Vegetation response to climate change: a functional traits-based approach

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> "Like roots finding water we always wind up moving towards what sustains us."
>
> – Mark Nepo

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THESIS ABSTRACT

Climate change influences all aspects of plant biology. The responses of vegetation to climate changes (particularly water availability in the world's drylands) constitute a critical and timely research agenda, with potentially significant ecological consequences. This doctoral thesis aimed to investigate vegetation response to climate change using a plant functional traits-based approach, with a specific focus on root traits in Southern Africa by undertaking three interlinked research objectives:

i) **Determination of globally important plant functional traits for coping with climate change (Chapter 4; Research Paper 1).** Here the aim was to synthesize the knowledge to date from the published literature on which traits are important in determining a positive response in plant performance and fitness to climate and associated environmental changes. A systematic review of 148 studies published between 2000-2017 was carried out. Results from this work present a suite of eight key traits that best predict positive plant responses: greater water-use efficiency (WUE), greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density, greater rooting depth, lower or higher specific leaf area (SLA) and lower or higher plant height (the latter two varying across biomes). These findings illustrate important and general trait-climate responses within and between biomes that enhance understanding of which plant phenotypes may cope with or thrive under current and future climate change. They also highlight the importance of generally understudied belowground traits in conferring plants the ability to cope with climate change.

ii) **Determination of how root traits vary within a dry biome (Chapter 5; Research Paper 2).** Here the aim was to quantify the contribution of belowground traits to overall trait variation in the semi-arid Fynbos biome of South Africa and analyse how this changed along regional and local water availability gradients. Fieldwork was conducted to collect root and aboveground traits of 124 individuals of dominant woody shrub species. Results from this work show that drier regions have greater root investment (rooting depth, length, dry matter content and root:shoot ratio) which was consistent intra-specifically and in post-fire environments. Additionally, roots accounted for significant whole-plant trait variation and, importantly, in drier conditions increased root allocation (at the expense of shoot allocation) deviated from expected global allometric relationships. These findings suggest that root investment will be especially crucial for plant performance and survival in a drier and warmer future predicted for dryland biomes. **Chapter 5 (Research Paper 2)** thus contributes to the still deficient field data on belowground traits in drylands.

iii) **Determination of the role that roots play in reducing sensitivity to climate variability in drylands (Chapter 6; Research Paper 3).** Here the aim was to use empirical belowground trait data and remote sensing imagery to explore belowground processes with space-borne, spatially continuous data that allow for regional assessments. A statistical analysis was conducted on the relationship between root depth data and remotely derived vegetation sensitivity to climate variability (VSI, after Seddon et al. (2016)) in Southern Africa. Results from this work show that a significant negative relationship between root depth and vegetation sensitivity exists in Southern Africa, as well as a significant positive relationship between root depth and temporal autocorrelation in vegetation productivity. These relationships were influenced by both biome and growth form, but generally imply that deeper roots reduce vegetation responses to concurrent climate variability and dampen temporal variability in aboveground productivity. These findings suggest that accessing deeper water resources during times of water stress through deeper roots is a potential resilience mechanism for drylands under future climate change.

In this thesis I conclude that traits play a key role in determining vegetation response to climate change. Specifically, I conclude that in dry biomes often-neglected root traits contribute significantly to overall plant trait variation and are thus key in reducing sensitivity to climate variability and determining positive plant responses to climate change. The novelty of this body of work includes but is not limited to the following findings: i) there is a global set of traits important across biomes to cope with multiple climate changes, ii) both local and regional drivers of water availability are significant drivers of belowground trait variation in the semi-arid Fynbos biome of South Africa and, iii) aboveground plant-climate interactions are reflected by belowground trait

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CHAPTER 1: INTRODUCTION

By: Nicola Kühn

> *"Look closely at nature. Every species is a masterpiece, exquisitely adapted to the particular environment in which it has survived."*
>
> *— E.O. Wilson*

1.1 THESIS RATIONALE

1.1.1 BACKGROUND

From the early Greek philosophical musings of Empedocles and Aristotle in the 4th and 5th century B.C., through the naturalist accounts of Darwin and Wallace more than 14 centuries later, right up to the present-day wealth of ecological studies fighting for their place in a scientific journal, plant and animal adaptations to their environments have continued to fascinate us. We are however, at a point in history where the knowledge of these characteristics or traits that allow organisms to persist and possibly thrive under harsh conditions is shifting from the interesting to the essential. Trait-based ecological studies utilise the concept of ecological filtering where plants with suitable traits can survive a set of climatic and environmental constraints and those that do not, are filtered out of the environment (Keddy, 1992). Trait information thus holds a key piece of the puzzle in determining how organisms will respond to the pervasive and fast-paced anthropogenic climate change that we are facing.

Both empirical and theoretical work indicates that there are general subsets of plant traits that best predict how plants will respond to climate change (Lavorel and Garnier, 2002; Moles *et al.*, 2014; Michaletz *et al.*, 2015). Recent studies have demonstrated that subsets of plant traits can play an important role in drought response (O'Brien *et al.*, 2017; Powell *et al.*, 2017; Feng, Ackerly and Skelton, 2018; Brodribb *et al.*, 2020) and temperature increase (Michaletz *et al.*, 2015; Wright *et al.*, 2017). However these are predominantly comparative in approach, they lack global synthesis and tend to have a focus limited to wetter, forested ecosystems (Wright *et al.*, 2010; Paine *et al.*, 2015). Traits in other ecosystems such as drylands, for example, are rarely studied, representing a significant knowledge gap as to how these communities may respond to climate change.

Another knowledge gap in traits-based research is the fact that the vast majority of studies consider aboveground traits with much less focus on the belowground components of plants (see **Fig. 1.1**, Kattge et al. (2019)). However it is well-established that the role of roots in determining vegetation response to climate and environmental changes is particularly important to understand because roots are key components defining plant form and function (Weigelt *et al.*, 2021) playing a significant role in maintaining ecosystem functioning and processes (Bardgett, Mommer and De Vries, 2014). For example, roots are essential for deep soil acquisition of water and nutrients (Jiang *et al.*, 2020; Tumber-Dávila and Malhotra, 2020) thus making them vital for ecosystem nutrient and water cycling (Freschet *et al.*, 2021), particularly under variable or decreasing precipitation (Maeght, Rewald and Pierret, 2013) and drought (Jackson *et al.*, 1996). Roots also play an important role in disturbance-driven ecosystems in helping plants to recover from and survive regular top-kill driven by fire and herbivory for example (Aubin *et al.*, 2016). Furthermore they are fundamental for plant anchorage (Jackson *et al.*, 1999) and relatedly ensure maintenance of soil stability and avoidance of landslides (Freschet *et al.*, 2021).

Of the few root-trait studies that have been carried out to date, the focus has been predominantly on root depth. Yet a variety of belowground plant traits are important for plant functioning, particularly in drier regions of the world that already experience hydroclimatic extremes including:

i) Root dry matter content (the ratio of dry mass to fresh mass of a root) is a representation of root construction costs and thus (alongside the related proxy root tissue density (Birouste *et al.*, 2013) influences root longevity and resource conservation in water-limited environments (Kong *et al.*, 2014; Fort *et al.*, 2017),

ii) Root thickness where roots with thicker diameters can penetrate into harder drier soils to access resources (Fort *et al.*, 2017),

iii) Greater overall belowground investment, including root biomass allocation, which influences the ability to resprout after disturbances such as drought and fire (Aubin *et al.*, 2016).

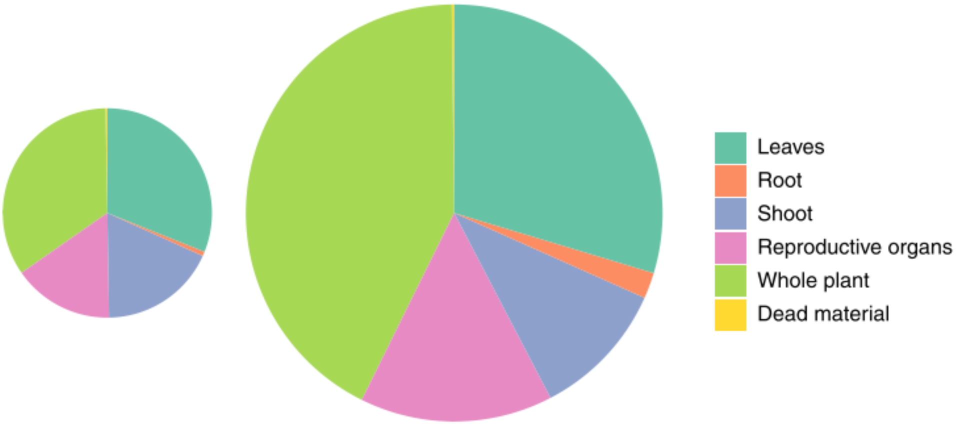

Figure 1.1: Representation of the distribution of plant trait records in the TRY trait database for different plant parts. Circle on the left represents data coverage in TRY version 1 (2.1 million trait records) and on the right TRY version 5 (11.8 million trait records), source: Kattge et al. 2019.

One reason for the lack in root trait data is that the study of belowground traits often involves labour-intensive root excavations (Iversen *et al.*, 2017). In addition, root data is normally measured at a small community scale and thus the spatial spread of this type of data is poor. To gain a proper understanding of how belowground traits influence the wider ecosystem processes or regional dynamics, we need a more spatially continuous understanding of root depth. It is therefore highly valuable to find a way to combine excavational data collection with predictive methods of estimating belowground traits (Yang, Donohue and McVicar, 2016; Jiang *et al.*, 2020; Chitra-tarak *et al.*, 2021; Liu *et al.*, 2021). One way this has been attempted is to establish links between above and belowground traits (Garnier, Navas and Grigulis, 2016) and then scale these relationships up to the ecosystem/landscape level using readily available aboveground data from space-borne imagery. Remotely sensed data are increasingly used in traits-based ecology (Asner *et al.*, 2015; Singh *et al.*, 2015; Jetz *et al.*, 2016) thus providing an opportunity to fill gaps in plant trait data (Pettorelli, 2019) including root trait data. For example, a recent study estimated rooting depth (Liu *et al.*, 2021) using vegetation optical depth (derived from remote sensing) in combination with water-mass balance equations. This approached refined previous estimates (Schenk and Jackson, 2009; Yang, Donohue and McVicar, 2016; Fan *et al.*, 2017) and holds much promise for the future of this research avenue.

However, as the authors themselves caution, the remote-sensing and ecology community need to align to generate these estimations and, beyond map generation, use existing root depth data to a) validate these results and b) directly link to satellite derived ecosystem patterns that describe vegetation sensitivity (for example the Vegetation Sensitivity index derived by Seddon et al. (2016)), in order to avoid circularity that may come about when comparing satellite-based ecosystem patterns to satellite-based root depth estimates.

1.1.2 KNOWLEDGE GAPS

Despite the surge in trait-based studies in relation to climate change over the last two decades (**Chapter 2** of this thesis: Fig 2.1), we are still lacking a global analysis of whether there is a general set of traits across biomes that will facilitate enhanced plant survival and performance under multiple climate and associated environmental changes, and which would enable species to cope with or even thrive under future changes. Without this, we are left without a clear understanding of which plant traits, and thus which species, may be important to target for restoration ecology, conservation, agroecology and maintenance of ecosystem services in a changing climate.

Many trait-based studies research the role of above-ground traits in response to climate/environmental changes with a significantly smaller proportion of the work focused on root traits. It is understood that roots are key in water uptake yet we lack clarity on how root trait variation can influence plant performance and fitness in water-limited environments (Funk, Larson and Ricks-Oddie, 2021), how this changes across environmental gradients and thus how root traits regulate responses to climatic and environmental change (Laliberté, 2017).

A lack of focus in drylands also represents a major research gap because roots play a disproportionately important role in determining plant's ability to access limited water resources in these environments and, in turn, survive drier periods. This is especially true in Africa, where despite recent efforts, it has the lowest overall trait coverage (Kattge et al., 2019) and includes 2 of the 4 drylands regions that have witnessed the greatest past vulnerability to climate change in the world

(Huang, Li, et al., 2017), a trend predicted to continue in the future (Huang et al., 2016; Davis and Vincent, 2017; Huang, Yu, et al., 2017).

One of these regions where there is a paucity of trait data is Southern Africa where rising temperatures, declining rainfall, increased evapotranspiration and increased frequency and intensity of droughts will interplay to enhance future water stress of the region (Davis and Vincent, 2017; Naik and Abiodun, 2019). This raises concern for the uniquely biodiverse ecosystems within Southern Africa and whether the traits required to survive drier conditions are apparent: a) across the functionally different biomes present (e.g. from Mediterranean shrublands of Fynbos, to succulents of the Desert, to the tree-grass mixes of the Savanna), b) within biomes and landscapes with different water-availability (driven by varying rainfall regimes or topography), and c) between and within species dominating the landscape.

Remote sensing offers an opportunity to address some of the gaps in understanding vegetation response to climate change that is potentially mediated by belowground components by linking belowground traits to aboveground patterns. In particular, responses to past climate variability as highlighted by the Vegetation Sensitivity Index (A. W. Seddon et al., 2016) which is a remotely sensed index derived from the analysis of temporal variability of enhanced vegetation productivity (EVI) response to changes in climatic conditions. The global application of this analysis on a 14-year period (2000–2013) employing the moderate-resolution imaging spectroradiometer (MODIS) dataset indicated variation in sensitivity to climate within regions of similar climatic conditions, with particularly stark differences across drylands. More work is required to understand what is driving these differences, including the potential role of traits in shaping these patterns. For example, could deeper roots play a role in reducing sensitivity to climate variability by allowing plants to access deeper water resources in drier times?

1.2 THESIS AIM AND OBJECTIVES

It is clear that there are knowledge gaps around how traits (particularly root traits) influence plant response to climate change. My thesis therefore aims to address the following question: What is the role of traits in determining vegetation response to climate change? Specifically, I address this research aim by undertaking the following three objectives:

I. Undertaking a global synthesis of which traits are important for determining response to climate change,

II. Determining how belowground (and aboveground) traits vary along water-availability in dry biomes, and

III. Investigating the role of root depth in defining vegetation sensitivity to climate variability and whether this can be examined using remote sensing.

To undertake objective *I*, I systematically reviewed 148 existing studies published between 2000-2017 with the aim of synthesizing our knowledge on which traits are important in determining a positive response to climate change across biomes and climate/environmental changes globally (**Chapter 4 (Research Paper 1)** of this thesis). In my review, I addressed the following research questions:

1) Which are the top traits across both biomes and climate/environmental changes that mediate positive responses in terms of plant fitness and performance to climate change?
2) What are the attributes (values or states) of these traits that confer a positive plant response to climate change?
3) Do these trait attributes vary across biomes and climate/environmental changes?

To address objective *II*, I examined root and aboveground traits of 124 woody shrubs across water availability gradients in the semi-arid Fynbos biome in South Africa. The aim was to quantify the contribution of belowground traits to overall variation across scales reflecting regional and localised (topographical) changes in water availability, between disturbance (fire) conditions and between and within species. To fulfil this objective, the following research questions were posed:

1) How do traits, specifically root traits, vary across water availability gradients (precipitation and topography) within a biome?
2) Do we observe intraspecific trait variation across these water availability gradients?
3) How do dominant traits in recently burnt vegetation differ from unburnt/more mature vegetation?
4) How important are root traits in whole-plant trait variation in our study system?
5) Is the belowground vs. aboveground investment by plants, higher in drier conditions?

To address objective *III*, I analysed the relationship between existing root depth data and remotely derived vegetation sensitivity to climate variability (using the vegetation sensitivity index (VSI) developed by Seddon et al. (2016)) across dry biomes in Southern Africa. The objective was to determine the potential role roots play in reducing sensitivity to climate variability and thus change and, in so doing, assess whether belowground plant traits can influence patterns we observe from aboveground plant/climate interactions as measure by space-borne remote sensing imagery. To fulfil this objective, the following research questions were posed:

1) How do biomes in Southern Africa differ in their sensitivity to climatic conditions (VSI)?
2) What is the relationship between root depth and VSI?
3) How is the above relationship affected by temporal autocorrelation in plant greenness as measured by VSI (*t-1*)?

1.3 THESIS STRUCTURE

This thesis is presented according to the requirements for the University of Oxford's Doctor of Philosophy in Geography and the Environment and follows the research article format. This thesis is divided into seven chapters. This chapter (**Chapter 1**) introduces the thesis background and sets out the primary research aim and objectives. **Chapter 2** places the research into its broader context by reviewing the literature and identifying the key research gaps addressed. **Chapter 3** presents the study area specifics and background knowledge about the methodological approaches adopted in this thesis. **Chapters 4 (Research Paper 1)**, **5 (Research Paper 2) and 6 (Research Paper 3)** are the research chapters of this thesis and thus address the objectives outlined in this chapter as three separate research papers. **Chapter 7** concludes this thesis by presenting a synthesis of results and the implications of this research and briefly discusses future directions identified by this thesis.

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CHAPTER 2: LITERATURE REVIEW

By: Nicola Kühn


Photo: Nicola Kühn

2.1 CLIMATE CHANGE ECOLOGY: WHY STUDY BIODIVERSITY RESPONSE TO CLIMATE CHANGE?

Climate change has been identified as one of the largest future threats to biodiversity (Bellard et al., 2012; Sala et al., 2000; Urban, 2015) and could, in decades to come, surpass habitat destruction to become the greatest global biodiversity threat (Leadley et al., 2010). This prediction and the inextricable relationship between climate and biological systems has led to the development of an expanding field of study concerned with the current and future impact of anthropogenic climate change on biodiversity.

Future climate and environmental projections indicate increases in global surface temperature, more frequent hot and fewer cold temperature extremes, more intense and frequent precipitation events (flooding and drought), increased sea-levels, increases in atmospheric CO_2 concentrations and more frequent and intense wildfires by the end of the 21st century (IPCC, 2015). These changes and their interactions have the potential to impact all levels of biodiversity (Parmesan, 2006). Consequently, predicting the impacts of climate change on biodiversity has become a priority (Dawson, 2011).

