: 200 – 700 m

HABITAT: Forest understory on white sandy soils.

SPECIMEN: SJH055 (-12 38.611, -71 16.082)

40: GENUS *AECHMEA*

DISTINGUISHING FIELD CHARACTERS: *Aechmea* can be distinguished by its epiphytic habit (although species in this genus are known to be facultatively terrestrial in other locations) and straight petals at anthesis (recurved in *Billbergia*)

23.2 *AECHMEA LONGIFOLIA* (RUDGE) L.B. SMITH & M.A. SPENCER

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished in flower from other *Aechmea* by the short-scaped inflorescence which is much shorter than the leaves.

Vegetatively this is the only *Aechmea* that forms an open rosette of long, narrow leaves, with very little water-impounding capacity.

LOCAL DISTRIBUTION: Tono area and below, MLC, Pantiacolla, Tambopata; PLOTS: TON, TAM3, TAM4.

ALTITUDE RANGE: 180 – 1200 m

HABITAT: Exposed trees in tropical rainforest and tropical montane forest and also on isolated trees in pasture. This species is sometime found with ants amongst the rosette, despite not forming a phytotelm.

SPECIMENS: SJH042 (-12.9596, -71.5660), SJH074 (-12.9533, -71.5493)

35. *AECHMEA MERTENSII* (G. MEYER) SCHULTES F. (FIGURE A55)

DISTINGUISHING FIELD CHARACTERS: This species is variable across these field sites and throughout its range. In flower can be distinguished from other *Aechmea* spp. by the pendulous red scape bracts.

LOCAL DISTRIBUTION: Lowland tropical rainforest including Tono, Pantiacolla, Tambopata; PLOTS: TON.

ALTITUDE RANGE: 180 – 1000 m

HABITAT: Isolated trees in pasture or forest trees in secondary forest.

SPECIMENS: SJH041 (-13.9258, -71.5653), SJH058 (-12 38.548, -71 14.265).

41. *AECHMEA LONGICUSPIS* BAKER (FIGURE A56)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from other *Aechmea* by the pendulous pale pink scape bracts, unbranched inflorescence and armed floral bracts.

Vegetatively the large glaucous tanks are distinctive.

LOCAL DISTRIBUTION: Pantiacolla, Tambopata; PLOTS: TAM4.

ALTITUDE RANGE: 180 – 400 m

HABITAT: Isolated and exposed trees in lowland tropical rainforest.

61. *AECHMEA ANGUSTIFOLIA* POEPPIG & ENDLICHER

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from other *Aechmea* by the scarlet red scape bracts, except for *A. mertensii* from which it is distinguished primarily by its larger size.

ALTITUDE RANGE: 600 – 800 m

HABITAT: Lowland rainforest

82. *AECHMEA PENDULIFLORA* ANDRÉ

DISTINGUISHING FIELD CHARACTERS: This species is superficially very similar to *A. angustifolia* but has a larger, wider inflorescence with more yellow colouration in the floral bracts.

ALTITUDE RANGE: 600 – 1000 m

HABITAT: Lowland rainforest

117.1. *AECHMEA MOOREI* H. LUTHER (FIGURE A57)

DISTINGUISHING FIELD CHARACTERS: This species can be distinguished from other *Aechmea* by neon pink scape bracts and once-branched inflorescence.

LOCAL DISTRIBUTION: Pantiacolla – Monk Saki trail

ALTITUDE RANGE: 400 – 500 m

HABITAT: Secondary tropical rainforest, typically in exposed locations on mature trees.

42: GENUS *BILLBERGIA*

DISTINGUISHING FIELD CHARACTERS: *Billbergia* can be distinguished by its epiphytic habit, narrow tubular growth form, leaves with distinctive white bands or spots on the abaxial surface, showy pink floral bracts, and recurved petals at anthesis.

40. *BILLBERGIA* CF. *BRACHYSIPHON* L.B. SMITH (FIGURE A58)

DISTINGUISHING FIELD CHARACTERS: The tubular rosette is narrower than in *B. decora* and the leaves are covered with white spots.

LOCAL DISTRIBUTION: Pantiacolla and MLC; PLOTS: TON, TAM3, MLC

ALTITUDE RANGE: 200-500m

HABITAT: Lowland tropical rainforest, epiphytic throughout the canopy often in large ramets.

SPECIMEN: SJH054 (-12.6538, -71.2563)

42. *BILLBERGIA DECORA* POEPPIG & ENDLICHER (FIGURE A58)

DISTINGUISHING FIELD CHARACTERS: The tubular rosette is covered with white bands across the entire width of the leaf (*B. brachysiphon* is spotted).

LOCAL DISTRIBUTION: Tono and below; PLOTS: TON, TAM3, MLC.

ALTITUDE RANGE: 180 - 1000 m.

HABITAT: Lowland tropical rainforest, typically epiphytic in the understory and very rarely terrestrial. Occasionally in more exposed locations. This species is a prolific clonal reproducer and mature colonies of this species can contain tens of individuals.

A4. DICHOTOMOUS KEY

The main part of this key was translated from Zevallos (2008). The key has been extended to include new species discovered as part of this research project. This dichotomous key is designed specifically for use with dried herbarium specimens, and hence the characters used are those which are well preserved. The use of an asterisk before a question shows it has been used directly from the key of Zevallos (2008). The generic characterisation is strongly based on the key from the BSI website by Derek Butcher (www.bsi.org), and includes the subfamilies updated to the classification of Givnish *et al.* (2007).

COUPLET KEY FOR FAMILY TO SUBFAMILY

*A. Ovary inferior. Fruit baccate, fleshy to coriaceous or sorosis. Leaves usually mucronate or spinose-serrate. Often epiphytic plants...Q1 Bromelioideae

*A'. Ovary superior to inferior. Fruit dehiscent capsule (indehiscent in some *Pitcairnia* species, but the seeds winged) ...B

*B. Seeds naked or appendices whole, not feathery. Ovary superior to inferior. Leaves often mucronate or spinose-serrate. Plants generally terrestrial ...C

*B'. Seeds plumose. Ovary superior. Leaves entire. Plants usually epiphytic ...Q5 Tillandsioideae

C. Petal blades showy; tightly spiralled after anthesis, broad and distinct from claws. Winged seeds ...Q11 Puyoideae (*Puya*)

C'. Petal blades remaining free after anthesis, or if slightly coiled, then not clawed. Seeds bicaudate ...Q13 Pitcairnioideae (*Pitcairnia*)

KEY FOR SUBFAMILIES TO GENUS

BROMELIOIDEAE

1'. Sepals asymmetric ...Q2

1. Sepals symmetric or nearly so ...Q3

*2. Inconspicuous inflorescence, covered by leaves that form a crown, white flowers ...Q1

Neoregelia

*2'. Inflorescence conspicuous, not cupped, yellow flowers ...Q3 *Aechmea*

3. Inflorescences multiple, lateral ...Q8 *Greigia*

3'. Inflorescences terminal ...Q4

4. Inflorescence with short peduncle, much shorter than leaves. Terrestrial ...Q9 *Bromelia*

4'. Inflorescence with long peduncle, exceeding leaves and often pendulous. Epiphytic ...Q10

Billbergia

TILLANDSIOIDEAE

*5. Petals connate or strongly conglutinated into a tube to the height of the sepals. Flowers always more than two rows (polystichous) ...Q6

*5'. Petals free or forming very short tube. Flowers usually distichous ...Q7

6. Petal bases always naked ...Q17 *Guzmania*

6'. Petal bases bearing appendages on the inside ...*Mezobromelia* [= *M. pleiosticha*]