The observed response of plant species and whole ecosystems to recent (Foden et al., 2013; Parmesan, 2006; Parmesan and Yohe, 2003; Seddon et al., 2016) and past (Dawson, 2011; Willis et al., 2010) climate change validate the concern that anthropogenic climate change has the potential to transform natural systems at an unprecedented rate. At the ecosystem level, these studies indicate that changes in species composition, resulting from different plant responses to climate change, can lead to an overall change in ecosystem structure, processes, functioning and integrity (Chapin, et al., 2000; Díaz et al., 2004, 1999b). Restructuring of ecosystems also has regional and global consequences because the biophysical responses of vegetation (via change in transpiration, sap flow, nutrient and water content fluxes) can influence climate, hydrology and carbon balance (Kearney and Porter, 2009). Research has indicated that across the world there is variation in the degree of sensitivity of vegetation to climate variability, with some ecosystems indicating higher sensitivity than others to changes in temperature, water availability and cloud cover/insolation (Seddon et al., 2016).

At the species-level, plant responses to climate change fall into the following categories: tolerance, environmental tracking (range shift and migration), adaptation or extinction (Aitken et al., 2008; Dawson, 2011; IPCC, 2015; Willis and MacDonald, 2011). These responses are thought to be underpinned by the presence (or absence) of certain trait attributes (e.g. (Estrada et al., 2016)), where having favourable trait attributes for a set of environmental limits would allow a species to persist or even benefit, whereas lacking these traits could mean population decline or local extinctions. Traits-based or functional approaches have therefore become increasingly useful in determining species response to climate change and this has stimulated an expansion of trait-based climate change studies (**Fig. 2.1**) over the last two decades.

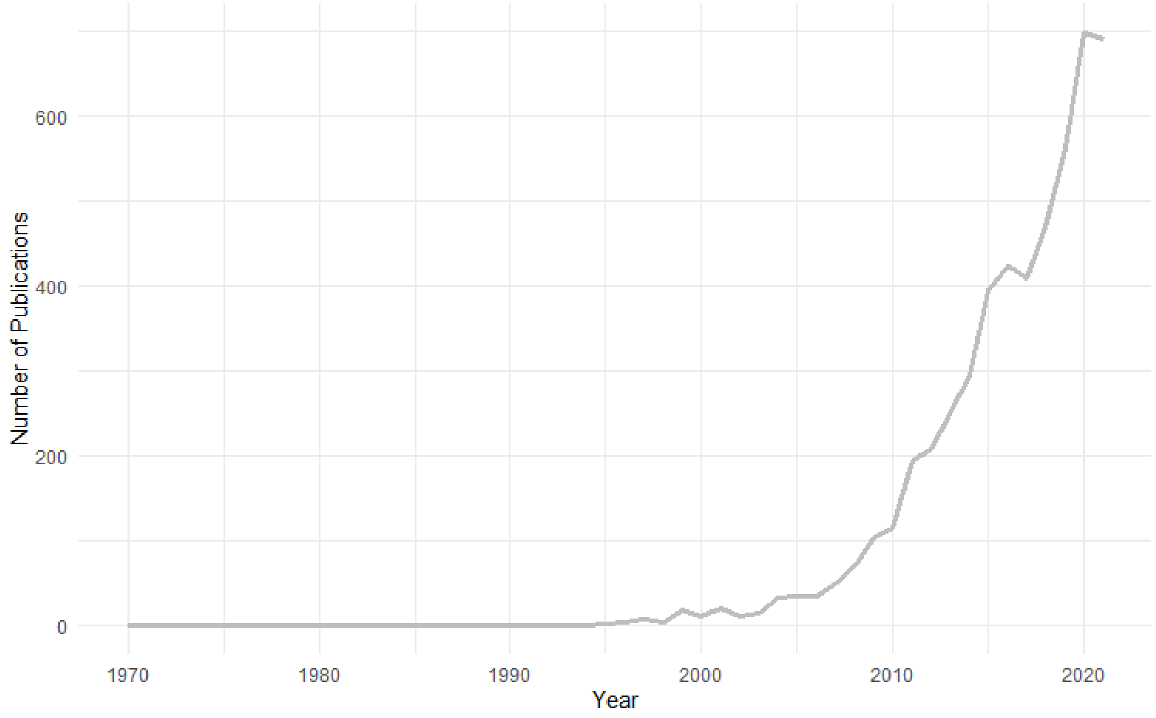

Figure 2.1: Number of publications in the SCOPUS database between 1970 – 2021 on trait-based climate change studies with an increasing trend demonstrated in the late 1990s early 2000s and which continues to climb up to the present day 2020. Search terms included "traits" OR "functional traits" AND "plants" AND "climate change" [accessed 16/10/2021].

2.2 TRAITS-BASED ECOLOGY AND ITS APPLICATION FOR CLIMATE CHANGE ECOLOGY

2.2.1 WHAT IS TRAITS-BASED ECOLOGY?

Traits-based ecology falls within the field of functional ecology which aims to describe species by their biological characteristics through the measurement of their functional traits (Calow, 1987). Functional traits are defined as any measurable morphological or physiological feature affecting plant performance and fitness directly or indirectly (Garnier et al., 2016; Lavorel et al., 1997; Pérez-Harguindeguy et al., 2013; Violle et al., 2007).

Traits-based thinking has seen a long history in the study of plant diversity, with Von Humboldt one of the first to officially recognise the relationship between plant form and function, as early as 1806. A whole century later in 1907, Raunkiaer developed the life-forms system that was later refined by Braun-Blanquet (1928). This field of research grew further in the late 1970s following seminal work on plant ecological strategies by Grime (1979). However, as a subject, traits-based ecology really came to the foreground between the late 90s to early 2000s (**Fig. 2.1**) when a number of research studies (Díaz et al., 1999a, 1999b, 1998; Díaz and Cabido, 2001, 1997; McIntyre et al., 1999) indicated that a traits-based approach may hold the key to understanding future changes in plant distribution and response to climatic change.

Environmental filtering is the central concept underpinning traits-based ecology and its application to understanding species response to climate change. It suggests that the establishment or persistence of a species in a location is determined by its traits. If a species lacks suitable traits to cope with the environmental factors of that particular location, it is “filtered out” i.e. cannot thrive or persist (Keddy, 1992). As a consequence of this filtering by the environment, consistent associations between plant traits and certain environmental conditions arise which are referred to as trait-environment linkages (Díaz et al., 1998; Keddy, 1992). A number of studies have demonstrated these relationships occurring along multiple environmental gradients (Fonseca et al., 2000; Gross et al., 2013; Metz et al., 2020; Ordoñez et al., 2010; Thuiller et al., 2004).

The traits present in an individual, are as a result of functional trade-offs between plant strategies suitable for the given environment and often combinations of traits are seen varying in response to changes in the environment. It is therefore important to consider plant responses through an ecological strategy lens, where suites of traits underpin ecological strategies and trait expressions determine where species fall along trait spectra.

2.2.2 ECOLOGICAL STRATEGIES AND TRAIT SPECTRA

Grime defined ecological strategies as ‘groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology’ (Grime, 1979). A more recent definition which emphasizes the process of natural selection by Craine (2009), proposes that ‘a strategy is a set of interlinked adaptations that arose as a consequence of natural selection and that promotes growth and successful reproduction in a given environment. Garnier et al. (2015) suggest that these two definitions which highlight slightly different facets of the concept (observation *vs.* mechanism) taken together provide us with a useful foundation to understand the concept of ecological strategies.

Ecological strategies and trait spectra have increased in complexity and scope over the last four decades (**Fig. 2.2**). The first significant plant ecological strategy scheme, which still influences the field today, is that of Grime’s Competitor-Stress-Ruderal Strategy (1979). Grime defined the threats to land plant existence as competition, stress and disturbance, and thus suggests that plants have evolved to cope with these threats by being competitors, stress tolerators or ruderals. This scheme is useful as it accounts for both life history phases namely the established vegetative phase and the reproductive/regenerative phase. However a fundamental downside to this scheme is that it is essentially a conceptual strategy without a simple protocol to position plants within it (Reich, 2014; Westoby, 1998). Westoby (1998) therefore attempted to develop a more operable scheme called the leaf-height-seed (LHS) scheme which allowed species to be easily placed along the axes of variation because these were directly reflecting trait differences of specific leaf area, height and seed mass. Westoby likened the variation in specific leaf area, to the C-S axis in Grime's scheme, reflecting a responsiveness to opportunities of growth and the variation in height and seed mass to the R axis, reflecting different aspects of coping with competition and disturbances.

Building on these earlier plant ecology strategy schemes, the next step was to examine the trade-off in resource allocation towards different traits – the so-called economic trait spectra. The first proposed was that of the leaf economics spectrum (LES) (Wright et al., 2004). The authors suggested that plants fall along axes of leaf trait variation that optimizes either a resource conservation or acquisition strategy of two key resources: carbon and nutrients. Generally, a conservative strategy (e.g. having lower photosynthetic capacity and SLA, but longer leaf life span) would be advantageous in resource-limited environments, where ensuring longer term, conservation of resources is key for success. In contrast, an exploitative strategy (e.g. having greater photosynthetic capacity, and higher SLA) would be advantageous in environments with high resource availability, where growing faster to outcompete surrounding plant species would be the key to success.

A similar line of thinking was applied to wood functional traits. Baas et al. (2004) for example, advocated for the existence of trade-offs in strategies defined by wood properties, a theory which was refined and then later proposed as the wood economics spectrum by Chave et al. (2009). According to this work, wood trait variation reflects trade-offs between the main wood functional properties of water transport and storage (e.g. hydraulic conductivity, water potential), mechanical properties (e.g. resistance to splitting/breakage), and defence properties (resistance to decay and embolism). One of the key traits in the wood economics spectrum which is involved in the multiple demands on wood structure is that of wood density, wherein higher wood density results in higher resistance to xylem cavitation (i.e. air pockets forming in the xylem thereby stopping water flow) during drought but is traded off against having less dense wood and rather growing taller (for light acquisition) due to the higher construction costs of denser wood.

Reich suggested that this organisation between fast-slow rates of resource acquisition and processing, should be extended to whole-plant thinking and thus include leaf, stem and root traits (2014). Equally importantly, they included water as a third key resource in addition to carbon and nutrients as well as extending the theory from individuals to community and ecosystem scales.

In comparison to the other traits described above, it was only relatively recently that thinking about resource allocation and the economic spectrum was applied to roots (de la Riva et al., 2018; Roumet et al., 2016; Weemstra et al., 2016). Although, some evidence exists to support a root economics spectrum (RES) mirroring the LES, recently this has been challenged by inconsistent relationships between root traits and a multidimensionality observed in root trait variation (Bergmann et al., 2020; Kong et al., 2019; Kramer-Walter et al., 2016; Weigelt et al., 2021). Bergman et al. (2020), empirically showed that alongside the resource acquisition/conservation gradient there exists a so-called collaboration gradient mediated by the association with mycorrhizal fungi, where root strategy varies between “do it yourself” (characterised by higher specific root length, and low mycorrhizal association) and “outsourcing” (characterised by lower specific root length, and high mycorrhizal association). A final additional axis of root variation has been recently proposed which is represented by maximum rooting depth (Weigelt et al., 2021). Subsequently this review identified root multidimensionality as being responsible for an overall multidimensionality in whole plant trait variation, indicating 4 axes of variation including: 1) conservation (as above), 2) collaboration (as above) 3) plant height and 4) root depth (Weigelt et al., 2021).

Another recent publication suggesting that roots are truly functioning differently from aboveground plant parts, shows that some root traits are unidirectional i.e. plants tend toward one expression of the trait under certain conditions, but not the opposite trait expression under opposite conditions (Laughlin et al., 2021). This fundamentally challenges classical ecological trade-offs as we know them. As new evidence emerges, it is becoming increasingly clear that ignoring difficult-to-collect root trait data (Maeght et al., 2013) is only giving us half of the picture. Accounting for resource uptake at depth and linking root form to function have become integral in understanding whole plant functioning (Jiang et al., 2020; Tumber-Dávila and Malhotra, 2020) and thus how plants may respond to climate and associated environmental changes, particularly considering the diversity in belowground strategies shown to cope with variation in environments (Li et al., 2017).

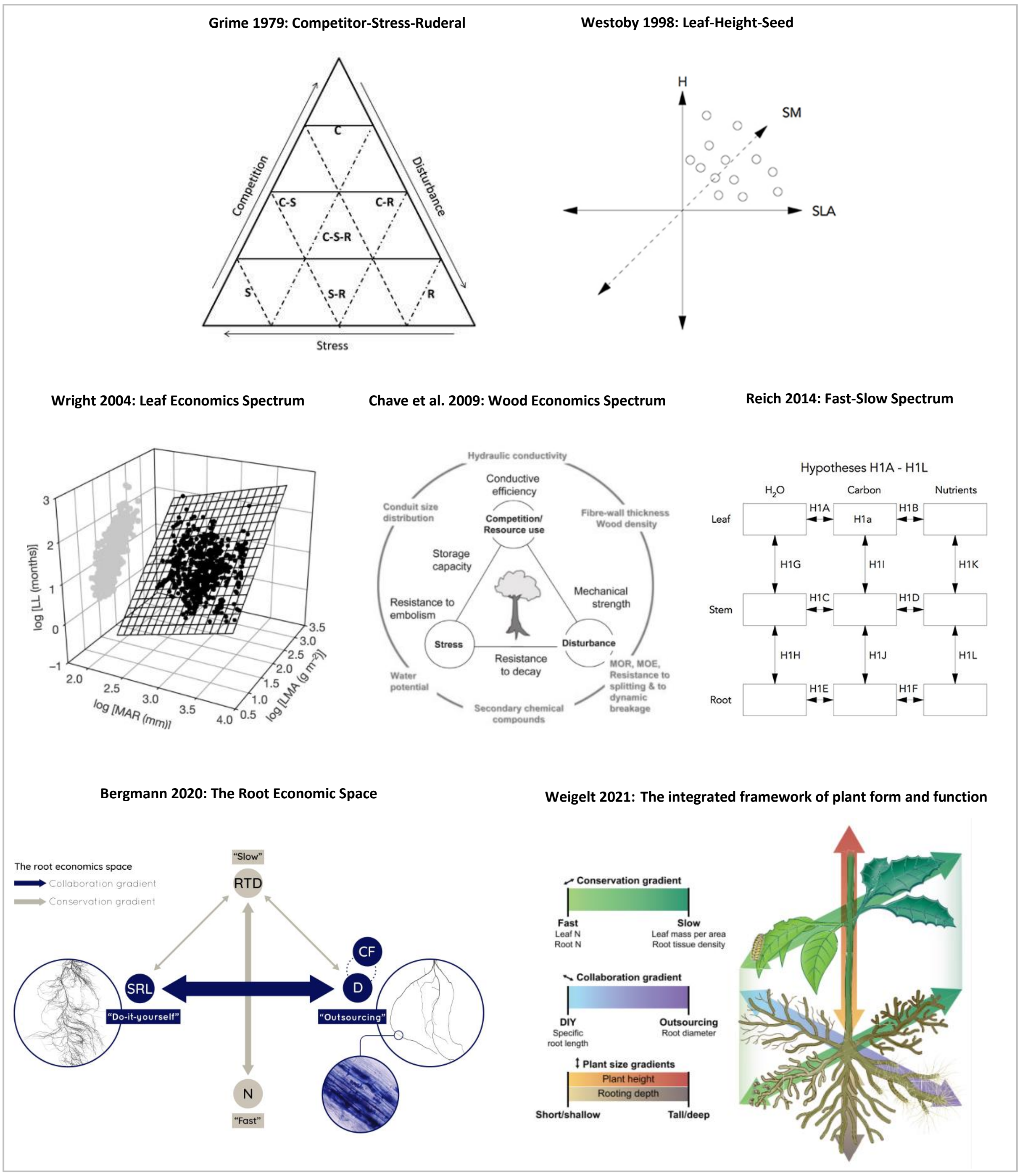

Figure 2.2: Conceptual frameworks of key ecological strategies and trait spectra which have increased in complexity and scope from early work through to the latest research. Source: original specified above each diagram excepting, Reich 2014 and Westoby 1998 schematic from (Watkins et al. 2021).

2.2.3 WHAT BENEFITS DO TRAITS-BASED APPROACHES OFFER CLIMATE CHANGE ECOLOGY?

Traits-based approaches are proving useful for studying species response to climate change and have certain key benefits. Firstly, through these approaches, we gain a deeper understanding of the constraints and opportunities faced by plants (Grime, 1979; Southwood, 1977) because traits allow us to explicitly link strategies to individuals and species and consequently to shed light on and test the mechanisms of plant response to change. This has implications for species/individual level studies but also for scaling up these analyses in trait-explicit species distribution models which can better predict species distribution in non-analogue conditions by incorporating traits in correlative models (Vesk et al., 2021).

Secondly, by shifting focus from species to traits we are able to determine potential responses to climate change across ecosystems that are taxonomically different (Cornwell et al., 2008; Díaz et al., 2004; Laliberté, 2017). In this way we can identify possible generalised trait-environment relationships across different biomes that make plants particularly vulnerable or indeed, particularly tolerant to climate changes, which is the topic of **Chapter 4 (Research Paper 1)** in this thesis.

Thirdly, trait-explicit approaches account for environmental disturbances, by looking at disturbance related traits (e.g., resprouting after fire or herbivory effects, bark thickness, presence of bud banks, belowground storage etc.). Further, these disturbances are predicted to interact with changing climatic conditions and in some cases become more frequent or severe (IPCC, 2015). Including disturbance related traits thus allows us to account for the additional influence of changes to existing disturbance regimes.

Another benefit of using a traits-based approach is in the context of restoration ecology where it can provide the basis on which to apply fundamental ecological theory, with the ultimate goal of maintaining ecosystem resilience and functioning under climate change (Laughlin, 2014). An example of this would be applying the theory of environmental filtering to generate functional trait targets that optimize fitness and performance under a set of environmental conditions. In this case, species with higher wood density – a resource-conservative trait – would be better suited to withstand drought conditions (Hacke et al., 2001; Markesteijn and Poorter, 2009; Mendivelso et al., 2013). A final key benefit to a traits approach is that we are able to make the link between changes in vegetation and the influence on human well-being and prosperity because traits-based analysis offer an understanding of how functional diversity underpins ecosystem process and thus ecosystem services (Chapin, et al., 2000; Hooper et al., 2002).

2.3 THE FUTURE OF TRAITS-BASED ECOLOGY

TRAIT DATA COLLECTION: WHERE, WHAT AND HOW?

Traits approaches can clearly offer major insight in our understanding of plant diversity, form and function and indeed response to climate change. However, it is limited in many regions by gaps in field trait data (Kattge et al., 2019). This is particularly the case for root trait data (**Fig. 2.3**), despite the recent and ongoing efforts to collate such information through online databases such as TRY, BIEN, GRooT and FRED (Enquist et al., 2009; Guerrero-Ramírez et al., 2021; Iversen et al., 2017; Kattge et al., 2019, 2011). These gaps need to be prioritized and especially so in drier biomes where root traits may play a proportionately greater role in determining response to future climate change. I contribute to this knowledge gap through my field work and the analysis presented in **Chapter 5 (Research Paper 2)** of this thesis.

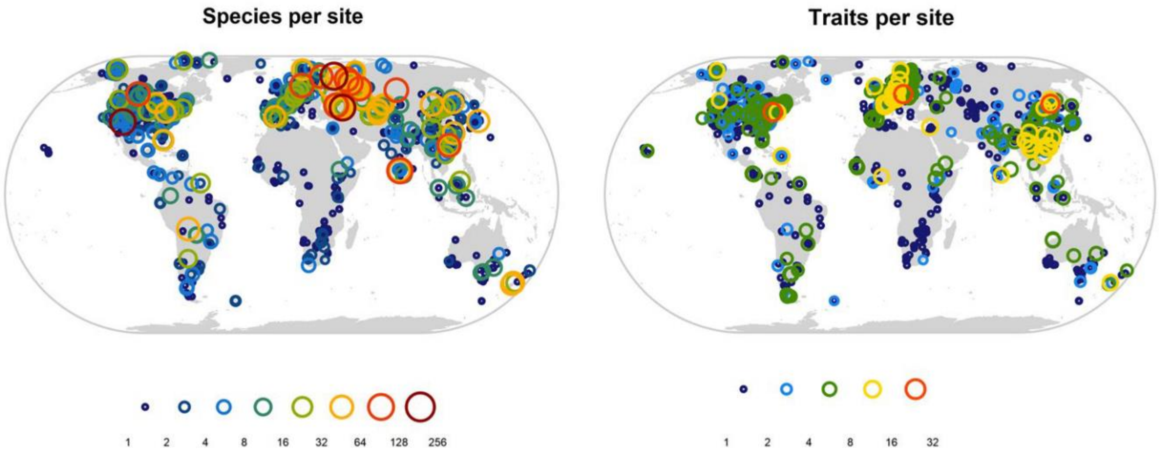

Figure 2.3: Maps depicting georeferenced data from field studies included in the Global Root Trait Database (GRooT). Circle size indicates the number of species per site (left) and traits per site (right). Source: Guerrero-Ramírez et al. *(2021)*.

Additionally, we are seeing more evidence emerging for the important role that intraspecific trait variation (ITV) is playing in contributing to overall trait variation (Albert et al., 2010) and thus in determining plant responses to environmental changes (Li et al., 2017). Most prior research has used species mean trait values or community weighted means, but this often neglects important information and variation at the intraspecific level. Albert et al. (2010) thus propose a framework for deciding when ITV is important to include in studies and suggest that at local level (individual, population and community), ITV is a significant component whereas beyond this scale (ecosystem and above), the effects from ITV may become negligible next to the effects of *interspecific* variation (between species). Greater attention to the potential effects of ITV are thus required when designing research and collecting data, which has up until now been neglected in favour of the accessibility and generalisability of species mean trait data. **Chapter 5** in this thesis also deals with this topic in more detail.

Wright and Westoby (2006) maintain that allometric differences should not be considered as a dimension within ecological strategy theory, and rather be considered complementary, but evidence suggests it is perhaps worth exploring how these are linked (Niinemets et al. 2007) and attempting to understand how allometry or isometric size scaling fits into or influences traits-based approaches. Isometric size scaling theory predicts that there are consistent relationships between plant parts in terms of their biomass partitioning or allocation (Enquist and Niklas, 2002) and thus should determine plant traits to an extent. Root:shoot ratios have been demonstrated to vary in different biomes (Ottaviani et al., 2020), but what has not been determined is whether in environmental extremes and across environmental gradients within a biome, these size scaling relationships still hold true, particularly in consideration of the multidimensionality of root traits. Or, rather, whether there is selection on greater root allocation in extreme limits of the environment that require more resource uptake from root systems, deviating from the theoretically expected allometric relationships (Enquist and Niklas, 2002). I examine this topic further in **Chapter 5 (Research Paper 2)** of this thesis.

A number of studies , to predict root depth and thus generate global gridded datasets using existing in-situ observations (Schenk and Jackson, 2009) or model simulations (Fan et al., 2017; Yang et al., 2016), have recently been complemented with studies predicting root depth from aboveground hydraulic traits (Chitra-tarak et al., 2021), isotopic analysis (Jiang et al., 2020) and, remotely sensed data for vegetation optical depth in combination with water mass balance equations (Liu et al., 2021). However, the outputs from these studies are still only estimated and often not based on field-measurements (excepting isotopic analysis). They therefore need to be used with caution when attempting to understand vegetation response to climate change due to the model uncertainties associated with local factors such as topographical variation, competition/facilitation, disturbance effects and/or phenotypic plasticity. The need to directly link trait observations to vegetation responses when attempting to understand the mechanisms behind response patterns therefore still remains an important knowledge gap. In **Chapter 6 (Research Paper 3)** of this thesis I address this by linking root depth observations to vegetation sensitivity patterns as defined by a Vegetation Sensitivity Index (VSI) based on remote sensing data (Seddon et al., 2016).

2.4 SUMMARY AND KNOWLEDGE GAPS

Review of the literature makes a case for a traits-based approach to climate change studies and thus for the body of work presented in this thesis. The key findings of this review can be summarised as follows:

1. Crucial research is still required in assessing species response to climate change due to the current and increasing threats biodiversity faces under altered climate and associated environmental conditions.
2. Traits-based approaches are grounded in theory of ecological strategies and spectra, which have become increasingly complex and comprehensive over time (**Fig. 2.3**).
3. Root trait variation presents many challenges to these historic ecological strategies and spectra, and challenge fundamental principles of plant form and function.
4. Traits approaches are beneficial in that they enhance understanding of the environmental constraints and opportunities faced by plants which can be compared within and between species and across biomes and disturbances.
5. Gaps remain in our understanding of the role of root traits in determining response to climate change (including how they vary intraspecifically and how allometric relationships influence them). This can be addressed through field data collection and connecting field observations with remote sensing data, especially in the under-sampled drylands of the world where roots play a disproportionately important role in determining plant form and function.

This thesis aims to address the research gaps identified by this literature review and outlined in more detail in **Chapter 1**.

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CHAPTER 3: METHODS AND STUDY SITES

By: Nicola Kühn

3.1 OVERVIEW

Addressing the research questions and objectives of this thesis outlined in **Chapter 1** requires using an array of methods, which are presented in detail in the three research papers (**Chapter 4 (Research Paper 1), 5 (Research Paper 2), 6 (Research Paper 3)**). The first research paper (presented in **Chapter 4**) collates existing research and identifies knowledge gaps through a systematic literature review and data synthesis. The gaps observed from this work inspired the research approach of the second article (**Chapter 5 (Research Paper 2)**), which involved local field studies with collection of below- and aboveground trait data of woody fynbos shrubs in South Africa. The final article (**Chapter 6 (Research Paper 3)**) utilised these and other field collected root trait data to explore the link between observational belowground traits and aboveground plant-climate interactions derived from space-borne remote sensing imagery across Southern Africa. The following section briefly outlines these three approaches, with more details available in each of the Research Papers.

3.2 METHODS USED IN SYSTEMATIC REVIEW AND DATA SYNTHESIS (CHAPTER 4; RESEARCH PAPER 1)

Systematic review of literature and consequent data syntheses are important tools to advance research by collating existing work and identifying key knowledge gaps. I therefore employed this approach for the first data chapter of this thesis **Chapter 4 (Research Paper 1)**, analysing studies published between 2007-2017. The systematic search was conducted globally per each of 12 selected biomes (Olson et al. 2001, Dinerstein et al. 2017). In my search, which was conducted in SCOPUS, I used a combination of search terms including “plant”, “climate”, “change”, “functional”, “trait”, and the name of each of the 12 selected biomes. This initial survey returned 1589 studies from which 148 studies which met the criteria of *a plant trait attribute that mediated a positive plant response to a simulated or observed climate/environmental change*. In my study, positive responses include both coping (e.g., survival) and thriving/enhanced fitness (e.g., increased vegetative biomass) under climate/environmental change. I classified the positive response data into three fitness categories (after Violle et al. (2007), **Fig. 3.1**): plant survival (e.g., delayed mortality, stress tolerance, survival), reproductive output (e.g., enhanced reproductive effort, seed germination, recruitment) and vegetative biomass (e.g., abundance, biomass, community dominant trait). Records used for this analysis were defined by the approach presented in **Fig. 3.2** (also see **Chapter 4 (Research Paper 1)**). Traits were standardized and grouped following Pérez-Harguindeguy et al. (2013), when possible, and new ones were added as required.

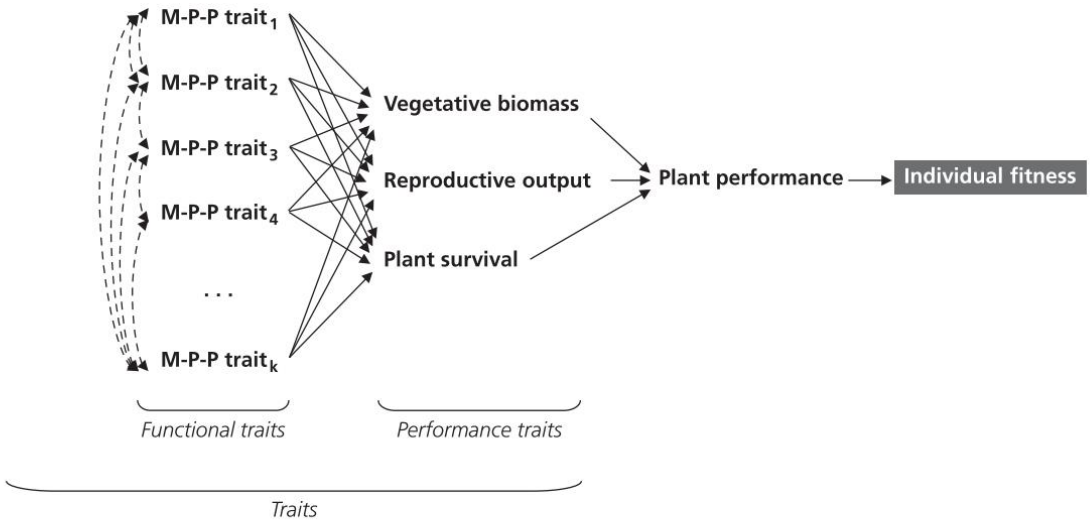

Figure 3.1: Chapter 4 (Research Paper 1) of this thesis used the concept of traits, as defined by Arnold (1983), to determine the link between plant traits (functional traits) and responses (performance traits). This concept consists of a three-level hierarchical structure where morphological, physiological, or phenological traits (here abbreviated as M-P-P traits) impact performance traits (vegetative biomass, reproductive output, plant survival), which in turn influence the performance and fitness of plants. The dashed arrows represent the inter-relatedness of M-P-P traits. Source: Violle et al. (2007).

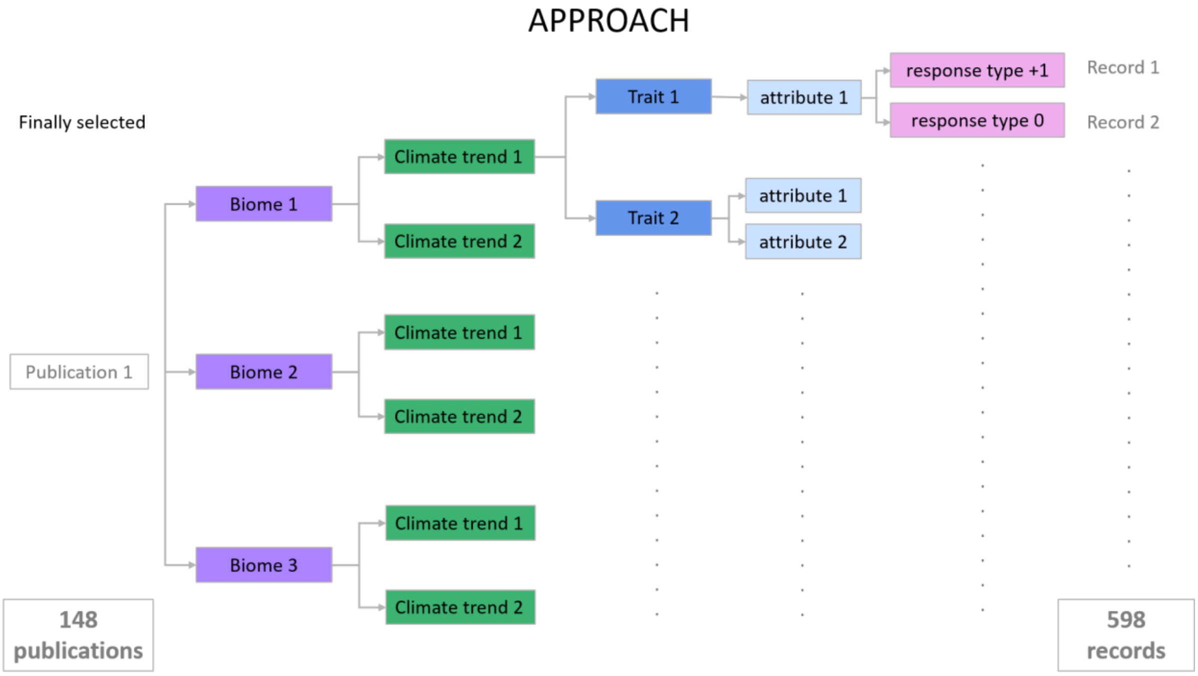

Figure 3.2: Approach to record data extracted from each publication for the data-synthesis of Chapter 4 (Research Paper 1) of this thesis, which consists of a global systematic review of literature identifying traits that mediate positive responses to climate change. The number of records was the unit of analysis since studies could contain several records. Attributes include the trend or state of the trait as well as the trait itself as defined by Garnier et al. (2016).

The most consistently important traits across biomes were identified using a scoring system that accounted for their representation across biomes and climate (and associated environmental) variables and was weighted by the proportion of positive records out of total records (i.e., positive plus null records) to provide confidence levels:

$$\text{Score} = \text{Pr}(\text{Pc}+\text{Pb})/2$$

where Pr=proportion of positive records, Pc=proportion of positive records per climate/environmental change and Pb=proportion of positive records per biome.

Important trait attributes, that is, the values or state of traits (Garnier et al. 2015), e.g., *deeper* roots, were also analysed per biome and climate/environmental change. Details on this methodology can be found in **Chapter 4 (Research Paper 1)**.

3.3 METHODS USED IN FIELD-BASED TRAIT DATA COLLECTION (CHAPTER 5; RESEARCH PAPER 2)

3.3.1 Study Site

The study presented in **Chapter 5 (Research Paper 2)** of this thesis was conducted in the Fynbos biome comprising most of the global biodiversity hotspot of the Cape Floristic Region of South Africa. This biome experiences a Mediterranean-type climate of cool wet winters and hot dry summers with periodic droughts and frequent fires. Most of the Fynbos biome receives annual precipitation between 300mm and 2000mm and soils in the Fynbos biome are typically acidic and nutrient poor. Despite this, the vegetation is characterised by a highly biodiverse assemblage of short-statured plants (predominantly from the Proteaceae, Ericaceae and Restionaceae families).

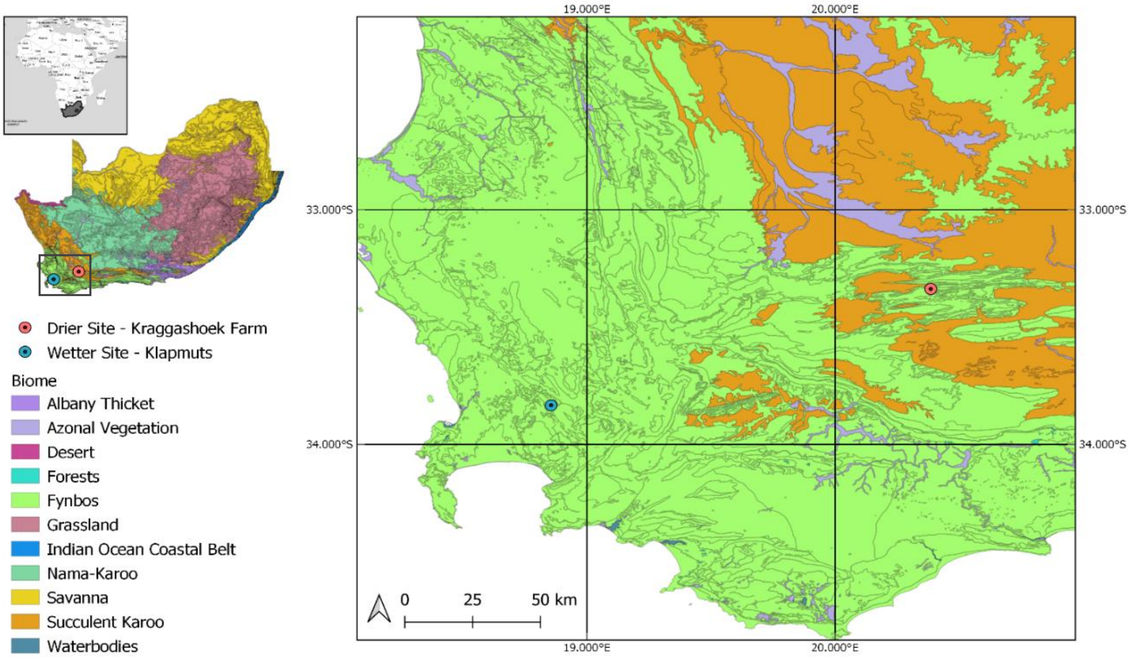

Figure 3.3: Location of study sites in the Fynbos biome, Western Cape, South Africa that were used in Chapter 5 of this thesis.