(*M. pleiosticha* is included in the key to *Guzmania* in case petals are absent)

*7. Petals small with rounded apex ...Q35 *Racinaea*

*7'. Petals with acute apex, flowers of medium size ...Q8

*8. Petals without basal appendage, inflorescence with distichous-flowered spikes or rarely simple or even a single flower ...Q43 *Tillandsia*

*8'. Petals with basal appendages on the inner side. Flowers usually distichous ...Q9

9. Flowers arranged distichously on inflorescence branches or inflorescence simple...Q57

Vriesea

9'. Flowers secund on inflorescence branches... *Werauhia* [= *Werauhia* cf. *gigantea*]

COUPLET KEY TO SPECIES

KEY TO *NEOREGELIA*

1. Inflorescence branched ...*Neoregelia eleutheropetala* var. *eleutheropetala*

1'. Inflorescence simple ...Q2

2. Leaves triangular, sheaths inflated ...*Neoregelia* cf. *leviana*

2'. Leaves linear, sheaths narrow ... *Neoregelia* sp.1

KEY TO *AECHMEA*

*3. Peduncle barely visible (inflorescence at base of leaves) ...*Aechmea longifolia*

*3'. Well-developed peduncle visible ...Q4

4. Inflorescence simple, floral bracts armed ...*Aechmea longicuspis*

4'. Inflorescence branched ...Q5

5. Inflorescence twice-branched ...*Aechmea penduliflora*

5'. Inflorescence once branched ...Q6

6. Peduncle bracts 15-20, bright pink ...*Aechmea moorei*

6'. Peduncle bracts 5-10, red... Q7

*7. Seeds 12-15 per fruit, plant 0.5 - 0.80 m high, leaves long deltoid ...*Aechmea angustifolia*

*7'. Seeds 10-11 per fruit, plant 0.4 - 0.55 m high, leaves deltoid ...*Aechmea mertensii*

KEY TO *GREIGIA*

8. Floral bracts armed, flowers sessile ...*Greigia vilcabambae*

8'. Floral bracts entire, flowers pedicellate ...*Greigia raporum*

KEY TO *BROMELIA*

9. Leaves less than 2m long ...*Bromelia* cf. *goeldiana*

9'. Leaves 4-6 (-7) m long ...*Bromelia* cf. *balansae*

KEY TO *BILLBERGIA*

10. Sepals narrowly acute, twice as long as wide ...*Billbergia cf. brachysiphon*

10'. Sepals broadly acute, distinctly less than twice as broad as long ...*Billbergia decora*

KEY TO *PUYA*

*11. Inflorescence branches visible, indumentum brown, more than 600 seeds per locule

...*Puya ferruginea*

*11'. Inflorescence branches not visible, indumentum another colour, Seeds 80-120 per locule ...Q12

*12. Petals blue, not succulent at the base, 80-100 seeds per locule ...*Puya leptostachya*

*12'. Petals yellow-green, succulent at the base, seeds 100-120 per locule*Puya membranacea*

KEY TO *PITCAIRNIA*

13. Plant with no or much reduced stem ...Q14

13'. Plant with elongated stem ...Q15

*14. Inflorescence simple, yellow flowers, leaves distichous ...*Pitcairnia lanuginosa*

*14 '. Inflorescence branched, red flowers, petals without basal appendages ...*Pitcairnia paniculata*

15'. Plant with solid stem supporting single or rarely 2-3 rosettes of leaves, inflorescence branched, Petal with basal appendages ...*Pitcairnia lechleri*

15'. Plant in climbing habit stem not providing support, leaves in one or more whorls along stem, inflorescence simple, flowers secund ... *Pitcairnia cf. scandens*

KEY TO *GUZMANIA*

16. Inflorescence simple ...Q17

16'. Inflorescence branched ...Q21

17. Floral bracts red or yellow ...Q18

17'.Floral bracts green ...Q19

18. Floral bracts and petals yellow, leaves linear...*Guzmania* sp. novo

18'. Floral bracts red, petals white, leaves lanceolate ...*Guzmania besseae*

19. Scape bracts foliaceous, green; Petals white ...Q20

19'. Scape bracts not foliaceous, red; Petals yellow ...*Guzmania melinonis*

*20. Floral bracts dense, overlapping ...*Guzmania retusa*

*20'. Floral bracts lax, spaces between flowers ...*Guzmania calothyrsus*

21. Lower primary bracts much exceeding the branches and enclosing them ...Q22

21 '. Primary bracts shorter than, or just equalling branches, branches exposed ...Q26

22. Primary bracts entirely red; Petals appendage present ...Q23

22'. Primary bracts green with red or yellow colouration ...Q24

23. Leaves deep red adaxially, floral bracts green, petals white ...*Guzmania* aff. *variegata*

23'. Leaves entirely green, floral bracts green with yellow tips, petals yellow ...*Mezobromelia pleiosticha*

24. Primary bracts glabrous, with single red strip at or near tip ...*Guzmania gloriosa*

24'.Primary bracts conspicuously lepidote, with faint red stripe and extensive spots, or red stripe with yellow stripe towards axis ...Q25

Q25. Primary bracts conspicuously red-lepidote with faint red stripe ...*Guzmania squarrosa*

Q25'. Primary bracts with strong red stripe outside a conspicuous yellow stripe ...*Guzmania* aff. *squarrosa*

*26. Flowers laxly or sub-densely arranged on spikes ...Q27

*26'. Flowers in dense spikes ...Q28

27. Plant mostly terrestrial, leaves to 1m, inflorescence with 20-30 branches, floral bracts red, petals yellow ...*Guzmania undulato-bracteata*

27'. Plant mostly epiphytic, leaves 50cm, inflorescence with 3-5 branches, floral bracts green, petals white ...*Guzmania roezlii*

*28. Spikes close together and concentrated at the apex ...*Guzmania morreniana*

*28'. Spikes lax, at least basally ...Q29

*29. Leaves with transverse lines ...Q30

*29'. Leaves without transverse lines ...Q31

*30. Plant terrestrial Primary bracts red, flowers yellow*Guzmania weberbaueri*

*30'. Plant epiphytic. Primary bracts with longitudinal red stripes, flowers white ...*Guzmania killipiana*

31. Inflorescence branches lax at base becoming denser towards tip ...Q32

31'. Inflorescence branches lax throughout ...*Guzmania acutispica*

*32. Spikes strict, globose ...*Guzmania cuzcoensis*

*32'. Spikes spreading ...Q33

33. Inflorescences branches elliptic ...*Guzmania atrocastanea*

33'. Inflorescences branches rounded ... *Guzmania sphaeroidea*

KEY TO *RACINAEA*

*34. Inflorescence simple or once-branched ...Q35

*34'. Inflorescence twice-branched ...Q41

*35. Leaves with longitudinal brown bands 1-2cm wide ...*Racinaea spiculosa* var. *ustulata*

*35'. Leaves uniform in colour, or at least without brown bands ...Q36

*36. Flowers clustered and floral bracts overlapping (imbricate) ...Q37

*36'. Flowers not clustered, visible spaces between them ...Q38

*37. 11 spikes, 14-16 flowered ...*Racinaea pendulispica*

*37. Spikes 6-8, 6-8 flowered ...*Racinaea seemannii*

38. Inflorescence erect, primary bracts green with brown scales, petals white ...Q39

38'. Inflorescence pendulous, primary bracts yellow with red tips, petals yellow ...*Racinaea tetrantha* var. *aurantiaca*

39. Inflorescence branches ascending. Primary bracts shorter than secondary peduncle ...

Racinaea pallidoflavens

39'. Inflorescence branches straight, divergent from axis ...Q40

40. Plant forming narrow pseudobulb, leaves linear, branches 10-18 flowered, primary bracts shorter than secondary peduncle ...*Racinaea parviflora*

40'. Plant forming open tank, leaves narrowly triangular, branches 6 flowered, primary bracts exceeding or equalling spikes ... *Racinaea schumanniana*

*41. Leaves linear, attenuate, 0.5-0.6 cm wide ...*Racinaea ropalocarpa*

*41'. Leaves deltoid, 1.7-2 cm wide ...*Racinaea penduliflora*

KEY TO *TILLANDSIA*

42. At least some inflorescences lateral ...Q43

42'. Inflorescence branched, terminal ...Q45

43. Inflorescences only lateral ...*Tillandsia complanata*

43'. Inflorescences both lateral and terminal ...Q44 *Tillandsia* sp. A (possible hybrids of *T. complanata*)

*45. Laxly arranged flowers with visible spaces between them ...Q46

*45'. Flowers clustered, no visible spaces between them ...Q48

*46. Spike axis thickened, curving upwards and branching, flowers secund ...*Werauhia* cf. *gigantea*

-
- *46'. Spike axis not thickened or branching, flowers distichous ...Q47
- *47. 20-30 spikes 6-10 cm long, 10-16 flowered ...*Tillandsia truncata* var. *major*
- *47'. 10-12 spikes 2-2.5 cm long, 2-3 flowered ...*Tillandsia biflora*
- *48. Primary bracts exceeding or equalling the spikes, especially in the lower branches
...Q49
- *48'. Primary bracts smaller than the spikes ...Q50
49. Primary bracts imbricate, inflorescence cylindrical ...*Tillandsia ionochroma*
- 49'. Primary bracts not imbricate, inflorescence sub-cylindrical ...*Tillandsia rubella*
- *50. Leaves narrowly triangular, inflorescence twice-branched ...*Tillandsia longifolia*
- *50'. Leaves lanceolate, inflorescence once-branched ...Q51
51. Floral branches ascending ...Q52
- 51'. Floral branches spreading to reflexed ...Q53
52. Secondary peduncle indistinct, primary bracts green with red tip, floral bracts green
...*Tillandsia stenoura* var. *mauroi*
- 52'. Secondary peduncle 2cm green, primary bracts red, floral bracts red ...*Tillandsia* cf.
pastensis
- *53. Seeds 30-40 per locule, plants under 60 cm tall ...*Tillandsia confinis*
- *53'. Seeds 75-100 per locule, plants flowering over 80 cm tall ...Q54
- *54. Plants 0.8-1.3 m tall, inflorescence primarily red ...Q55
- *54'. Plants flowering more than 1.8 m tall, inflorescence of another colour ...*Tillandsia*
stenoura
55. Floral bracts green with red tip ...*Tillandsia wurdackii*
- 55'. Floral bracts red ...Q56
-

*56. Inflorescence branches flattened, 10-20 flowered, floral bracts keeled 1/3 from apex, 2.5 × 0.6 cm ...*Tillandsia pyramidata*

*56'. Inflorescence branches recurved to reflexed, 6-10 flowered. Floral bracts keeled 2/3 from the apex, 4.3 x 0.7 cm ...*Tillandsia superba*

KEY TO *VRIESEA*

57. Inflorescence branched ... Q58

57'. Inflorescence simple, erect ...*Vriesea* cf. *chrysostachys*

58. Leaves cinereous-lepidote, inflorescence pendulous, floral bracts pink, petals green
...*Tillandsia patula*

58'. Leaves glabrous, inflorescence erect, floral bracts red with white tips, petals white
...*Vriesea dubia*

A5. REFERENCES

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A6. IMAGES TO ACCOMPANY SPECIES CHECKLIST

The following images are referred to in the species checklist, and are included here together for ease of reference.



Figure A1. *Pitcairnia paniculata*. (a) flowering plant in natural habitat, roadside verges with open vegetation (b) view of flower with zygomorphic petals

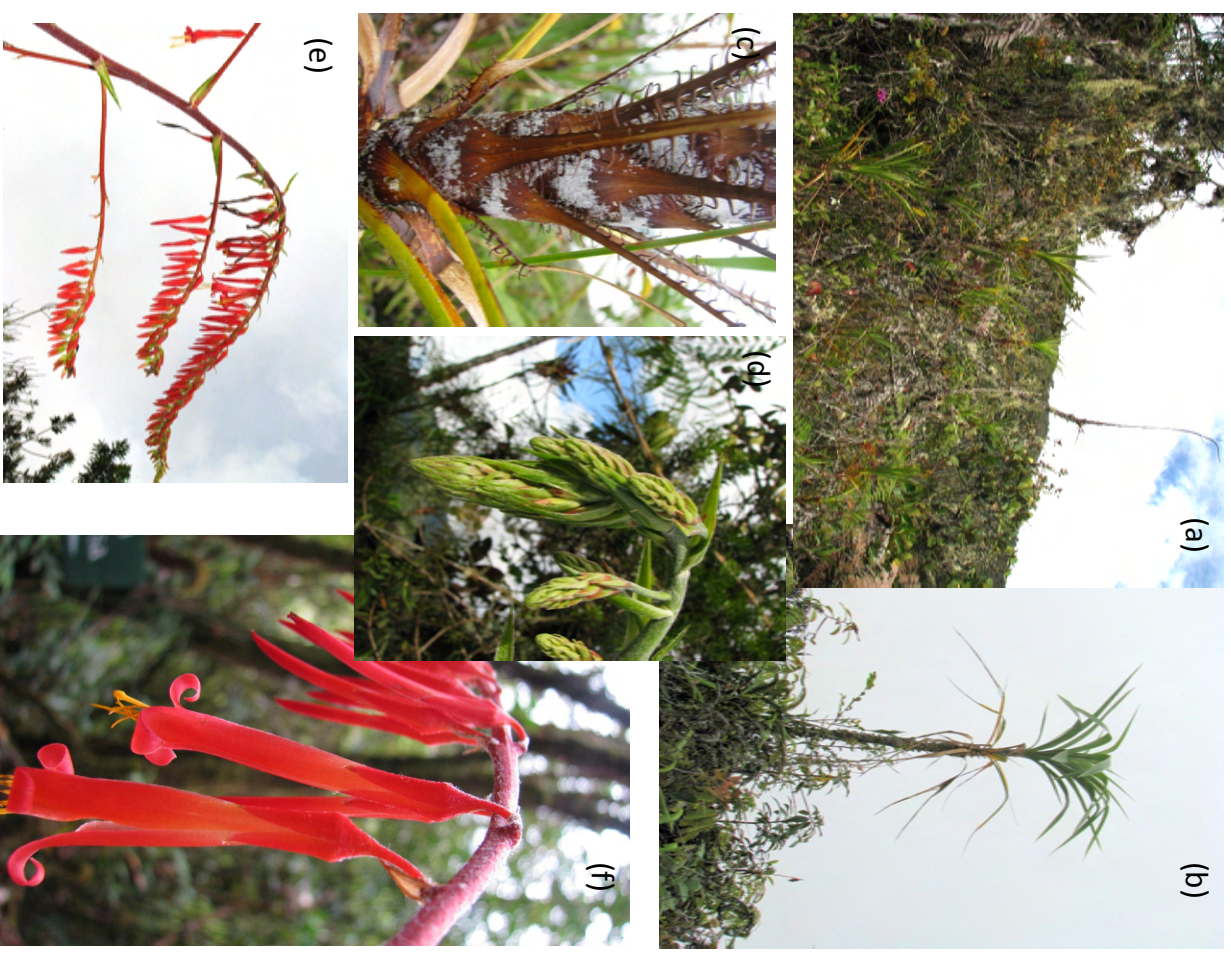


Figure A2. *Pitcairnia lechleri* (a) habitat (b) growth form with elongated woody stem raising leaf rosette above surrounding vegetation (c) much reduced stem leaves (d) immature inflorescence (e) mature inflorescence (f) flower detail showing petals coiled at anthesis