3.3.2 Sampling design, data collection and analysis

Fieldwork was conducted over four field campaigns between November 2018-November 2019. Above and belowground plant traits of 124 individuals of dominant woody shrub species were sampled along a regional precipitation gradient in Fynbos at a wetter and drier site (600-700mm *vs.* 250-300mm annual precipitation) (**Fig. 3.3**). Both sites had fires in January 2016 leaving patches of recently burnt and unburnt/more mature (8-10+ years) vegetation (e.g., **Fig. 3.4**), which offered an opportunity to sample across post-fire conditions and thus constituted the sub-sites for this study. Within each sub-site, sampling was done at three locations along a topographical gradient presenting locally wetter (bottom of slope) and drier (top of slope) locations. See **Chapter 5 (Research Paper 2), Fig. 5.1** for sampling design and for methodological details.

Figure 3.4: Photographs showcasing vegetation at the dry site before the January 2016 fire (left), and ~3 years later in December 2018 (right), showcasing the patches used for sub-sampling sites.

Traits were selected due to their perceived importance for coping with dry conditions, their role in determining global plant strategies (Díaz et al. 2016), and their collection feasibility. See individual trait justifications in **Table 5.1** in **Chapter 5 (Research Paper 2)**. For each individual, five root traits, one stem trait, one whole plant trait, five leaf traits, and five traits that comprise allocation components were collected (see **Table 1**, **Chapter 5 (Paper 2)**).

Species dominance was first determined at each location using line-intercept surveys. Dominant species were defined as those making up more than 70% shrub cover. Then at each location within a sub-site and within a site, at least 5 individuals of each dominant species were sampled. To collect sufficient trait data from each individual, entire plants were excavated (see **Fig. 3.5 for examples of techniques used for root excavation**). This involved careful attention to the root systems: the primary root system was prioritized, but in most cases, most of the secondary systems were excavated too. Fresh measurements were taken before plant material was dried (70 ° C for 72 hours) for further measurements. Trait data was then analysed across sites, sub-sites and locations and at inter- and intraspecific levels, and was statistically compared using t-tests, analysis of variance (ANOVA) and Principal Component Analysis (PCA). Further methodological details in **Chapter 5 (Research Paper 2)**.

Figure 3.5: Root excavation involved removing dirt around the root system with jackhammers, spades, pickaxes, hammers, and chisels, and then the finer work of following the primary root system and brushing/chiselling away ground from roots with brushes and smaller gardening tools.

3.4 METHODS USED FOR LINKING OBSERVATIONAL BELOWGROUND TRAIT DATA TO REMOTE SENSING DATA (CHAPTER 6; RESEARCH PAPER 3)

3.4.1 Study Site and Vegetation

The study extent for **Chapter 6 (Research Paper 3)** was Southern Africa between 20°S and 40°S and 10.59°E and 39.20°E and included South Africa, Lesotho, Eswatini and portions of Namibia, Botswana, Zimbabwe, and Mozambique. Overall analyses of remotely sensed data (described below) were conducted across all biomes present in **Fig. 3.6**. Root analysis was restricted to those biomes containing root trait data, which included Savanna, Fynbos, Nama Karoo, and Succulent Karoo.

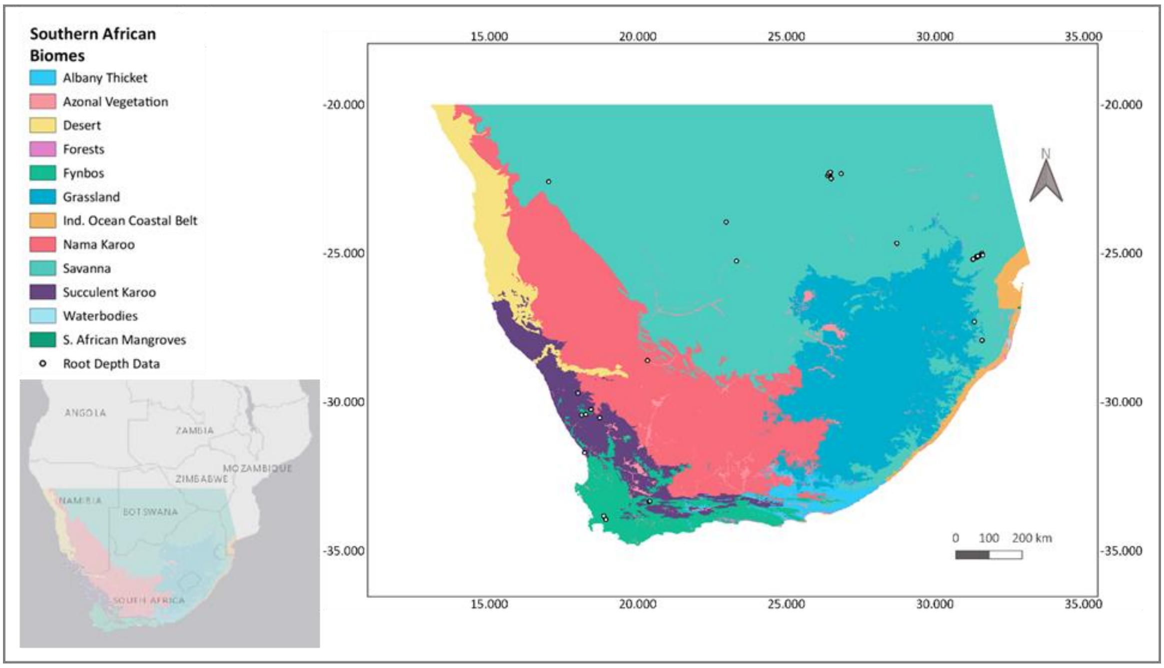

Figure 3.6: Map of the study region for Chapter 6 of this thesis in Southern Africa, which covers South Africa, Lesotho, Eswatini and portions of Namibia, Botswana, Zimbabwe, and Mozambique.

3.4.2 Data collection and Analysis

The remote-sensing derived Vegetation Sensitivity Index (VSI) and associated temporal autocorrelation in productivity, Coefficient *t-1* (*t-1*) used in this analysis was calculated for our study extent at a spatial resolution of 1km for the period 2000-2019 in Southern Africa using the methodology by Seddon et al. (2016). This involved the following key spatiotemporal raster-based datasets employed at a monthly temporal resolution:

- Enhanced vegetation Index (EVI) – a widely used vegetation index that has been correlated with aboveground vegetation productivity. Obtained from MODIS monthly Enhanced Vegetation Index (EVI) (Didan 2015).
- Climate variables evapotranspiration (obtained from MODIS 8-day composite ratio of actual *vs.* potential evapotranspiration (Running et al. 2019)); cloudiness (obtained from MODIS daily cloudiness (Vermote and Wolfe 2020) and calculated following Wilson & Jetz (2016); and air temperature (obtained from the CHELSA monthly timeseries of maximum temperature (Karger et al. 2017, Karger 2018)).

Computation of the VSI involves modelling the relationship between monthly EVI and the three climatic variables (evapotranspiration, cloudiness, and temperature) and the *t-1* variable (which is obtained as the temporal 1st order autocorrelation on the monthly EVI timeseries) by running a principal component regression on a pixel-by-pixel basis. Regression coefficients (or "climate weights") were obtained for each of the climate variables, which were then averaged over all months for which a significant relationship was found, multiplied by the relative variance of EVI compared to the climate variance and summed to give the vegetation sensitivity (VSI) (see **Chapter 6 (Research Paper 3)** and Seddon et al. (2016) for further details). High values of VSI identify regions where the variability in remotely sensed productivity can be largely explained by climate, and vice-versa. Areas with low VSI values in drylands tend to show high *t-1* coefficients, suggesting that their relationship with climate operates over longer timescales (Seddon et al. 2016). Biome data for

Southern Africa (National Vegetation Map Project (VEGMAP2018)[1], Atlas of Namibia Project[2], WWF Ecoregions[3]) was collated and used to compare mean and median VSI and *t-1* for random samples of pixels (10% of total number of 1-km pixels) for each biome to determine whether these indices differed significantly across biomes.

Next, root traits were compared to aboveground signals of VSI and *t-1*. Root trait data was collated from prior fieldwork **(Chapter 5 (Research Paper 2))** and online databases (GRooT (Guerrero-Ramírez et al. 2021); FRED (Iversen et al. 2017). For each pixel in our raster datasets where root depth data was present, VSI and *t-1* values were extracted and used to statistically explore the relationship between root depth and VSI/*t-1*. The models used included growth form and biome as variables.

A complementary part of this analysis aimed to identify areas where vegetation productivity was less correlated with concurrent monthly precipitation, suggesting the presence of an adaptation to survive drier conditions. This involved the comparison of remotely derived vegetation productivity using the MODIS monthly Enhanced Vegetation Index (EVI)[4] and monthly total precipitation[5] across the study extent in Southern Africa. This was then compared with VSI, *t-1* and the root depth data described above to determine if lower sensitivity (low VSI, high *t-1*) areas with deeper roots also showed a lack of relationship between EVI and concurrent monthly precipitation.

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[1] South African National Biodiversity Institute (2018) http://bgis.sanbi.org/vegmap [Accessed 01/10/2021]

[2] Atlas of Namibia Project (2002) Directorate of Environmental Affairs, Ministry of Environment and Tourism (http://209.88.21.36/Atlas/Atlas_web.htm)

[3] World Wildlife Fund Terrestrial Ecoregions (2012) https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world

[4] MOD13A3 https://lpdaac.usgs.gov/products/mod13a3v006/

[5] CHELSA monthly time series of total rainfall version 2.1 https://chelsa-climate.org/timeseries/

3.5 SUMMARY

The methods used in these papers allowed for local, regional and sub-continental scales in analysing trait variation and the role of traits – with a focus on largely data-deficient belowground traits – in determining response to climate change:

1. **Chapter 4 (Research Paper 1)** uses a systematic literature review to consider the global patterns emerging on which traits are key across different biomes and climate changes.
2. **Chapter 5 (Research Paper 2)** uses a field study to consider the regional variation in below and aboveground traits across precipitation regimes of the two main field sites in the Fynbos biome of South Africa.
3. **Chapter 5 (Research Paper 2)** also considers local intra- and interspecific variation of below and aboveground traits, along local topographical gradients as well as in post-disturbance conditions within the landscape.
4. **Chapter 6 (Research Paper 3)** connects field observations and remote-sensing data to consider regional variation in the relationship between root depth and vegetation sensitivity (as derived by VSI) across biomes of Southern Africa.

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CHAPTER 4 (RESEARCH PAPER 1): GLOBALLY IMPORTANT PLANT FUNCTIONAL TRAITS FOR COPING WITH CLIMATE CHANGE

By: Nicola Kühn, Carolina Tovar, Julia Carretero, Vigdis Vandvik, Brian J. Enquist, Kathy J. Willis

Linking statement: The research approach of the first paper of this thesis (**Chapter 4 (Research Paper 1)**) was inspired by the lack in global consensus on whether there are key traits that consistently mediate a positive response of plant fitness and performance across biomes and under multiple climate changes. The following chapter therefore presents results of a data synthesis based on a systematic literature review of existing studies on this topic. The research presented in this chapter is published in the journal *Frontiers of Biogeography* (in issue 13.4 available December 2021) and is available online at https://doi.org/10.21425/F5FBG53774.

Author contribution statement: NK, KJW and CT conceptualised the research and designed the approach. NK, JC and CT collected the data and NK and CT performed the data-synthesis. NK and CT wrote the first draft and received substantial contribution from other authors.

ABSTRACT

The last decade has seen a proliferation of studies that use plant functional traits to assess how plants respond to climate change. However, it remains unclear whether there is a global set of traits that can predict plants' ability to cope or even thrive when exposed to varying manifestations of climate change. We conducted a systematic global review which identified 148 studies to assess whether there is a set of common traits across biomes that best predict positive plant responses to multiple climate changes and associated environmental changes.

Eight key traits appear to best predict positive plant responses to multiple climate/environmental changes across biomes: lower or higher specific leaf area (SLA), lower or higher plant height, greater water-use efficiency (WUE), greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density, and greater rooting depth. Trait attributes associated with positive responses appear relatively consistent within biomes and climate/environmental changes, except for SLA and plant height, where both lower and higher trait attributes are associated with a positive response depending on the biome and climate/environmental change considered.

Overall, our findings illustrate important and general trait-climate responses within and between biomes that help us understand which plant phenotypes may cope with or thrive under current and future climate change.

HIGHLIGHTS

- Our research identifies a set of key traits that best predict positive plant responses to multiple climate/environmental changes across biomes: lower or higher specific leaf area (SLA), lower or higher plant height, greater water-use efficiency (WUE), greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density, and greater rooting depth.

- We find consistence in the trait attributes (values/states of traits) associated with positive responses for most of our key traits.
- There is a) an overrepresentation of studies focusing on leaf traits, although other traits are more consistently linked to beneficial responses, b) an overrepresentation of studies on decreased precipitation/drought compared to other changes c) an underrepresentation of studies in Deserts in relation to their global coverage, and an underrepresentation of studies in the Tundra biome in relation to expected climate changes.
- Our research supports that there are general trait-climate responses within and between biomes.
- Our results take us a step closer to understanding which plants can cope or thrive under climate change because of their trait makeup.

Keywords: climate change, functional traits, plant response, trait-based ecology, trait-environment relationship

4.1 INTRODUCTION

Plant functional traits are heritable characteristics of morphology, physiology or phenology that influence individual performance and fitness and ultimately the responses of species to changes in the environment (Violle et al. 2007, Pérez-Harguindeguy et al. 2013, Garnier et al. 2016). The development of trait-based ecology has relied on the working hypothesis that there are general trait-environment relationships that can predict how biodiversity responds to climate (Enquist et al. 2015). Some studies have focused on quantifying variation within specific individual traits along environmental gradients (Moles et al. 2009, Wright et al. 2017, Boonman et al. 2020), whereas others have focused on identifying coordination and trade-offs between different traits across species and landscapes (Díaz et al. 2016). Understanding both the type and consequences of trait variation is critical to determining species response to climate change, because a suite of traits can directly affect ecological tolerance, diversity and distribution of species (Díaz et al. 2016, Wright et al. 2017, Feng et al. 2018, Rueda et al. 2018). Whilst many studies have focused on those trait attributes that may restrict a species' ability to cope with environmental change, leading to vulnerability (Foden et al. 2008, Williams et al. 2008, Dawson et al. 2011, González-Suárez et al. 2013), less focus has been placed on those trait attributes that may enhance a species' ability to withstand climate and associated environmental change.

Climate change is one of the largest threats to current and future biodiversity (Sala et al. 2000, Bellard et al. 2012, Urban 2015, IPBES 2019). Future earth system projections indicate a suite of climatic and associated environmental changes with projections indicating: increases in atmospheric CO_2; an increase in global surface temperature by more than 2°C (under all but one emission scenarios); more frequent hot and fewer cold temperature extremes; more intense and frequent extreme precipitation events; a rise in sea-level; and an increased frequency and intensity of wildfires by the end of the 21st century (IPCC 2015). Additionally, indirect effects of climate change are suggested to have an impact on ecosystems such as subarctic peatlands where increased temperatures are predicted to enhance permafrost thaw, which in turn increases available nitrogen (Keuper et al. 2012).

Evidence from palaeoecological, present-day and modelling studies shows that species can have different responses to climate changes. These include adaptation, migration, extinction, or persistence (i.e., tolerance) (Aitken et al. 2008, Dawson et al. 2011, Willis and MacDonald 2011, IPCC 2015). All these responses are thought to be closely linked to the presence (or absence) of certain functional traits or specifically, trait attributes (value or state of a trait in a given location at a given time (Garnier et al. 2016)) (e.g. Estrada et al. 2016). Thus, having 'favourable' traits or trait attributes can allow a species to cope with a changing climate, whereas a lack of these can result in population decline or local extinctions.

Both empirical and theoretical work indicate that there should be a general subset of traits that best predict plant responses to global change (Lavorel and Garnier 2002, Moles et al. 2014, Michaletz et al. 2015). Recent theoretical advances have identified subsets of traits that are more central to how plants respond to drought (O'Brien et al. 2017, Powell et al. 2017, Feng et al. 2018, Brodribb et al. 2020) and temperature (Michaletz et al. 2015, Wright et al. 2017). Nonetheless, most studies indicating support for a general set of trait responses are empirical and comparative in approach (Wright et al. 2010, Paine et al. 2015). For example, a global meta-analysis that explored plant recovery performance from water stress found that trade-offs of specific traits, mainly related to plant hydraulic architecture, leaf anatomy and physiology, affect plant recovery (Yin and Bauerle 2017). Similarly, a recent study in the Neotropics highlighted wood density and vessel size as important traits to help trees withstand drought (Esquivel-Muelbert et al. 2017).

Other studies have examined which specific trait attributes might be more favourable to tolerate climate change. For example, denser wood, lower specific leaf area and deeper roots have been found to be associated with lower tree mortality in the face of drought (Greenwood et al. 2017, O'Brien et al. 2017). However, to date, there has been no global study that assesses whether there is a general set of functional traits across global biomes that will allow plants to cope with, or even thrive under, multiple manifestations of climate change (i.e. a positive response).

In this study, we aimed to examine whether current studies indicate a general set of trait-environment relationships that underlie positive species responses to climate change. Specifically, we undertook a systematic review process of the literature to identify 148 studies which analysed responses of plants with different traits to climate and associated environmental changes (hereafter climate/environmental changes). We used biomes as the units of analysis (following Olson et al. (2001)) to determine whether positive trait–environment relationships are generalizable globally, irrespective of a region's history or differences in species assemblages (e.g. see Van Bodegom *et al.* 2012; Sandel *et al.* 2016).