Figure A3. *Pitcairnia cf. scandens* (a) climbing stem with rosette of leaves (b) an old inflorescence with secund arrangement of flowers/seed pods (c) underside of leaves (d) new shoot emerging from base of leaf rosette



Figure A4. *Tillandsia fendleri* (a) plant in habitat in the Urbamba valley (b, c) inflorescence detail (d) lower inflorescence branches with entirely foliaceous bracts (e) floral bracts detail (f) roots of the same plant growing into the leaf base

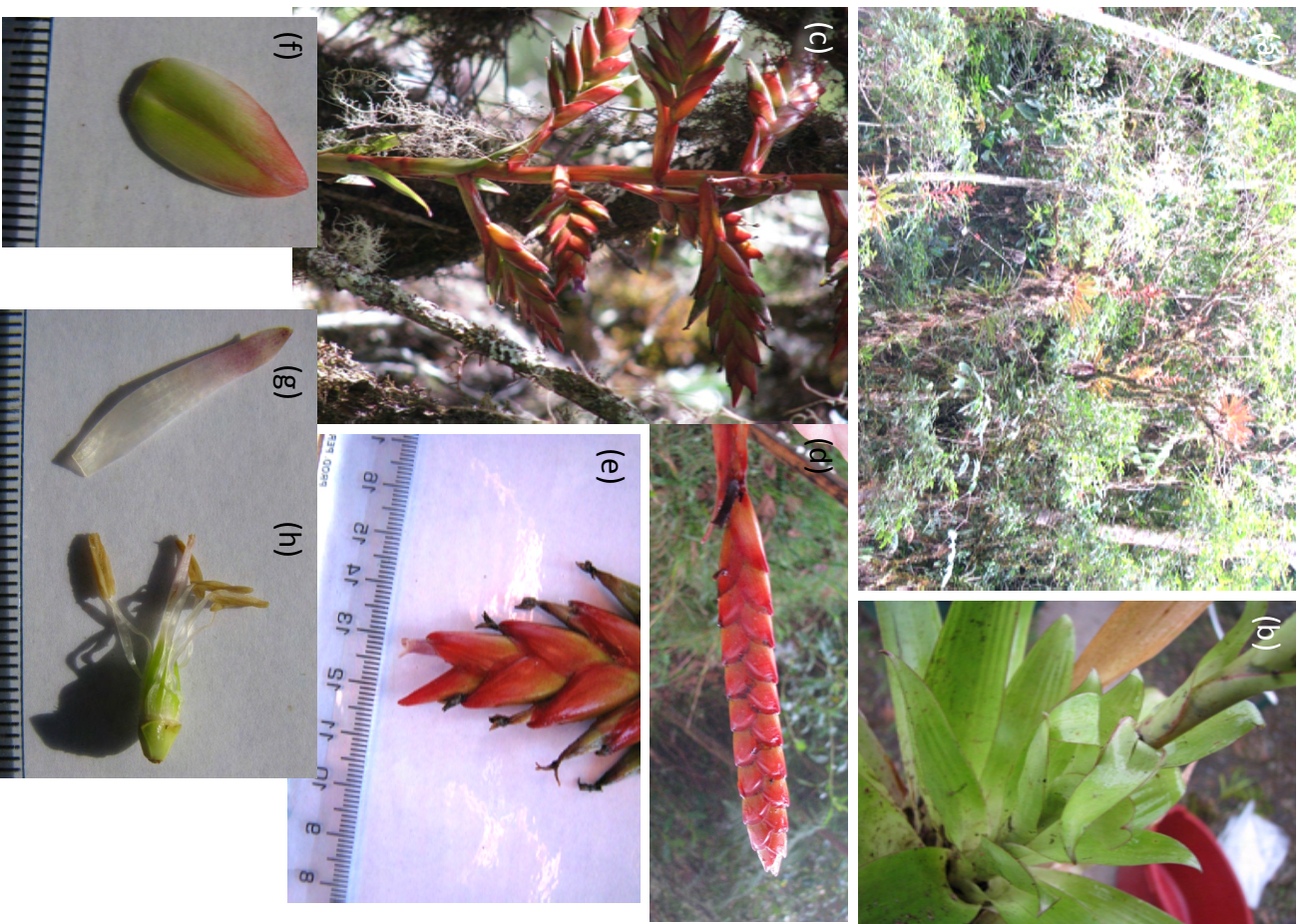


Figure A5. *Tillandsia pyramidalata* (a) plants in habitat (b) detail of leaves and peduncle bracts (c) flowering inflorescence (d) inflorescence branch from plant with larger inflorescence (e) detail of flower branches with flower showing flowering at tip while seed pods are maturing towards base (f) detail of flattened sepal (g) petal (h) stamens still attached to superior ovary

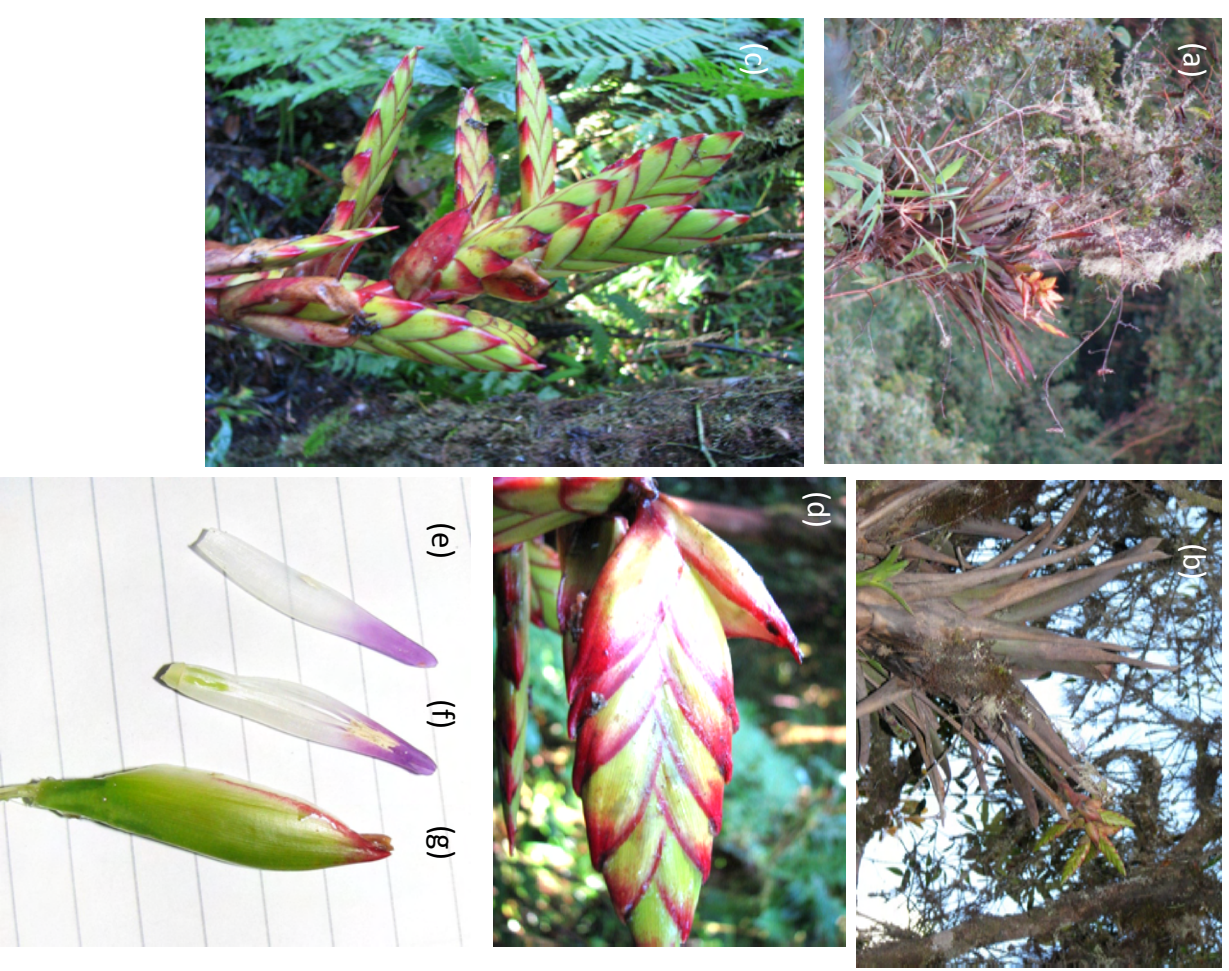


Figure A6. *Tillandsia wurdackii* (a) plant in exposed habitat (b) plant in sheltered habitat (c) inflorescence (d) detail of inflorescence branch (e) petal (f) petal with stamens and ovary (g) floral bract



Figure A7. *Tillandsia confinis* (a) plant often found in dense colonies on exposed trees (b) plant showing pale underside of leaves and immature inflorescence (c) inflorescence (d) detail of inflorescence branch with flower (e) floral bract (f) sepals and petals (g) petals with stamens



Figure A8. *Tillandsia stenoura* (a) plant in exposed habitat (b) inflorescence (c) plant detail (d, e) *T. stenoura* has significant variation in branch lengths, with longer branches often simultaneously flowering and setting seed (f) petal with stamens and ovary (g) sepal s(h) floral bract



Figure A9. *Tillandsia stenoura* var. *mouroi* (a) plant (b,c) inflorescence branch and primary bract detail (d) inflorescence (e) petals (f) sepals (g) stigma, style and ovary



Figure A10. *Tillandsia superba* (a) plant in open habitat (b) plant in forest understory habitat (c) inflorescence branch (d) primary bract and floral axis detail (e) anther detail (f) petals (g) sepals (h) flori bract



Figure A11. *Tillandsia rubella* (a) plant in forest habitat (b) plant in habitat at treeline (c) inflorescence (d) flower with petals spreading at anthesis (e) lower floral bract (f) branch with flower and exposed rachis (g) upper floral bract (h) details of petal, stamens and carpel

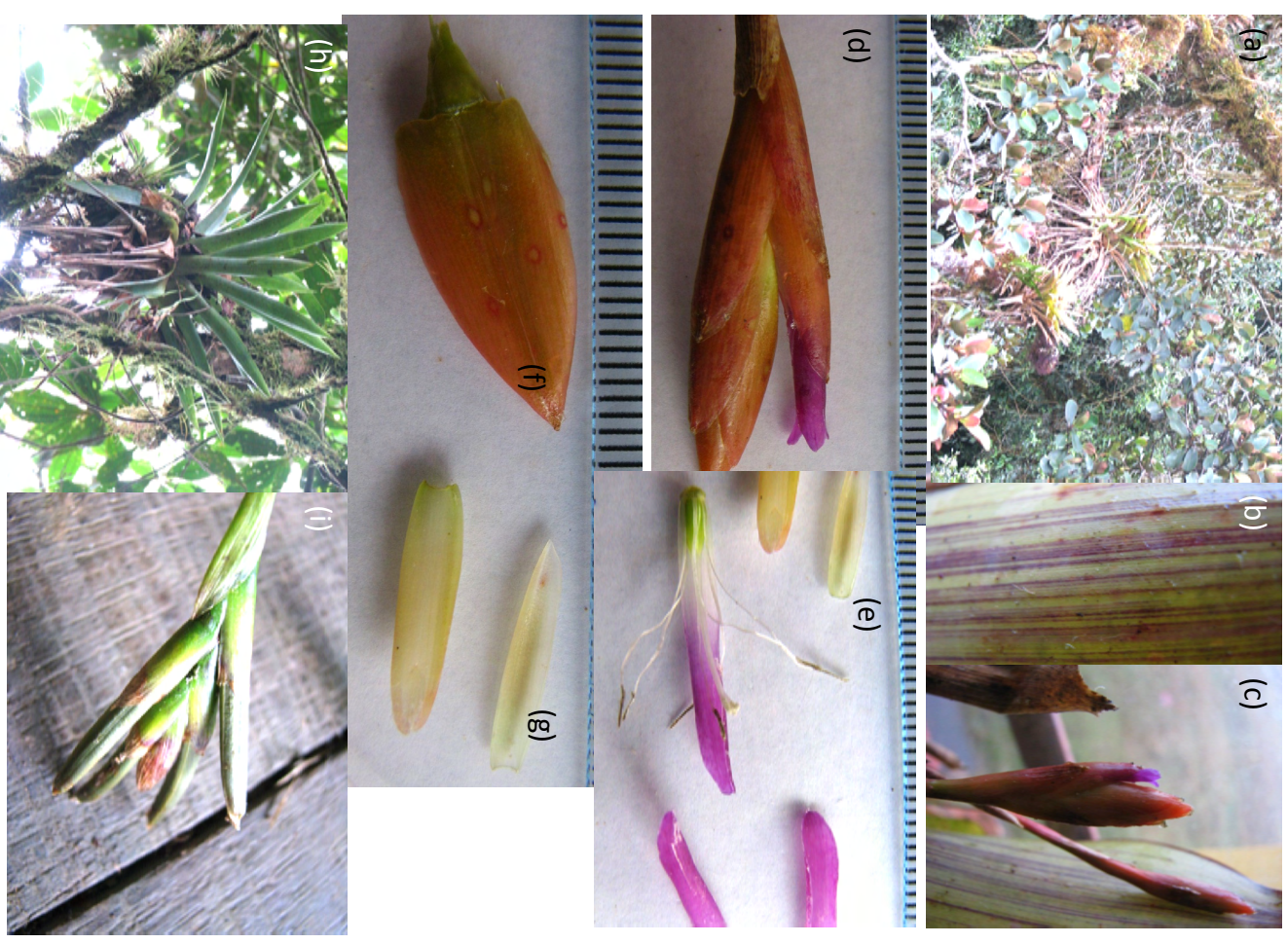


Figure A12. *Tillandsia complanata* (a) habitat (TMC) (b) leaf showing red lines (c) inflorescence detail (d) petal with stamens and carpel (e) floral bract (f) sepals (h) seedling inflorescence of lowland form