4.2 METHODS

4.2.1 BIOME MAP AND ESTIMATION OF PROJECTED CHANGES IN TEMPERATURE AND PRECIPITATION

We used a modified version of the biome map of Dinerstein and colleagues (2017) (see Appendix S1, Supplementary Material) and reconstructed expected mean annual temperature and total annual precipitation projected for each biome for year 2050 (CMIP5 data) (IPCC 2015) RCP 6.0). This involved downloading model outputs from Worldclim v1.4 (Hijmans et al. 2005) at 30 arc-seconds pixel resolution together with the baseline maps (climate representing 1960-1990) (Hijmans et al. 2005). Then, for each climatic variable we summarized the mean value per biome per future climate model and calculated the absolute change in temperature and the relative change in precipitation in comparison to the mean value per biome of the baseline maps.

4.2.2 SYSTEMATIC LITERATURE SURVEY

We conducted a systematic survey to identify published studies in international journals spanning the years 2007-2017 that focused on traits which are associated with positive plant responses to climate/environmental change. In our study, positive responses include both coping (e.g. survival) and thriving/enhanced fitness (e.g. increased vegetative biomass) despite climate/environmental change. The search was conducted per biome, therefore constituting a global analysis.

In our search, conducted in SCOPUS, we used a combination of search terms including “plant”, “climate”, “change”, “functional”, “trait”, and the name of each of the 12 selected biomes. This initial survey returned 1589 studies from which we selected 148 studies which met our criterion, that is: identifying a plant trait attribute that mediated a positive plant response to a simulated or observed climate/environmental change (see Appendix S2, **Table S1** for the list of studies and Appendix S1, Supplementary Material for further methods). We classified the positive response data into three fitness categories (after Violle et al. (2007), see Appendix S2, **Table S2**): plant survival (e.g. delayed mortality, stress tolerance, survival), reproductive output (e.g. enhanced reproductive effort, seed germination, recruitment) and vegetative biomass (e.g. abundance, biomass, community dominant trait).

We extracted all records of traits that were either associated with a positive response (positive record), or not associated with a response (referred to as null records) to climate/environmental changes (see Appendix S1, Supplementary Material and **Fig. S4.1**). In this way, we obtained a total of 598 records (446 positive responses and 152 null responses) from the 148 studies (see Appendix S2, **Table S4.1**).

All 101 traits were standardized and grouped into the five categories proposed by Pérez-Harguindeguy and colleagues (2013) (see, Appendix S1, Supplementary Material and Appendix S2, **Table S4.3**): below-ground, leaf, stem, regenerative and whole-plant traits. We also kept a few traits with a low number of records under the group category of “others”.

4.2.3 DATA SYNTHESIS

We summarized the data from the 148 studies using the records as a unit of analysis (since some studies contained several records) (see Appendix S1, Supplementary Material and **Fig. S4.1**).

In order to identify the most consistently important traits across biomes, we scored all traits reported in our selected studies according to their representation across biomes (proportion out of 12 total biomes) and climate/environmental changes (proportion out of six total changes – see below). These were weighted by the proportion of positive records out of total records (positive plus null records) to provide a level of confidence in that trait being consistently associated with a positive response to climate/environmental change. This scoring was calculated by the following equation, where Pr=proportion of positive records, Pc=proportion of positive records per climate/environmental change and Pb=proportion of positive records per biome:

$$\text{Score} = \text{Pr}(\text{Pc}+\text{Pb})/2.$$

Using this approach, the scores ranged from 0 to 1 and higher scoring traits (values closer to 1) thus representing those traits that are associated with multiple biomes and climate/environmental changes, according to our systematic survey. Once the globally important traits were identified, we extracted the information of their trait attributes per biome and climate/environmental change. Lastly, we analysed plant traits for each of the top three studied climate/environmental changes and the associated attributes to analyse how consistent an attribute was within traits.

4.3 RESULTS

4.3.1 FUTURE PROJECTED CLIMATE CHANGE PER BIOME

IPCC projections show that all biomes will experience an increase in temperature that ranges from 1 to 5 degrees (°C). The Tundra and Boreal Forests are projected to undergo the highest increase, while Tropical Forests biomes and Mangroves are expected to see the least increase in temperature (**Fig. 4.1c**). Projections of relative change in precipitation indicate that both the Mediterranean and the Mangrove biomes are projected to have a decrease in relative precipitation while Tundra and Boreal Forests are expected to have an increase in total annual precipitation (**Fig. 4.1c**). Additionally, precipitation shows variability in the direction of the trend (positive vs. negative). There is thus considerable variability in the projected trends, even at the coarse resolution of biomes.

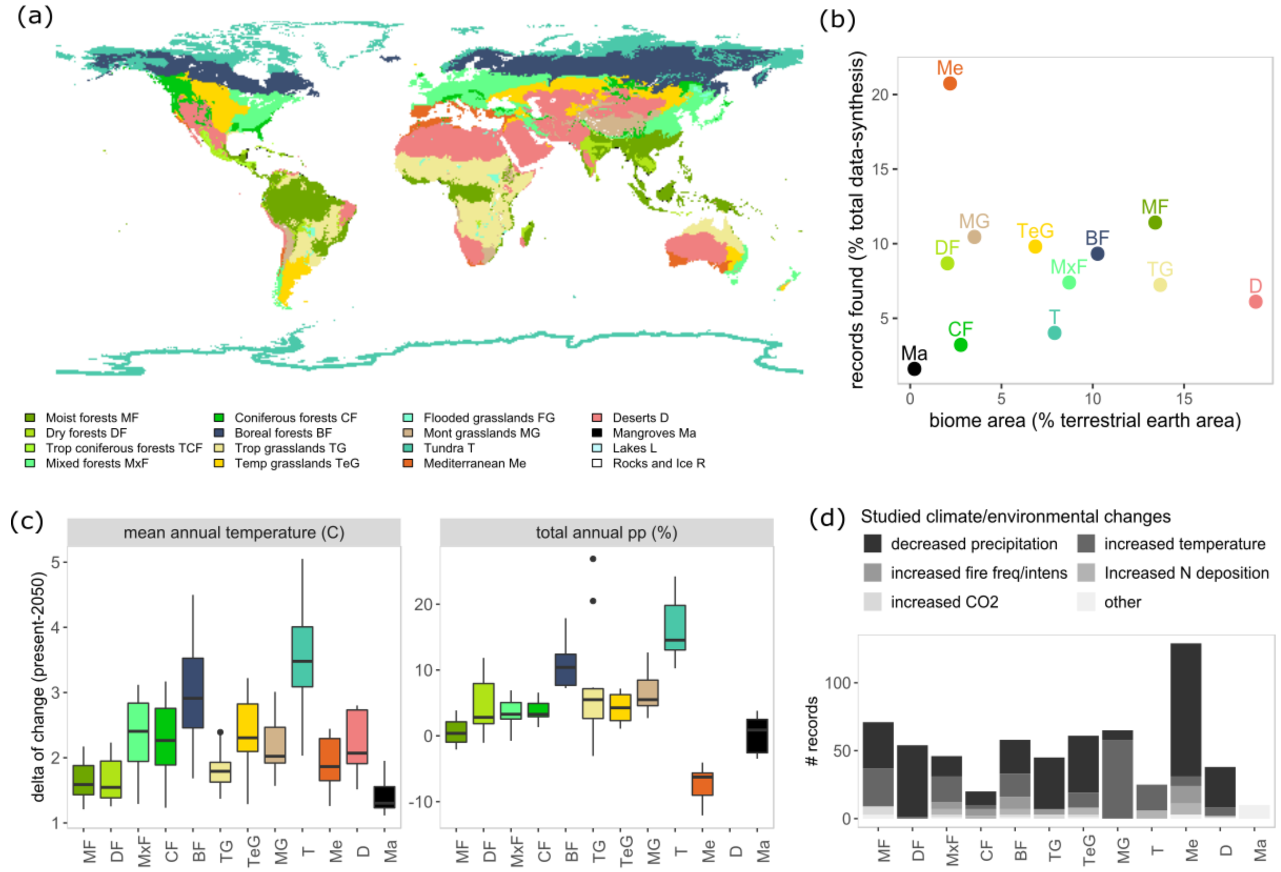

Figure 4.1. a) Biomes map (based on Dinerstein et al. (2017)), b) Percentage of records found per biome in our data-synthesis in comparison to each biome area, c) box and whisker plots of projected future change in temperature and precipitation (present – 2050) under scenario RCP 6.0 per biome, d) Number of records found in our data-synthesis per climate/environmental change for each biome. Abbreviations follow those in 1a. The number of studies increased over time 2007-2017 (Appendix S1, Fig. S4.2) and employed a range of methods (Appendix S1, Fig. S4.7).

4.3.2 SYNTHESIS OF STUDIES

There has been an increase in the number of studies focusing on plant trait attributes associated with a positive response under climate change over the past ten years (see Appendix S1, **Fig. S4.2**). We found that the highest number of relevant studies and records have taken place in Mediterranean Forests, Woodlands and Scrubs (**Fig. 4.1b** and see Appendix S1, **Fig. S4.3**), while the lowest number of studies have occurred in Mangroves and Coniferous Forest. In addition, the Desert biome and Tropical Grasslands and Savannas, the two largest in aerial extent, are among the biomes with the lowest number of records found by our data-synthesis (**Fig. 4.1b**). The peer-reviewed studies found in our systematic search have an uneven geographic cover. Countries with the highest number of publications are USA, China and France (see Appendix S1, **Fig. S4.4a**), whereas the highest density of studies are concentrated in Europe and a few countries in South and Central America (see Appendix S1, **Fig. S4.4b**). The African continent has the poorest coverage of records (see Appendix S1, **Fig. S4.4**).

Plant responses to decreased precipitation were the most studied (**Fig. 4.1d** and see Appendix S1, **Fig S4.5**) but other climate/environmental changes studied included: increased temperature, increased frequency/intensity of fires, increased N deposition, and sea-level rise.

We identified 101 traits in the analysed studies (see Appendix S2, **Table S4.3**) that were linked to a positive plant response (see Appendix S2, **Table S4.2**) to a specific climate/environmental change. Of these, 34 are leaf traits, 19 are whole-plant traits, 17 are below-ground traits, 11 are regenerative traits, 8 are stem traits, 7 are flowering traits and 5 are classified as "others".

The traits with the highest number of total records (weighted by the proportion of positive records) were specific leaf area (SLA), followed by plant height, water-use efficiency (WUE), root depth and wood density (see Appendix S1, **Fig. S5a**). Leaf traits were by far the most recorded (see Appendix S1, **Fig. S4.5b**), however all, but one, of the other trait groups had a higher proportion of positive records than leaf traits (67%). Notably high proportions of positive records were seen in regenerative (84%), whole-plant (82%) and below-ground traits (82%) (see Appendix S2, **Table S4.4**).

4.3.2 GLOBALLY IMPORTANT TRAIT ATTRIBUTES

Our data-synthesis indicates that overall, lower or higher SLA, better water-use efficiency, lower relative growth rate, greater plant height, and higher wood density are traits consistently linked to a positive response across most biomes (**Fig. 4.2a**, **Fig. 4.3**). When looking across the suite of different climate/environmental changes, in addition to higher or lower SLA and higher or lower plant height, clonality/bud banks/larger below-ground storage, greater resprouting ability and greater rooting depth also appear to be traits linked to a positive response across the different climate/environmental changes (**Fig. 4.2b**, **Fig. 4.4**). By combining all traits in a biplot (**Fig. 4.2c**) and the associated combined score (see Appendix S2, **Table S4.5**), we identified eight traits as the “top” traits related to positive responses for both multiple climate/environmental changes and multiple biomes. Each of these top traits had a proportion of >0.4 along both axes. The “top” traits emerging as globally important are higher or lower SLA, higher or lower plant height, greater water-use efficiency, greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density and greater rooting depth (**Figs. 4.2-4.4**).

Although most of the trait’s attributes were consistent across biomes, we found two (SLA and plant height), where both lower and higher attributes were found to be important for plant performance and fitness under climate change across different biomes (**Fig. 4.3**).

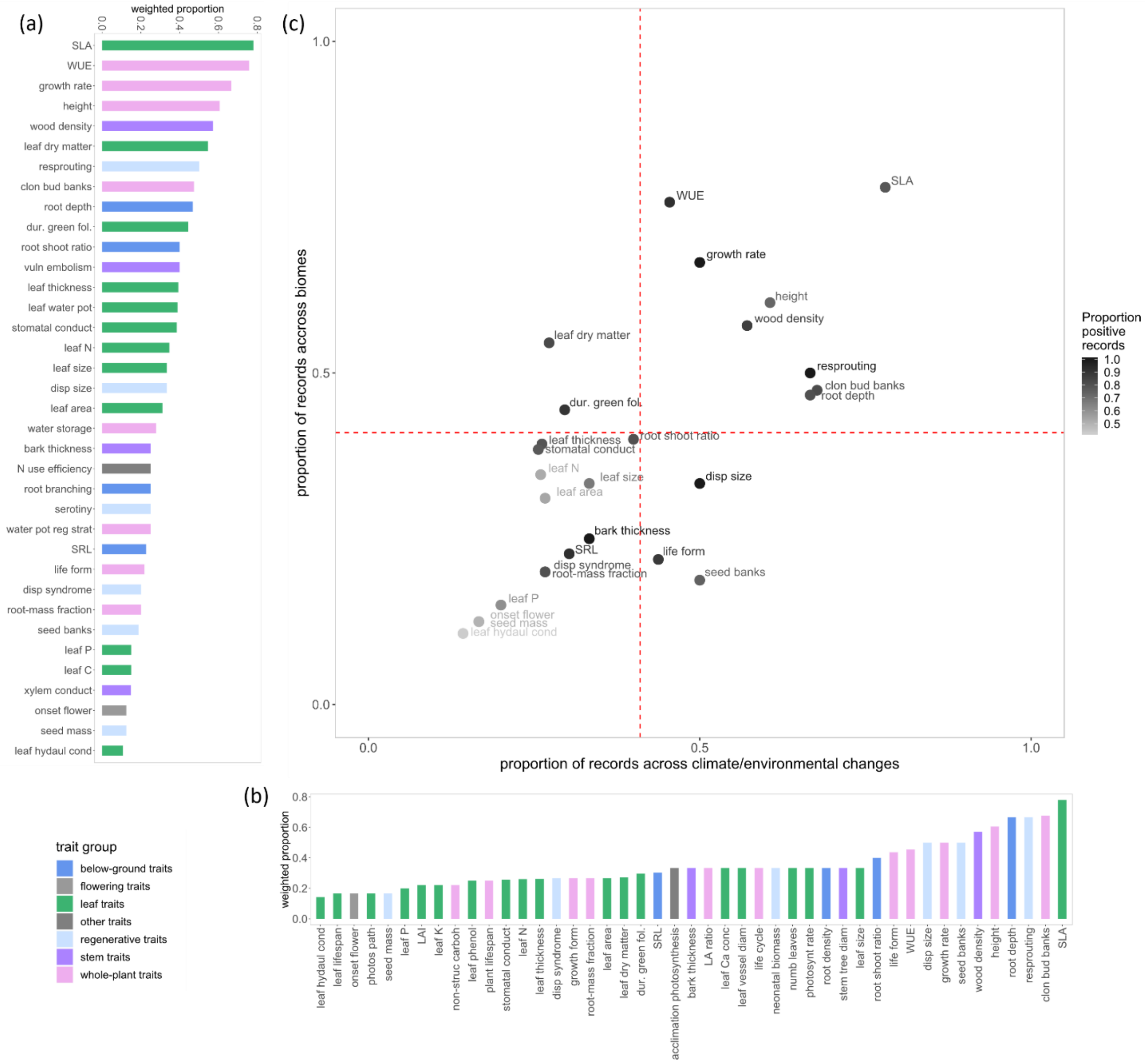

Figure 4.2. Scoring of traits that are linked to a positive response to climate and associated environmental change. The y-axis (a) represents the scoring of traits across biomes weighted by the confidence in the trait mediating a positive plant response (proportion of positive records out of all records including null), where higher values (closer to 1) are given to traits that are recorded as important for plant performance and fitness in a higher number of biomes while lower values (closer to 0) are for traits limited to lower number of biomes. The x-axis (b) represents the scoring of traits across climate/environmental changes (see Fig. 1d) weighted by the confidence in the trait being associated with a positive response (proportion of positive records), where higher values (closer to 1) are assigned to traits that are linked to multiple climate/environmental changes while lower values (closer to 0) are linked to only few climate/environmental changes. Overall scores represented in (c) were determined by combining positive records of traits reported in our selected studies according to their representation across biomes and climate/environmental changes, weighted by the proportion of positive records out of total records (see methods for further details). Traits included in this figure were

those with proportion of biomes and proportion of climate/environmental changes greater than 0.2 for enhanced clarity. Dotted red lines represent the cut-off for top traits at 0.4 proportion for each axis. Top traits are therefore those in the top right section of the figure. Full traits names in Appendix S2, Table S4.1.

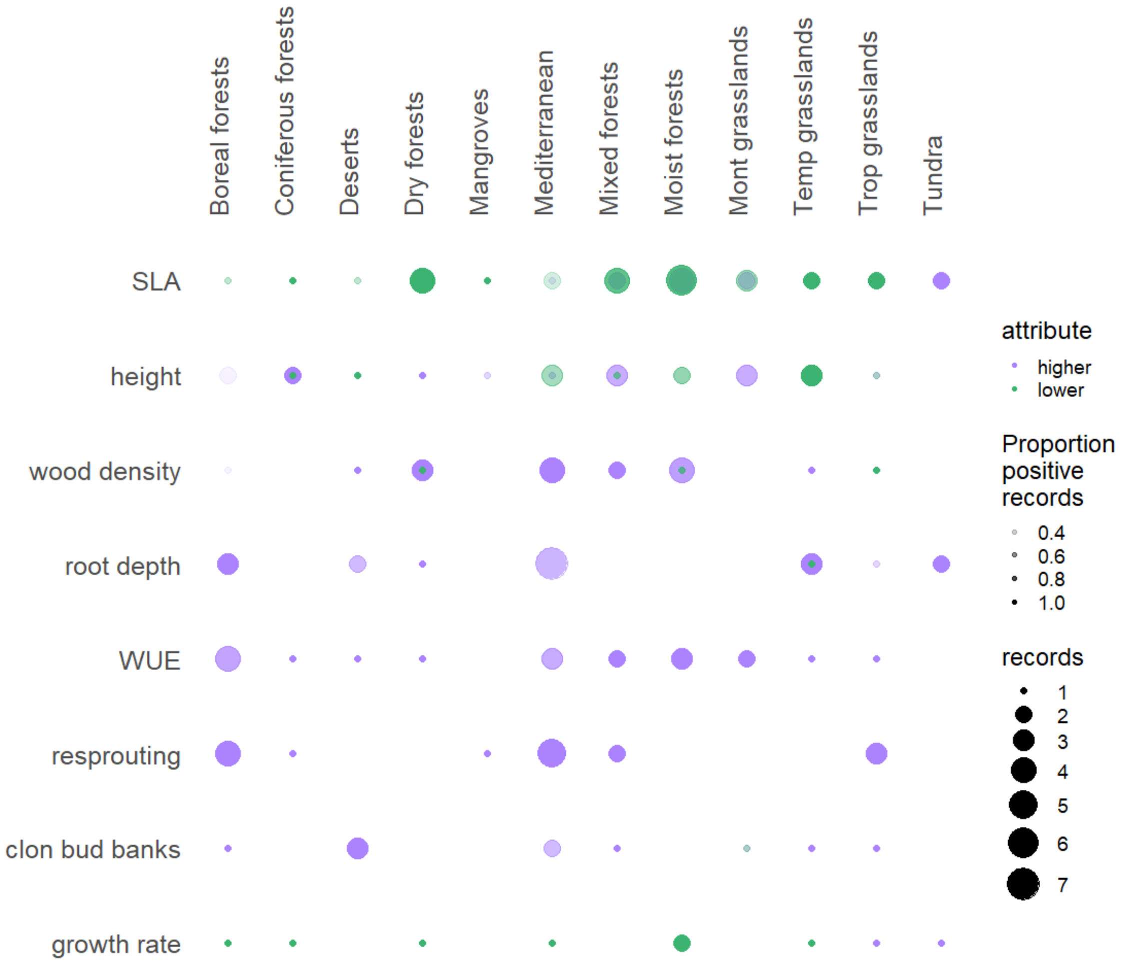

Figure 4.3: Top eight traits identified by this data-synthesis as important for plants to withstand climate change showing their trait attributes ("attribute"), support in number of records ("records") and the confidence in the observed records ("proportion of positive records" out of total number records). Where there are both higher and lower attributes, circles overlap and therefore the total number of records is a sum of both circle sizes.

The top five trait attributes that emerged for coping with decreased precipitation are lower SLA, higher WUE, higher wood density, deeper roots and greater plant height (**Fig. 4.4a**). The top trait attributes for coping with increased temperature are both lower and higher SLA, and greater plant height. Other attributes with less support in terms of number of records but which may also facilitate positive plant responses under increased temperatures, include having higher or lower leaf dry matter content, deciduous or evergreen foliage, higher WUE and higher relative growth rate (**Fig. 4.4b**). The top trait attributes to cope with fires are greater resprouting ability, greater clonality/bud banks/below-ground storage, greater serotiny, deeper roots and thicker bark. In general, there seems to be consistency in the trait attributes that are favourable to cope with fires (**Fig. 4.4c**). Not enough records on trait attributes were available for the remaining climate/environmental changes to make any significant inferences on these changes.

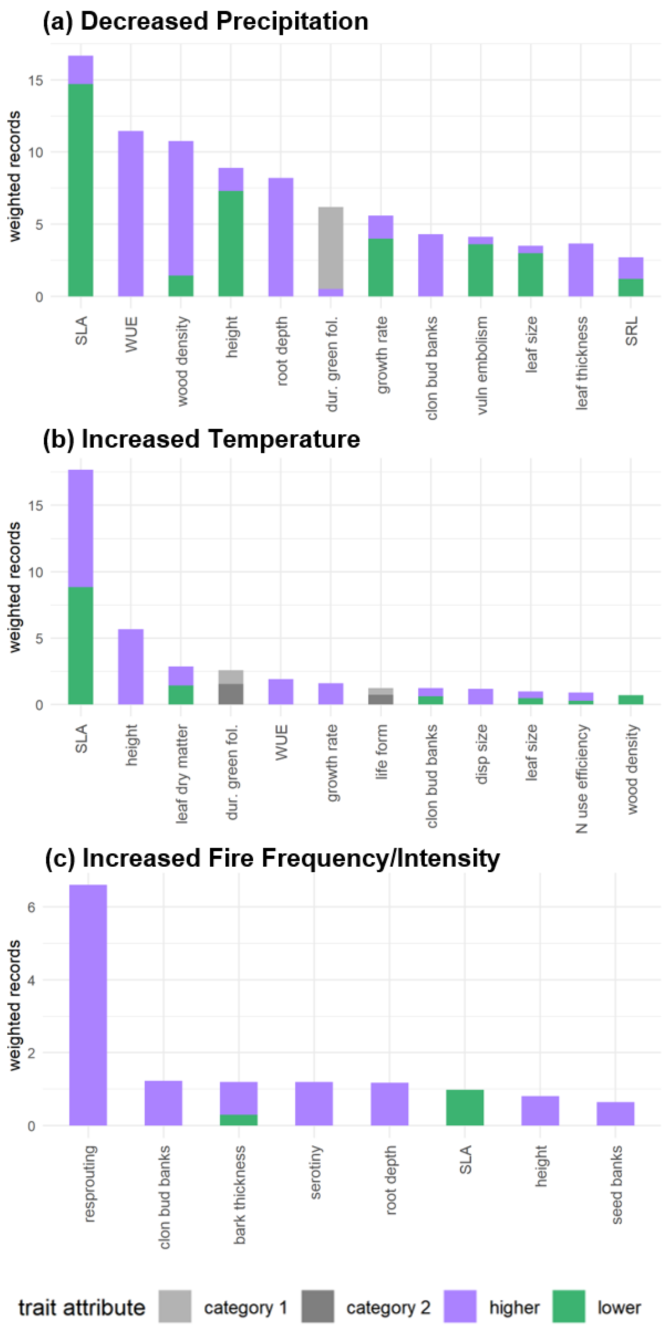

Figure 4.4. Number of records weighted by the proportion of positive records out of total records that were found in our literature survey that support each trait as important for a plant to cope with climate/environmental change for a) decreased precipitation, b) increased temperature, c) increased fire frequency/intensity. Traits included were the top up to 12 for each climate/environmental change. Colours indicate the different trait attributes recorded by the studies. “Lower” and “higher” indicate attributes for quantitative traits. “Category 1” and “Category 2” indicate attributes of qualitative traits. Full traits names in Appendix S2, Table S4.1.

4.4 DISCUSSION

GLOBALLY IMPORTANT TRAITS AND ASSOCIATED ATTRIBUTES FOR COPING WITH CLIMATE CHANGE

Our data-synthesis identified eight main traits that are important for plants across biomes in coping with, or thriving under climate change (decreased precipitation, increased temperature, increased CO_2) and associated environmental changes (increased frequency and intensity of fires, increased nitrogen deposition and others (see Appendix S1, **Fig. S4.6**) (**Fig. 4.2c**). These are higher or lower SLA, higher or lower plant height, greater water-use efficiency, greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density and greater rooting depth. In comparison with the largest existing trait database (TRY Kattge et al. (2011)), our top traits do not meaningfully match those that are most often measured, with only plant height and wood density falling within the top 10 most sampled traits and with most of our traits falling outside the top 100 sampled traits (see Appendix S2, **Table S4.6**). This, along with accounting for the instances where traits were not associated with a response to climate/environmental change (null records), suggest that our presented traits are not merely those most sampled. Below we describe each of the globally important top traits we identified, together with how the trait attributes are related to climate changes and associated environmental changes in different biomes.

Specific leaf area (SLA)

Specific leaf area, defined as “one-sided area of a fresh leaf divided by its oven-dry mass” (Pérez-Harguindeguy et al. 2013), reflects a trade-off between leaf construction costs and carbon assimilation rates (Díaz et al. 2016). Previous work has identified that SLA positively scales with leaf nitrogen concentration and carbon assimilation rate and negatively with leaf life span (Reich et al. 1997, Blonder et al. 2011).

Our data-synthesis shows that in nine out of the twelve biomes, lower SLA is important for plant performance and fitness under *decreased precipitation* (**Fig. 4.3**, **4.4**). For example, in Moist forests of Costa Rica, modelling and plot data indicate that species with lower SLA will better survive drought conditions and become dominant (Uriarte et al. 2016). The authors attribute this to smaller exposed leaf surfaces reducing water loss through evapotranspiration. The same pattern was also found in the Deserts of Australia (Baruch et al. 2017), the Savannas of Brazil (Ribeiro et al. 2016), the Ecuadorian (Chirino et al. 2017) and Bolivian Dry Forests (Markesteijn and Poorter 2009), where plants with lower SLA showed greater persistence under decreased precipitation. In these latter studies, lower SLA was also related to higher sclerophylly, suggesting that plants invested more resources in building robust leaves (lower SLA = more mass per unit of area) and thus adopted a conservative water use strategy (Chirino et al. 2017).

In contrast, studies focusing on plant responses to increased temperature found less consistent responses in SLA, in that both higher and lower values could result in positive responses, depending on the biome (**Fig. 4.3**, **4.4**). For instance, in the Montane Grassland biome in Chongqing, China (Song et al. 2012) and in southern Norway (Guittar et al. 2016), species with higher SLA are more abundant in warmer temperatures at lower elevations. However, in Montane Grasslands of North-western Caucasus in Russia (Soudzilovskaia et al. 2013), species with lower SLA are more abundant in warmer climates. Similarly, in Temperate forests across Europe, some herbaceous species show decreasing SLA, together with smaller and thicker leaves, is linked to reduced evapotranspiration under warming, while other herbaceous species of these same biomes show increasing SLA under warmer climates (Lemke et al. 2015).

Plant height

Plant height is the distance from the ground level to the upper boundary of the main photosynthetic tissues of a plant at maturity, often expressed as maximum height (Pérez-Harguindeguy et al. 2013, Díaz et al. 2016) and is the most common measure of whole plant size (Díaz et al. 2016). Plant height is associated with competition for light resources (Moles et al. 2009), where taller plants are able to display their leaves above others. This, however, trades off against the construction costs that come with growing taller (Poorter et al. 2008). Plant height is considered relevant for carbon storage capacity (Moles et al. 2009, Kattge et al. 2011) and is associated with and influenced by growth form, potential lifespan, competitiveness and other size-related traits (Pérez-Harguindeguy et al. 2013).

In our data-synthesis, plant height emerged as an important trait for plant performance and fitness in response to multiple climate/environmental changes across biomes. We found that for climatic warming, the attributes reported for this trait, i.e. being taller or shorter, differed across biomes. For example, greater grass height was associated with positive plant responses in two grassland biomes, in the Montane Grasslands of France (de Bello et al. 2013) and Norway (Guittar et al. 2016) and in Temperate Grasslands of California, USA (Sandel and Dangremond 2012). In the Boreal Forest, however, shorter trees seem to have higher growth rates than taller trees (Ratcliffe et al. 2016).

Under high water stress, plant height is generally an important trait, where shorter statured plants coped better across biomes (**Fig. 4.3**, **4.4**). For instance in the Moist Broadleaf Forests of the Dinghushan Biosphere Reserve of China, the abundance of shorter-stature species increased in response to decreased precipitation (Zhou et al. 2013). Another example is found in Temperate Grasslands of California (USA), where shorter plants were more stress tolerant to decreased precipitation than taller plants (Fernandez-Going et al. 2012).

Water-use efficiency

Unlike SLA and plant height, water-use efficiency is a complex trait as it is determined by a number of different variables including but not limited to carbon gain per unit of water lost (Pérez-Harguindeguy et al. 2013), water transport features (Holloway-Phillips and Brodribb 2011), stomatal traits (Lawson and Blatt 2014) and leaf (Brodribb et al. 2007) and root architecture (White and Snow 2012). Despite this, our analysis indicates high coherency in results which indicate that across biomes and three climate/environmental changes, higher water-use efficiency is found to be positive for plant performance and fitness. Examples from the drier biomes indicate that greater WUE enabled Mediterranean trees in Sardinia (Italy) to cope better with drought stress (Altieri et al. 2015) and it was also a trait found to be more prevalent among shrubs in the drier sites of the Balearic Islands (Spain) (Lazaro-Nogal et al. 2013).

In Deserts of Arizona (USA), Huang *et al.* (2016) found that seedlings of herbaceous plants with greater WUE had higher stress tolerance and thus seedling survival in drought conditions. Similarly, examples from drier forested biomes such as the Boreal Forests of Canada showed that higher WUE in trembling aspen enhanced the cavitation resistance and thus survival of these plants in drought (Schreiber et al. 2011), and in Dry Forests of Bolivia higher WUE enhanced drought tolerance of trees (Slot and Poorter 2007).

In wetter biomes, trait attributes were consistent i.e. higher WUE was important for plant performance and fitness under a variety of climate/environmental changes. For example, higher WUE was important under drought conditions for Moist Forest tree species in Bolivia (Slot and Poorter 2007). Under increased CO_2 conditions (measured experimentally), higher WUE was also associated with positive plant responses for coniferous trees of the Moist Forests in Panama (Dalling et al. 2016). Finally, field studies in Montane Grasslands of China indicate that under increased temperature, grasses with higher WUE had greater vegetative biomass and thus higher plant performance (Song et al. 2012, Li and Wu 2016).

Resprouting

Resprouting capacity can broadly be defined as the ability of plants to grow new shoots after destruction of above-ground biomass using below-ground and basal (Pérez-Harguindeguy et al. 2013) resources or sometimes, if the entire shoot is not damaged, from aerial resources (Clarke et al. 2013). Another important trait identified by our analysis is that of the presence of bud banks, which is a key determinant of resprouting ability (see further details below). The ability to resprout is important for plants to persist after disturbances such as fires, wind, mechanical removal, drought, frost, grazing and erosion events (Clarke et al. 2013, Pérez-Harguindeguy et al. 2013). In some fire-driven systems like Mediterranean ecosystems, resprouting is often traded off against serotiny as a regenerative strategy which involves seeds being protected by seed capsules during fire and then released after fire.

Our study indicated that in biomes with and without a natural fire regime, resprouting was an important trait to cope with fire. However, the studies considered suggest that the benefit of resprouting vs. serotiny depends on the severity (Hollingsworth et al. 2013) and frequency of the fire (Buma et al. 2013) and on the stage of the post-fire cycle (Tavşanoğlu and Gürkan 2014).

In the Boreal Forest, being able to resprout was important after lower severity fires (Hollingsworth et al. 2013) and more frequent fires (Buma et al. 2013). In the Mediterranean biome, resprouting was important in conditions of increased fire frequency in SW Australia (Enright et al. 2014), however the study noted that seedling recruitment was additionally important in maintaining these resprouting species. In Turkey, resprouting species appeared to recover better over the longer term than reseeder species in post-fire recovery (Tavşanoğlu and Gürkan 2014). The ability to resprout epicormically was identified as important under increased fire frequency in Eucalypt trees in the Australian savanna (Clarke et al. 2015). In Mixed Forests, resprouting enhanced the population recovery after fire in the central Yunnan plateau (China) (Su et al. 2015) and in Coniferous Forests of New Mexico and Arizona (USA) (Haire and McGarigal 2008). Furthermore, resprouting has also been found to be important under conditions of drought and wind in Mediterranean systems (Sánchez-Pinillos et al. 2016, Parra and Moreno 2017).

Relative growth rate

Relative growth rate (RGR) is defined as the increase in size of the plant relative to its initial size over a given time. It is different from the response variables “enhanced growth” or “biomass accumulation” used in this study as it is an inherent trait that is a time-associated variable (i.e. a rate with plants having faster or slower RGRs). Relative growth rate is a good indicator of plant productivity related to environmental stress and disturbance regimes (Pérez-Harguindeguy et al. 2013). Our data-synthesis shows that a high number of studies have demonstrated that under decreased precipitation conditions a lower relative growth rate is important for plant performance and fitness (**Fig. 4.3**, **4.4**). These include studies in Temperate Coniferous Forests in Oregon, USA (Kerr et al. 2015) and Moist Broadleaf Forests species of Ecuador (Chirino et al. 2017), which link lower RGR with greater resistance to drought and extreme temperatures. However, in Moist Forests of Costa Rica, higher growth in the previous year allowed for greater survival in drought conditions (Uriarte et al. 2016). Also, Mediterranean grass species from California (USA) with greater summer dormancy, predominantly characterised by higher spring growth rate, had enhanced dehydration tolerance (Balachowski et al. 2016).

Several studies have also indicated that a faster RGR is an advantage with increased atmospheric CO_2 concentration. In Savannas of South Africa, woody species taking advantage of the CO_2 fertilisation effect, and thus able to grow faster, could escape the 'fire-trap', i.e. grow to a large enough stature to survive a surface fire (Bond and Midgley 2012). In experiments conducted on Moist Forest species of Panama, conifers with inherently slower growth rates benefitted more than angiosperms from the increase in atmospheric CO_2 because it stimulated enhanced growth (Dalling et al. 2016), a trend that could influence the composition in these forests.

Clonality, bud banks and below-ground storage organs

Clonality, the ability to reproduce vegetatively, allows plants to form bud banks, which enhances ability to recover and persist after disturbance through branching, shoot replacement and regrowth after severe seasons or injury (Pérez-Harguindeguy et al. 2013). Below-ground clonal organs can also serve as carbohydrate carbon storage, which provides resource for growth in future years (Soudzilovskaia et al. 2013).

Outputs from our data-synthesis show that reproducing clonally and/or increasing investment in bud banks and/or below-ground storage, has been found to be important by different studies across biomes and multiple climate/environmental changes. For instance, studies in the warmer and drier Desert and Mediterranean biomes report that species with greater biomass allocation to roots (Tian et al. 2014, Tardella et al. 2016), greater carbohydrate reserves (Volaire et al. 2014) and below ground storage (Evans et al. 2014) showed enhanced drought tolerance, survival and post-drought recovery. In another study in the cooler biome of Temperate Grasslands and Savannas, species with bud banks had greater drought resistance in tall prairie grasslands of Kansas, USA, which ultimately lead to a shift in species composition (VanderWeide et al. 2014). In the even cooler forests of Boreal and Temperate Broadleaf and Mixed Forests biomes, the ability to reproduce vegetatively after severe dieback, enhanced drought tolerance and recovery at the population and individual level (Aubin et al. 2016).