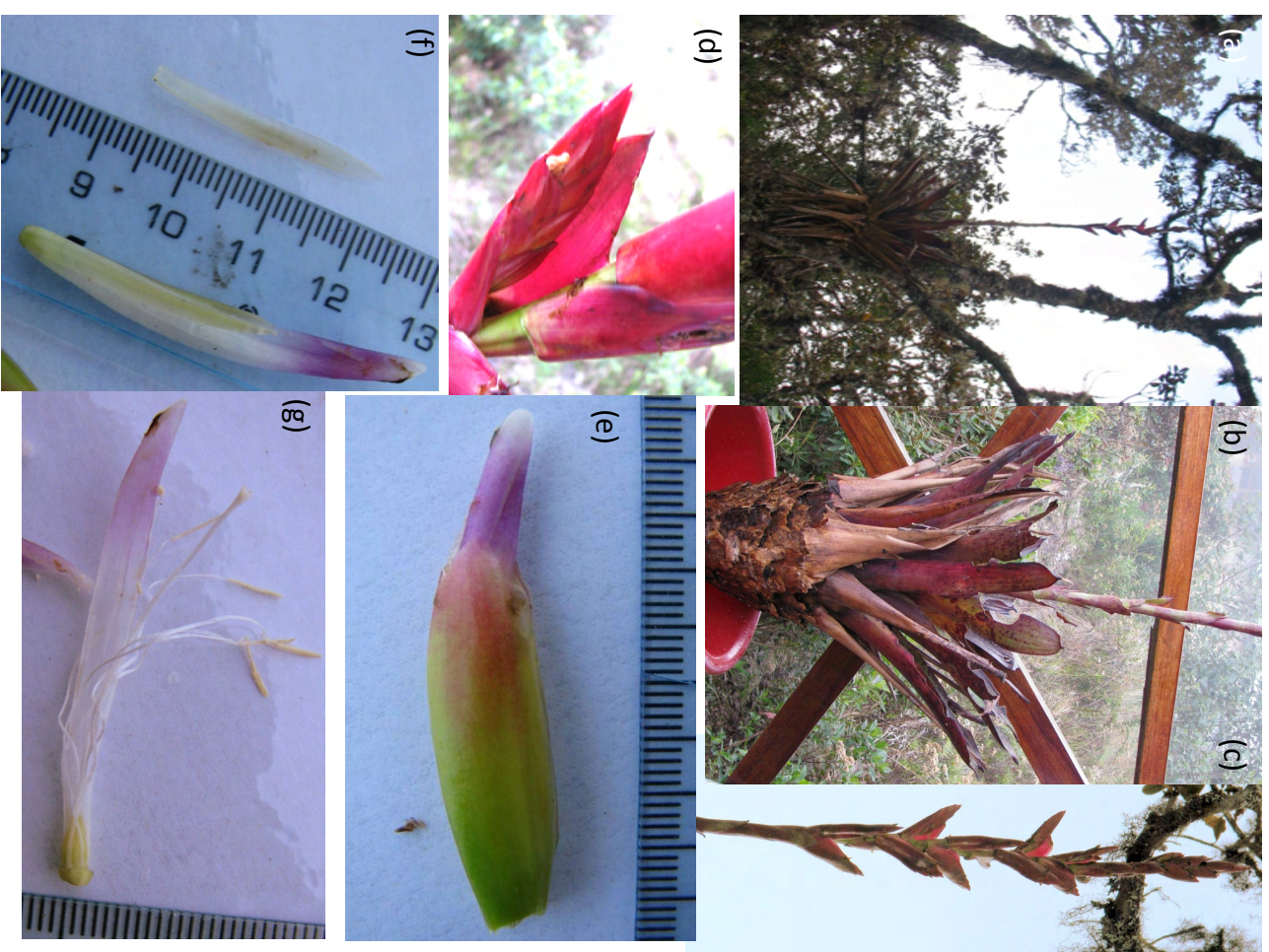




Figure A15. *Tillandsia longifolia* (a) in habitat (right) next to *T. truncata* (b) inflorescence



Figure A16. *Tillandsia paraensis* (a) inflorescence (b) plant



Figure A17. *Tillandsia parula* (a) habitat (b) immature inflorescence detail (c) flowering inflorescence detail (picture courtesy Isau Huamantupa) (d) seeds (e) flower detail (picture courtesy Isau Huamantupa)



Figure A18. *Tillandsia* species A (potential hybrids) 1) with compound inflorescence (a) habitat (b) leaves with branching lateral inflorescences (c) immature inflorescence (d) lateral inflorescence maturing after the plant has died; 2) with simple inflorescence (e) plant (f) habitat (g) rosette with lateral inflorescences



Figure A19. *Racineoa seemanii* (a) habitat (b) seedling and flowering plants (c) flower detail (d) simple inflorescence (e) branched inflorescence (picture courtesy Taló Treviño Zevallos) (f) floral bract and sepal detail



Figure A20. *Racinoa spiculosa* var. *ustulata* (a) habitat (b) inflorescence (c) inflorescence branch with post-dispersal fruits



Figure A21. *Racinoa pallidoflavens* (a) plant (b) inflorescence (c) flower detail

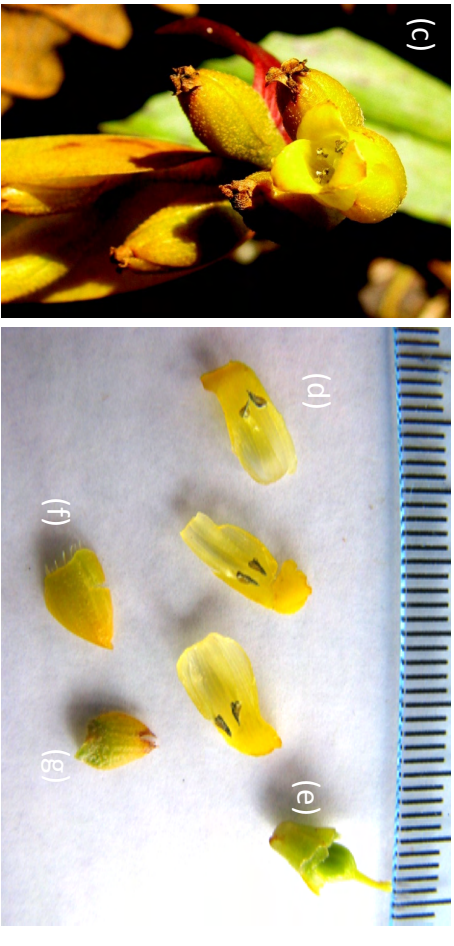


Figure A23. *Rocinoea tetrantha* var. *aurantiaca* (a) inflorescence (b) inflorescence branch (c) flower detail (d) petals and stamens (e) carpel (f) asymmetric sepal (g) floral bract

Figure A22. *Rocinoea penduliflora* (a) habitat (b) inflorescence (c) foliage details (d) flower detail (e) petals, stamens and carpel inflorescence branch (f) flower detail (g) petals, stamens and carpel



Figure A24. *Rochnoea schumanniana* (a) habitat (b) inflorescence (c) primary bract and inflorescence branch (d) floral bract (e) sepals (f) petals, stamens and carpel.