In conditions of increased temperature these traits also proved important: greater investment in below-ground storage to support the following year's buds was the best predictor of species abundance of grasses in Montane Grasslands along a gradient of increasing temperature (Soudzilovskaia et al. 2013). Further, increased biomass allocation to roots was also associated with enhanced post-fire recovery in the Boreal Forest biome (Aubin et al. 2016).

WOOD/STEM-SPECIFIC DENSITY

Wood density and stem-specific density (SSD) are used interchangeably with the distinction being that SSD can be measured for non-woody species (herbaceous) and that it includes the stem bark. This trait is calculated as dry mass per unit of fresh volume of a stem and is linked to the stability, hydraulics, growth, defence and architecture of plants (Pérez-Harguindeguy et al. 2013, Garnier et al. 2016). As a result, this trait is a central component of the "wood economic spectrum", which aims to describe functional trade-offs in woody plants (Chave et al. 2009). Species with higher wood density have enhanced resistance to hydraulic cavitation and physical damage/disease, but tissue costs associated with denser wood impose a limit on this.

Our analysis indicates that, across eight biomes, higher wood density was important for plant performance and fitness under decreased precipitation. For example, in Dry Forests of Bolivia seedlings with greater wood density had a reduced risk of cavitation during drought (Markesteijn and Poorter 2009) and in adult trees growth was less sensitive to reduced water availability for species with denser wood (Mendivelso et al. 2013). Similar trends were noticed in Moist Forests of M'Baïki (Central African Republic) (Ouédraogo et al. 2013), the Caribbean lowlands of Costa Rica (Uriarte et al. 2016) and Ecuador (Sakschewski et al. 2016), where studies combining monitoring and modelling indicated that under increased aridity or drought, trees found to be more resilient in terms of lower growth/biomass reduction and greater survival had greater wood density. In Mediterranean environments, modelled plant community structure indicated that woodier species would be more prevalent under conditions of increased aridity (Frenette-Dussault et al. 2013). However, in Tropical Grasslands there seems to be a trade-off: in the Cerrado (Brazil), high wood density was found to be important as it prevents cavitation in stems, but low wood density allowed for higher water storage capacity (Hao et al. 2008).

Rooting depth

The root system of plants is the primary organ for water and nutrient uptake and is also responsible for resource transfer from the soil to above-ground parts of the plant. Rooting depth is an important morphological trait which determines from where in the soil profile the plant can acquire water and nutrients (Pérez-Harguindeguy et al. 2013). Plants with deep roots contribute disproportionally to the water and carbon balance of dry systems (Oliveira et al. 2005) and have an important role in ecosystem functioning under variable or decreasing precipitation (Maeght et al. 2013). Plant rooting depth therefore has an influence on ecosystem resilience during environmental stress such as drought, when deeper-rooted plants can tap groundwater more efficiently (Fan et al. 2017). Rooting depth is a trait rarely measured despite its perceived representation of hydraulic regulating strategies due to the difficulty of obtaining these data, which often involves labour-intensive root excavation (Iversen et al. 2017). Despite this, rooting depth was consistently identified as an important trait in our data-synthesis, across climate/environmental changes as well as biomes. The clearest trend that emerged from the studies we analysed associated with roots was that deeper roots were important for plant performance and fitness in drought conditions or in drier climates

(**Fig. 4.3**). For example, reports from experiments on grassland species of the Temperate Grassland and Mediterranean biomes indicated that deeper roots enhanced potential depth of water uptake, which avoided dehydration and thus increased plant survival and recovery (Zwicke et al. 2015, Barkaoui et al. 2016). Additionally, deeper rooting was found to be important for fire survival by a number of studies, particularly for high-severity fires in trees of Boreal Forests, whereby deeper roots are protected from the lethal temperatures associated with fire (Aubin et al. 2016), potentially resulting in higher species abundances for those possessing these traits (Hollingsworth et al. 2013).

IMPLICATIONS AND FUTURE DIRECTIONS

Future changes in the climate system will lead to regional key risks where some regions are projected to be more vulnerable to decreased precipitation and/or increased temperature than others (IPCC 2015) (**Fig. 4.1c**). Our data-synthesis identified plant traits that enable species to cope with, or thrive under, specific climate/environmental changes (**Fig. 4.4**). The consistency observed in trait attributes within climate/environmental changes suggests generalizable response to climate change exists, and thus provides insights on key trait attributes for regions where these environmental changes are projected. In this way, we provide information that could be useful for prediction, management and/or restoration actions.

Our data synthesis also informs which traits can be focused on going forward in climate change studies. For example, less focus on those commonly sampled leaf traits that are not consistently associated with positive responses and more focus instead on other whole plant, regenerative and below-ground traits (See Appendix S2, **Table S4.5** and S1, **Fig S4.6**) may be preferable when prioritising which traits to measure in the field. Furthermore, a greater focus on climate/environmental changes that remain relatively unstudied, but which are predicted to be significant in the future such as increased CO_2 and increased nitrogen deposition, would provide an enhanced understanding of plant responses to the full suite of factors associated with climate change. Finally, there should be enhanced effort to study plant traits in relation to climate change in

Deserts, Temperate grasslands and Tundra as they remain under-sampled relative to their extent and perceived climate change vulnerability (**Fig. 4.1b**) (however see recent efforts to advance the literature on traits in the Tundra (Anne D. Bjorkman et al. 2018, Anne D Bjorkman et al. 2018, Myers-Smith et al. 2019, Thomas et al. 2020).

There are several layers that need to be combined to have a complete picture of how the potential plant responses to climate changes are mediated by traits. There is a body of work focusing on responses at the molecular level that are related to individual phenotypic plasticity, showing that changes in trait attributes within individuals occur in response to environmental changes (Nicotra et al. 2010, Anderson 2016). This is a key point that is not addressed by our analysis but should be considered in future research as it may alter the relative abilities of different species responding positively to climate change where some species benefit from changing their traits (plasticity) (Nicotra et al. 2010), and some cannot but benefit from resource conservatism (bet-hedging) (Power et al. 2019). Another important consideration for future studies which is gaining momentum in the functional ecology community is that of intraspecific variation in traits. Although most trait studies use the mean trait value/attribute per species, intraspecific variation can contribute significantly to overall trait variation and should therefore not be overlooked (Albert et al. 2010, Mitchell et al. 2018). Explicitly analysing these elements requires detailed analysis of a) the change in trait attributes in response to environmental change (plasticity), (as above) and b) the variation in trait attributes both between and within species (intraspecific variation). This level of analysis is not yet widely available (Kattge et al. 2020) and remains an important future direction of study.

4.5 CONCLUSIONS

Although climate change has contributed to shaping plant form and function over millions of years, the speed at which current climate change is being observed is unprecedented. We focused on identifying whether there are general patterns of plant functional traits that are associated with positive plant responses (ability to cope or thrive) under predicted climate and associated environmental changes, across biomes. Our data-synthesis identified a subset of top traits and their associated attributes namely higher or lower specific leaf area, higher or lower plant height, greater water-use efficiency, greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density, and greater rooting depth. Significantly, these findings do not merely reflect traits highly sampled. We found that trait attributes are quite consistent across the globe for the top traits that help plants to cope with decreased precipitation (i.e. higher wood density, lower SLA, higher WUE, deeper roots). Although more data are required to sufficiently compare other climate/environmental changes, both higher and lower SLA are reported to be important under increased temperature, and resprouting ability is reported to be important under increased frequency or intensity of fire.

Knowledge of which plant traits and attributes are important under different climate and associated environmental changes is key when developing a range of management decisions. For instance, it could help breeding programmes select species or varieties with key traits and trait attributes. It could also help conservation and restoration actions identify species that are resistant vs. vulnerable to climatic changes. Further, our analysis has implications for which ecosystem services will be more resilient to climate change, as many are linked to specific traits (e.g. the size and architecture of root and shoot systems regulate climate, water, and soils of ecosystems, Garnier et al. (2016)). More effort is needed to overcome the knowledge gaps we identified, such as which traits and climate/environmental changes future studies should focus on and which biomes these studies should target.

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AUTHOR CONTRIBUTIONS

KJW, NK and CT conceived the study and designed the approach, NK, JC and CT collected the data, NK and CT performed the data-synthesis, all authors substantially contributed to discussion of results, NK and CT wrote the first draft and received substantial contribution from other authors.

DATA ACCESSIBILITY

We do not have new data but have synthesized information from published papers that are listed in Appendix S2 **Table S4.1**.

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4.6 SUPPLEMENTARY MATERIALS:

Appendix S1, Supplementary Methods and Supporting Figures

Globally important plant functional traits for coping with climate change

Nicola Kühn, Carolina Tovar, Julia Carretero, Vigdis Vandvik, Brian J. Enquist, Kathy J. Willis

Supplementary methods

Biome selection

We used a modified version of the biome map of Dinerstein and colleagues (2017) (which, additional to Olson et al. (2001), contains updated Mangroves distribution). From the 14 global biomes, we excluded Tropical and Subtropical Coniferous Forests and Flooded Grasslands and Savannas from our analysis due to the relatively small area and restricted global coverage represented by these biomes. However, we kept Mangroves because despite its small area, it is globally distributed.

For each biome we used all projected climate model outputs (CMIP5 data) (IPCC2015) and chose RCP 6.0 as an intermediate scenario.

Systematic literature review

Our search often resulted in several records per study. Each of our records represents a unique combination of the following variables: biome, studied climate/environmental change (e.g. decreased precipitation, increased temperature, etc.), response type (positive or null), fitness surrogate defining the positive response (e.g. survival, increase in biomass or reproductive output), trait (e.g. specific leaf area), and trait attribute associated with the positive response (e.g. higher, lower, etc) (see **Fig. S4.1** in Supporting Information).

The inclusion of specific climatic changes and associated environmental changes was dependent on this change being associated with climate change, because the search terms included “climate” “change” and not individual climate or environmental changes (e.g. “drought”, “fire”). Increased fire frequency and intensity were grouped in the analysis because most studies looked at changes in fire regime which included both increased frequency and intensity of fires.

Traits were standardized following Pérez-Harguindeguy *et al.* (Pérez-Harguindeguy et al. 2013), when possible, and new ones were added as required. We also checked whether traits were listed in the Thesaurus Of Plant characteristics (Garnier et al. 2017).

Supporting figures

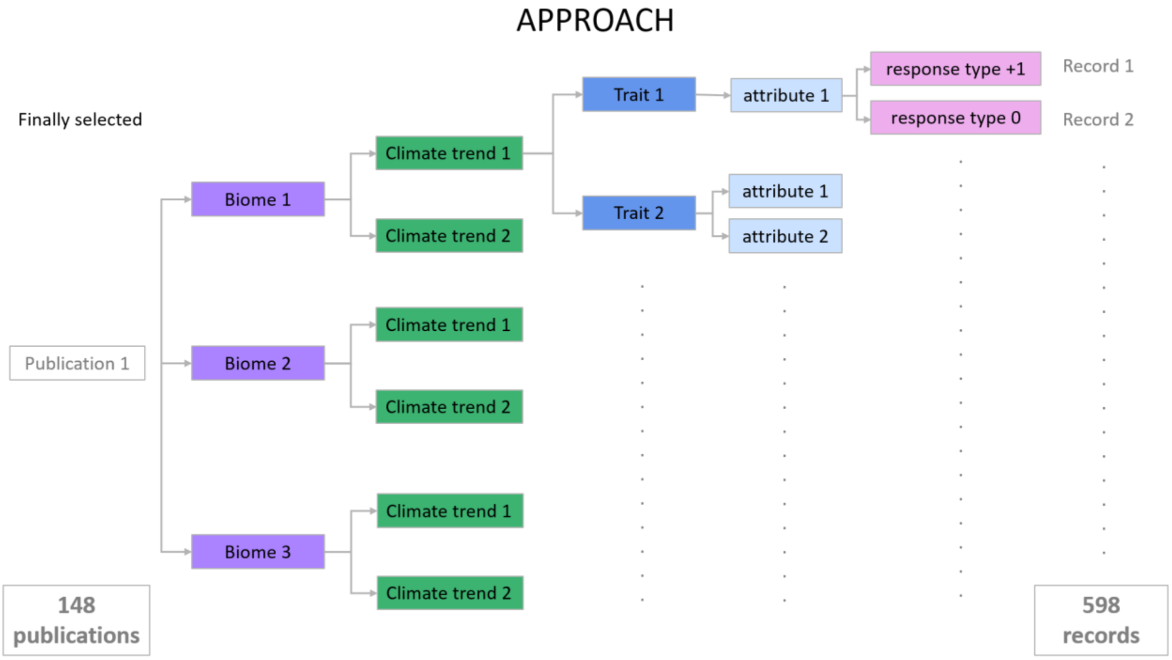

Figure S4.1 Approach to record data extracted from each publication for our data-synthesis based on the global systematic review of literature identifying traits that mediate positive responses to climate change between 2007-2017. Multiple biomes, climate trends, traits, attributes, and response types were recorded per publication resulting in multiple records per publication. A total of 598 records were extracted from 148 publications.

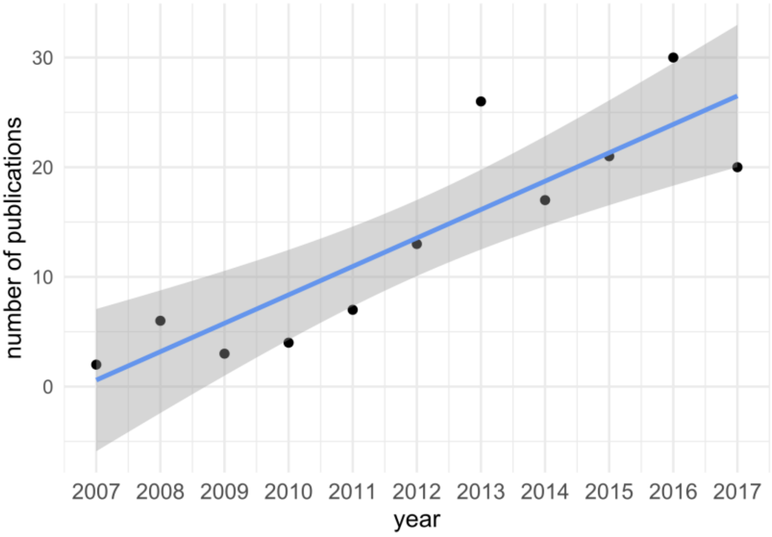

Figure S4.2 Number of publications by publication year (2007-2017) used in our data-synthesis based on the global systematic review of literature which identified positive responses to climate change.

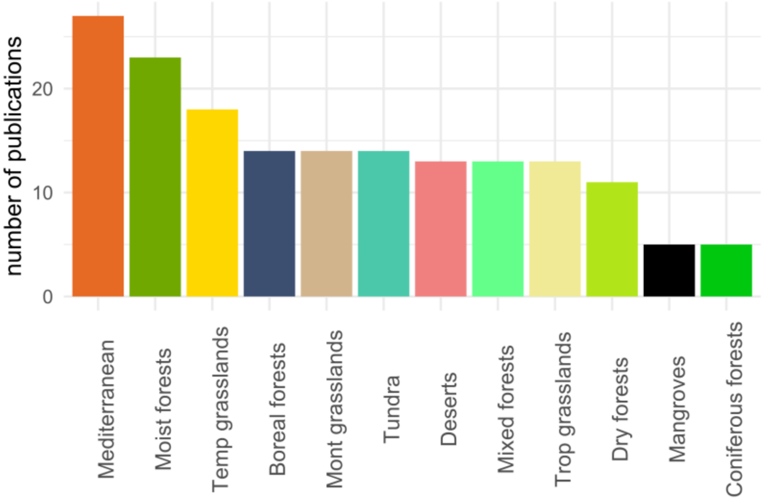

Figure S4.3 Number of publications per biome used in our data-synthesis based on the global systematic review of literature which identified traits mediating positive responses to climate change.

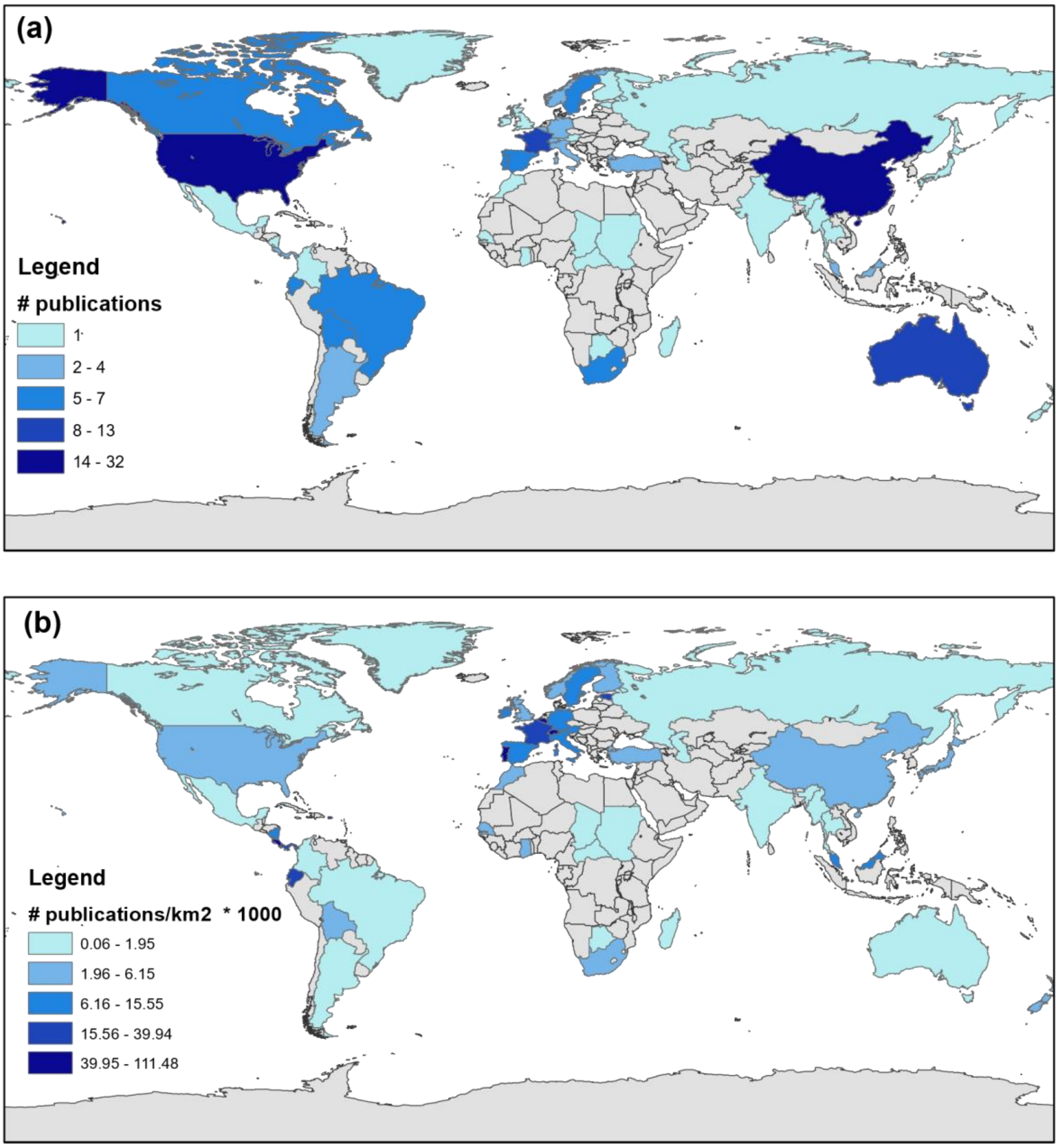

Figure S4.4 Map showing number of publications per biome for each country found by our data-synthesis based on the global systematic review of literature which identified traits mediating positive responses to climate change (a) and the number of publications related to area of each country (b).