Figure A25. *Rochnoea ropalocarpa* (a) plant (b) inflorescence branch (c) sepals (d) petals, stamens and carpel



Figure A26. *Rocinaea parviflora* (a) plant



Figure A27. *Vriesea cf. chrysostachys* (a) plant (b) inflorescence



Figure A28. *Vriesea dubia* (a) plant (b) inflorescence branch with flower (photos courtesy Isau Huamantupa)



Figure A29. *Werahia cf. gigantea* (a) habitat (b) inflorescence



Figure A30. *Guzmania roezlii* (a) plant (b) inflorescence branch with flower (images courtesy Isau Haunantupa)



Figure A31. *Guzmania* aff. *variegata* (a) plant (b) inflorescence with flower



Figure A32. *Guzmania weberbaueri* (a) plant in cultivation at the InkaNatura Lodge in San Pedro (b) plant in epiphytic habitat (c) leaf details showing dark green transverse lines (d) peduncle bract details (e) inflorescence details



Figure A33. *Guzmania sphaeroides* (a) plant in habitat showing discoloured foliage typical of this species (b) inflorescence (c) fruiting inflorescence details

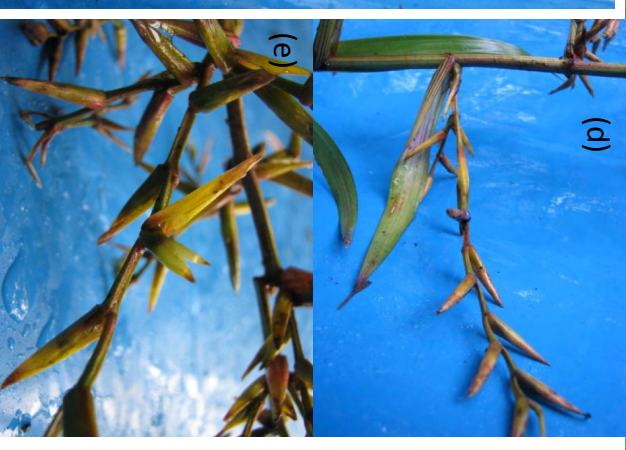
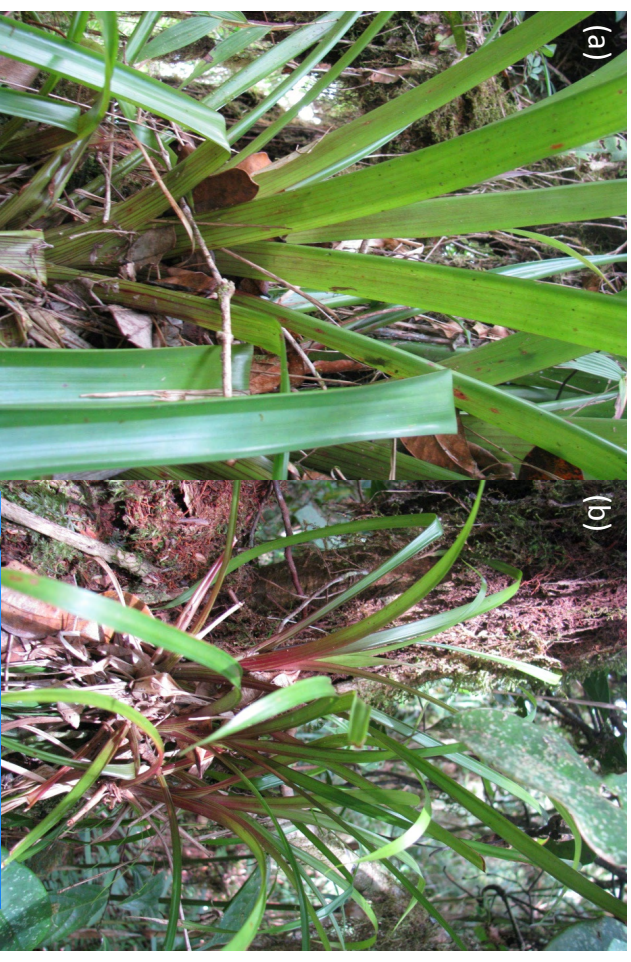


Figure A34. *Guzmania undulato-bracteata* (a) plant in habitat showing red lines on lower parts of leaf blades (b) immature plants with strong red colouration (c) inflorescence (d) inflorescence branch and primary bract (e) post-anthesis flower detail



Figure A35. *Guzmania kilipiana* (a) plant in habitat (b) inflorescence (c) inflorescence detail with flower (d) inflorescence branch with flower (e) floral bract (f) flower with sepals (g) stamens and carpel with a sepal still attached



Figure A36. *Guzmania acutispica* (a) fruiting plant in habitat (b) inflorescence (c) inflorescence detail with fruiting branches (d) inflorescence branch with flower (e) flower details showing stamens and carpel



Figure A37. *Guzmania cf. cuzcoensis* (a) plant in habitat – the only sighting of this plant in tropical montane cloud forest at 2600 m.

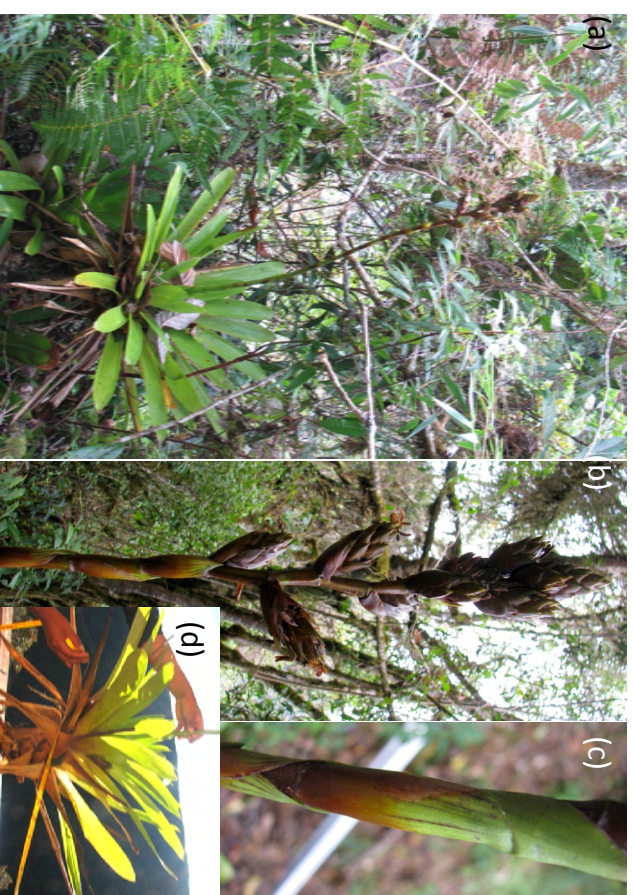


Figure A38. *Guzmania atrocastanea* (a) plant in habitat (b) inflorescence (c) peduncle bracts (d) foliage detail (e) flower details showing stamens and carpel (and a drop of rainwater)



Figure A39. *Guzmania inkerterae* (a) fruiting plant in habitat (b) flowering inflorescence (photo courtesy Italo Trevino Zevallos) (c) peduncle bracts (d) immature inflorescence (e) detail of inflorescence branch

Figure A40. *Guzmania retusa* (a) plant in habitat (b) plant with fruiting inflorescence

Figure A41. *Guzmania besseae* (a) inflorescence (b) flower detail



Figure A42. *Guzmania colothyrusus* (a) plant in habitat (b) plant with furting inflorescence

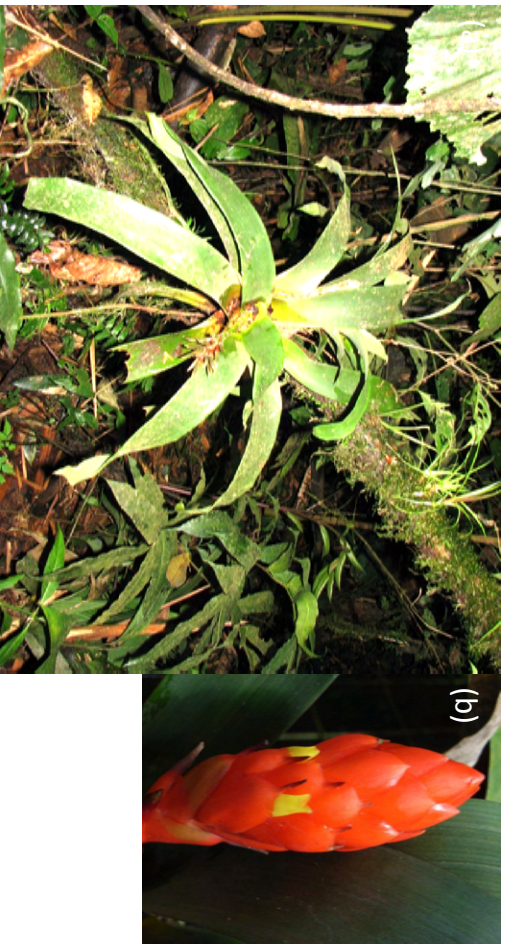


Figure A43. *Guzmania melnensis* (a) habitat (b) inflorescence detail (Image from Isau Huamantupa)



Figure A44. *Guzmania cf. squarrosa* (a) habitat (b) plant (c) inflorescence detail (d) primary bract detail (e) primary bracts showing red band and progressive shortening of blade length (f) seed pods at base of primary bract



Figure A45. *Guzmania squarrosa* (a) habitat (b) plant (c) inflorescence detail showing spotty foliage and red stripes on bracts (d) offshoot showing spotty foliage (e) inflorescence detail showing arrangement of bracts



Figure A46. *Guzmania gloriosa* (a,b) plant (c) inflorescence detail (d) upper part of inflorescence with primary bracts and flowering inflorescence branches (e) floral bract (f) sepal (g) petal

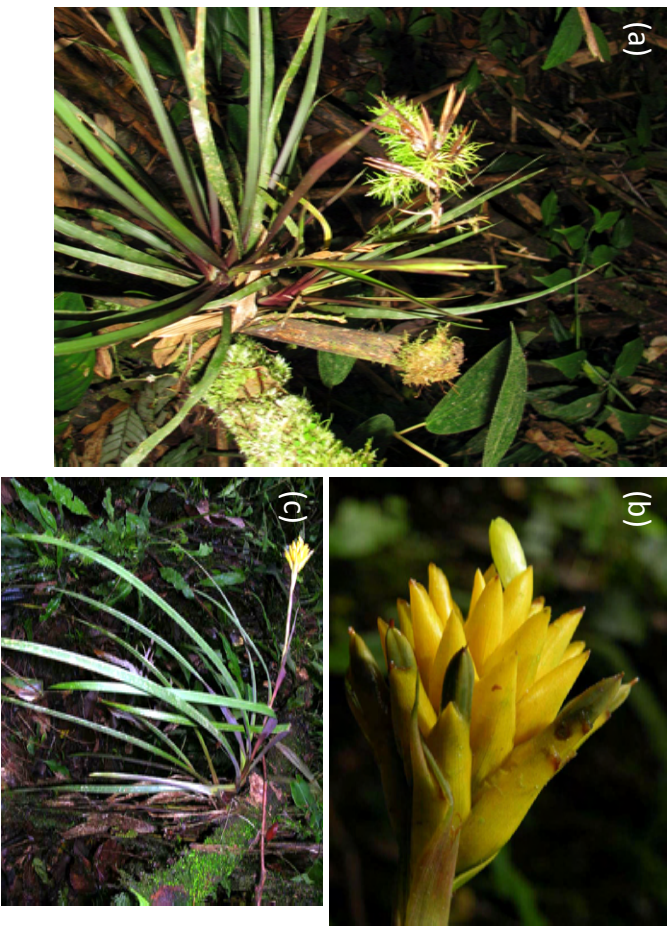


Figure A47. *Guzmania* sp. A (a) plant with seedlings developing on old inflorescence (b,c) plant and inflorescence (photos courtesy Atrium biodiversity network)



Figure A48. *Mezobromelia pleiositchia* (a) habitat (b) plant (c) flowering inflorescence (d) inflorescence dispersing seed (e) flora bract with flower showing gelatinous liquid contained in the bracts (f) branch (g) flower (h) petals, stamens and carpel (i) petal base showing appendage



Figure A49. *Neoregelia eleutheropetala* (a) plant (b) inflorescence detail



Figure A50. *Neoregelia* sp. A (a,b) plant



Figure A51. *Neoregelia* cf. *lewiana* (a) habitat (b) plant showing inflated leaf bases (c) plant showing sunken inflorescence (d) inflorescence detail (e) part of the inflorescence (f) petal with stamen and carpel (g) flower with inferior ovary and floral bract

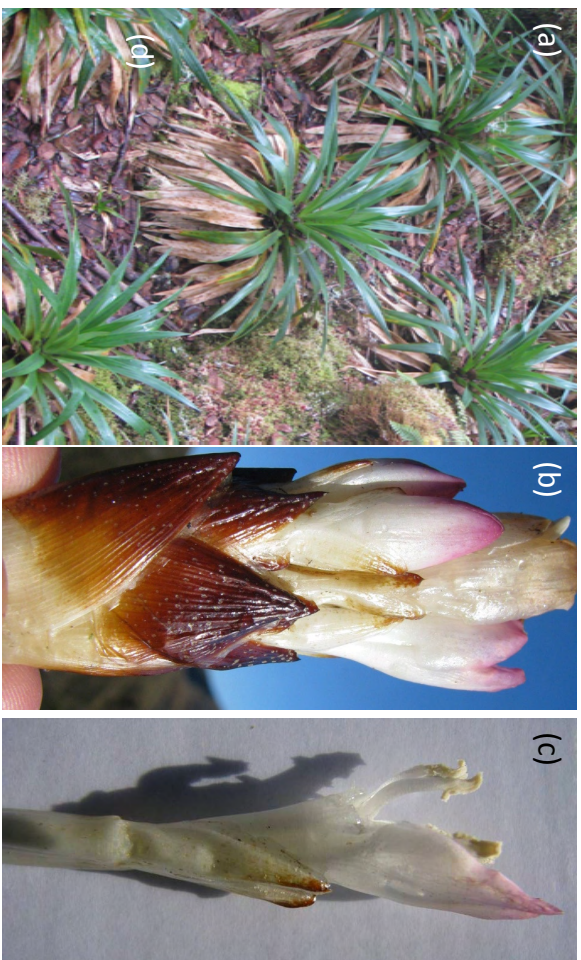


Figure A52. *Greigia raporum* (a) habitat (b) inflorescence detail showing stem bracts (c) flower detail showing sepals, petal and stamens (d) petal, stamens and carpel.



Figure A53. *Greigia wilvabambae* (a) habitat showing dense covering often formed by this species (b) detail of leaf bases showing dense scales and inflorescences (c) an exceptional individual in which the leaf rosette is lifted off the ground by the woody stolon (d) offshoots developing in the leaf bases (e) inflorescence (f) all the stem and floral bracts and flowers from a single inflorescence (g) petal with stamens (h) flower with floral bracts and sepals (i) carpel



Figure A54. *Bromelia* spp. (a) *Bromelia* cf. *goeldiana* in white sand forest at the Pantiaicola lodge (b-d) *Bromelia* cf. *balansae* (b) plant showing red coloration of juvenile leaves (c) showing tangle of exceptionally long leaves and stilt roots of palm protecting plant base (d) base of plant



Figure A55. *Aechmea mertensii* (a) inflorescence (b) inflorescence covered with ants (c) inflorescence detail with fruit (d) fruit opened to show seeds (e) primary bract detail (f) flower detail



Figure A56. *Aechmea longicuspis* (a) Habitat (b) plant (c) inflorescence detail (d) leaf bases



Figure A57. *Aechmea moorei* (a) habitat (b) inflorescence detail



Figure A58. *Bilbergia* spp. (a) *Bilbergia decora* (b) *Bilbergia cf. brachysiphon*