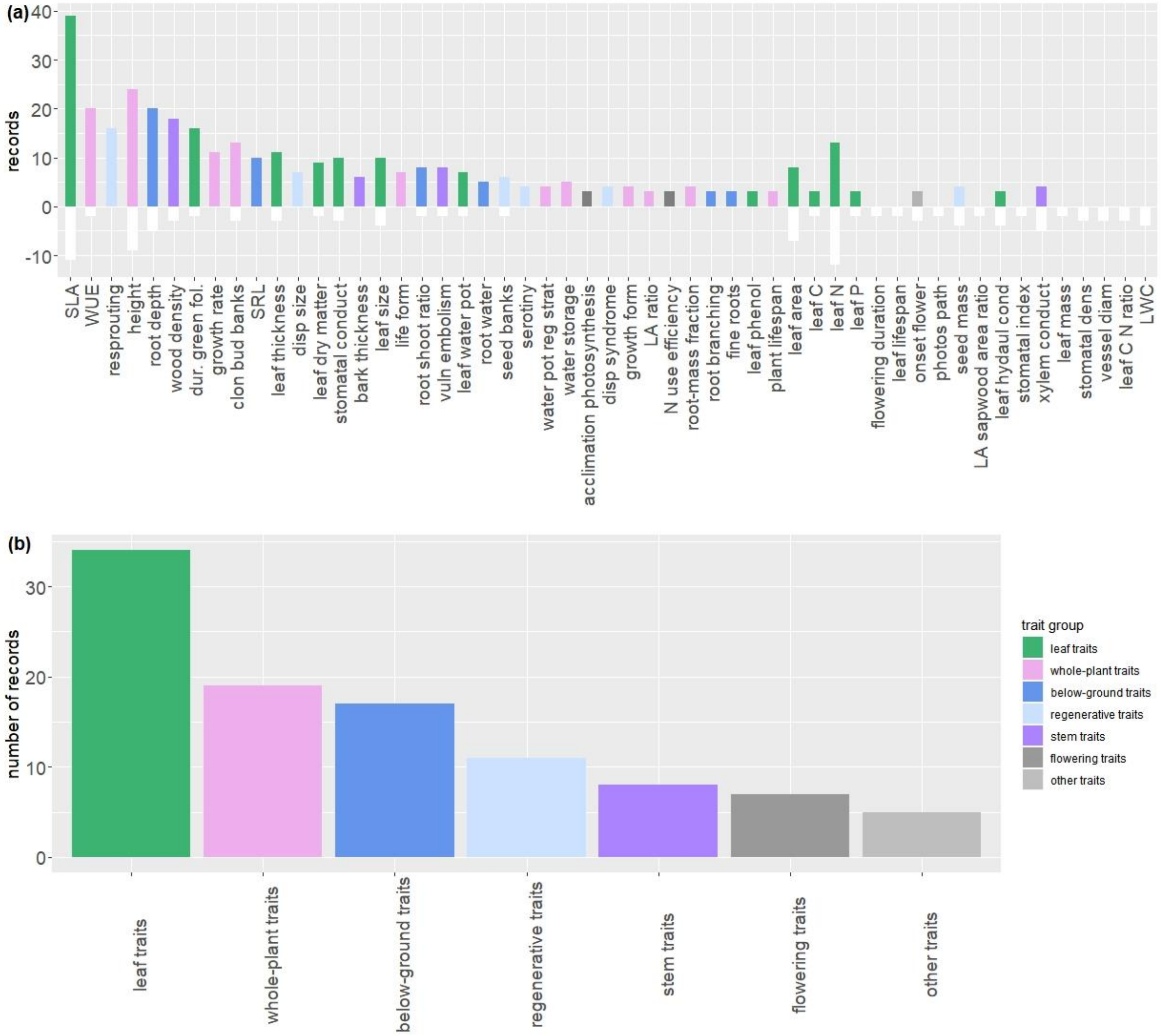

Figure S4.5 Recorded traits of our data-synthesis based on a global review of literature that identified traits mediating responses to climate change. Number of records per trait (a) associated with a positive response to a studied climate/environmental change obtained from 148 studies. Number of records per trait categories (b). Colours represent the different trait categories. Records where a trait was measured but not found to be positive (i.e. null) in (a) are represented below the axis in white.

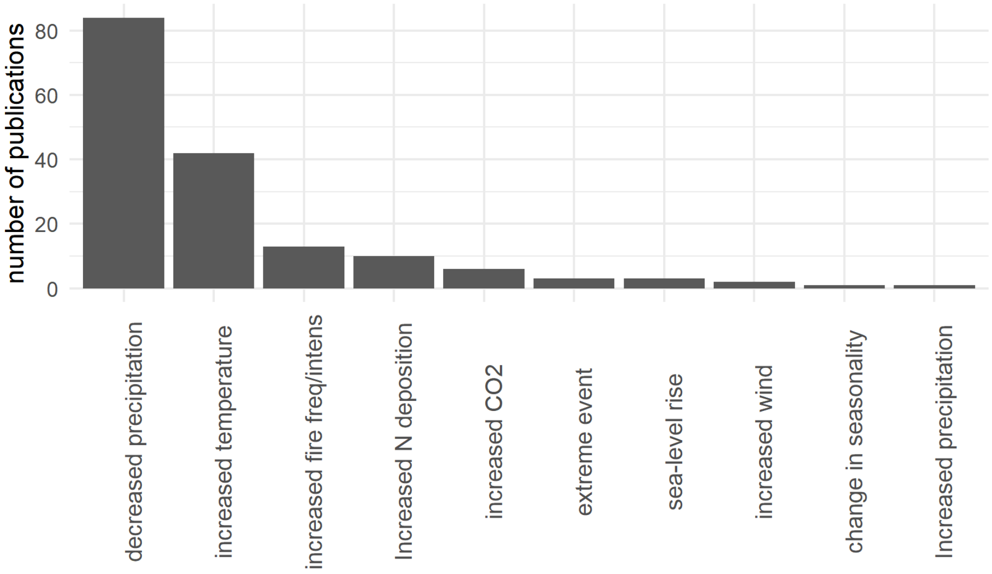

Figure S4.6 Number of publications for each climate/environmental change analysed in this data-synthesis based on a global review of literature identifying traits that mediate positive responses to climate change.

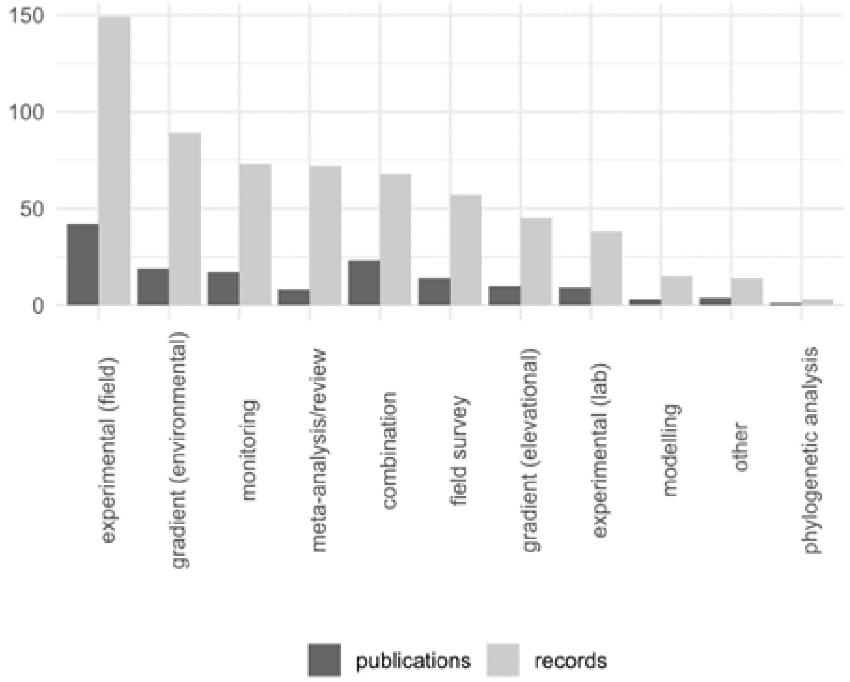

Figure S4.7 Number of publications and records for each of the recorded methods used by the studies examined by our data-synthesis based on a global review of literature identifying traits that mediate positive responses to climate change.

Supplementary Materials: Appendix S2, Supporting Tables

Globally important plant functional traits for coping with climate change: Nicola Kühn, Carolina Tovar, Julia Carretero, Vigdis Vandvik, Brian J. Enquist, Kathy J. Willis

SUPPORTING TABLES

Table S1 List of studies used for this data-synthesis based on the global systematic review of literature identifying traits that mediate positive responses to climate change.

Nº	First Author	Year	Title	Journal	Volume	Issue	Pages
1	Alatalo, Juha M.	2016	Impacts of different climate change regimes and extreme climatic events on an alpine meadow community	Scientific Reports	6	1	21720
2	Allen, Kara	2017	Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes?	Environmental Research Letters	12	2	023001
3	Almeida, Juan P.	2013	Patterns and origin of intraspecific functional variability in a tropical alpine species along an altitudinal gradient	Plant Ecology & Diversity	6	3-4	423-433
4	Altieri, Simona	2015	Tree-ring carbon and oxygen isotopes indicate different water use strategies in three Mediterranean shrubs at Capo Caccia (Sardinia, Italy)	Trees	29	5	1593-1603
5	Amissah, Lucy	2014	Functional traits, drought performance, and the distribution of tree species in tropical forests of Ghana	Dissertation			
6	Arndt, Stefan K.	2015	Vulnerability of native savanna trees and exotic Khaya senegalensis to seasonal drought	Tree Physiology	35	7	783-791
7	Asner, Gregory P.	2016	Convergent elevation trends in canopy chemical traits of tropical forests	Global Change Biology	22	6	2216-2227
8	Aubin, I.	2016	Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change	Environmental Reviews	24	2	164-186
9	Aung, Toe Toe	2013	Prediction of recovery pathways of cyclone-disturbed mangroves in the megadelta of Myanmar	Forest Ecology and Management	293		103-113
10	Balachowski, Jennifer A.	2016	Summer dormancy, drought survival and functional resource acquisition strategies in California perennial grasses	Annals of Botany	118	2	357-368
11	Baltzer, J. L.	2008	The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula	Functional Ecology	22	2	221-231
12	Barkaoui, Karim	2016	Mean root trait more than root trait diversity determines drought resilience in native and cultivated Mediterranean grass mixtures	Agriculture, Ecosystems & Environment	231		122-132

13	Baruch, Zdravko	2017	Leaf trait associations with environmental variation in the wide-ranging shrub Dodonaea viscosa subsp. Angustissima (Sapindaceae)	Austral Ecology	42	5	553-561
14	Benomar, Lahcen	2015	Fine-scale geographic variation in photosynthetic-related traits of Picea glauca seedlings indicates local adaptation to climate	Tree Physiology	35	8	864-878
15	Binks, Oliver	2016	Plasticity in leaf-level water relations of tropical rainforest trees in response to experimental drought	New Phytologist	211	2	477-488
16	Bjorkman, Anne D.	2017	Climate adaptation is not enough: warming does not facilitate success of southern tundra plant populations in the high Arctic	Global Change Biology	23	4	1540-1551
17	Bohlman, Stephanie A.	2010	Landscape patterns and environmental controls of deciduousness in forests of central Panama	Global Ecology and Biogeography	19	3	376-385
18	Bond, William J.	2012	Carbon dioxide and the uneasy interactions of trees and savannah grasses	Phil. Trans. Roy. Soc. B: Biological Sciences	367	1588	601-612
19	Buitenwerf, R.	2012	Increased tree densities in South African savannas: >50 years of data suggests CO2 as a driver	Global Change Biology	18	2	675-684
20	Buma, Brian	2013	The Impacts of Changing Disturbance Regimes on Serotinous Plant Populations and Communities	BioScience	63	11	866-876
21	Byrne, Kerry M.	2017	Contrasting effects of precipitation manipulations in two Great Plains plant communities	Journal of Vegetation Science	28	2	238-249
22	Chirino, Esteban	2017	Morpho-functional traits and plant response to drought conditions in seedlings of six native species of Ecuadorian Ecosystems	Flora	233		58-67
23	Clarke, Peter J.	2015	A synthesis of postfire recovery traits of woody plants in Australian ecosystems	Science of The Total Environment	534		31-42
24	Dalling, James W.	2016	Two tropical conifers show strong growth and water-use efficiency responses to altered CO2 concentration	Annals of Botany	118	6	1113-1125
25	Bello, Francesco de	2013	Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps	Ecography	36	3	393-402
26	Deines, Jillian M.	2011	Traits associated with drought survival in three Australian tropical rainforest seedlings	Australian Journal of Botany	59	7	621
27	DeMarco, Jennie	2014	Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra	Ecosphere	5	6	art72
28	Eamus, Derek	2016	Mulga, a major tropical dry open forest of Australia: recent insights to carbon and water fluxes	Environmental Research Letters	11	12	125011
29	Enquist, Brian	2017	Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient	Global Ecology and Biogeography	26	12	1357-1373
30	Enright, Neal J.	2014	Resistance and resilience to changing climate and fire regime depend on plant functional traits	Journal of Ecology	102	6	1572-1581
31	Ertl, Siegrun	2013	Positive effects of an extremely hot summer on propagule rain in upper alpine to subnival habitats of the Central Eastern Alps	Plant Ecology & Diversity	6	3-4	467-474
32	Eskelinen, Anu	2015	Erosion of beta diversity under interacting global change impacts in a semi-arid grassland	Journal of Ecology	103	2	397-407

33	Euskirchen, Eugénie S.	2014	Changes in the structure and function of northern Alaskan ecosystems when considering variable leaf-out times across groupings of species in a dynamic vegetation model	Global Change Biology	20	3	963-978
34	Evans, M.	2014	Insights on the Evolution of Plant Succulence from a Remarkable Radiation in Madagascar (Euphorbia)	Systematic Biology	63	5	697-711
35	Fernandez-Going, B.M	2012	Temporal variability in California grasslands: Soil type and species functional traits mediate response to precipitation	Ecology	93	9	2104-2114
36	Frenette-Dussault, Cédric	2013	Trait-based climate change predictions of plant community structure in arid steppes	Journal of Ecology	101	2	484-492
37	Gotsch, Sybil G.	2015	Life in the treetops: ecophysiological strategies of canopy epiphytes in a tropical montane cloud forest	Ecological Monographs	85	3	393-412
38	Guittar, John	2016	Can trait patterns along gradients predict plant community responses to climate change	Ecology	97	10	2791-2801
39	Guo, Chengyuan	2017	Morphological, physiological and anatomical traits of plant functional types in temperate grasslands along a large-scale aridity gradient in northeastern China	Scientific Reports	7	1	40900
40	Haire, Sandra L.	2008	Inhabitants of Landscape Scars: Succession of Woody Plants after Large, Severe Forest Fires in Arizona and New Mexico	The Southwestern Naturalist	53	2	146-161
41	Hao, Guang-You	2008	Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems	Oecologia	155	3	405-415
42	Hartnett, David C.	2013	Variation in root system traits among African semi-arid savanna grasses: Implications for drought tolerance	Austral Ecology	38	4	383-392
43	He, Binyuan	2007	Comparison of flooding-tolerance in four mangrove species in a diurnal tidal zone in the Beibu Gulf	Estuarine, Coastal and Shelf Science	74	1-2	254-262
44	Hedwall, Per-Ola	2016	Trait variations of ground flora species disentangle the effects of global change and altered land-use in Swedish forests during 20 years	Global Change Biology	22	12	4038-4047
45	Heskel, Mary	2013	Differential physiological responses to environmental change promote woody shrub expansion	Ecology and Evolution	3	5	1149-1162
46	Hofer, Daniel	2016	Yield of temperate forage grassland species is either largely resistant or resilient to experimental summer drought.	Journal of Applied Ecology	53	4	1023-1034
47	Hoiss, Bernhard	2012	Combined effects of climate and management on plant diversity and pollination type in alpine grasslands	Diversity and Distributions			n/a-n/a
48	Hollingsworth, Teresa N.	2013	Fire Severity Filters Regeneration Traits to Shape Community Assembly in Alaska's Boreal Forest	PLoS ONE	8	2	e56033
49	Hoover, David L.	2014	Resistance and resilience of a grassland ecosystem to climate extremes	Ecology	95	9	2646-2656
50	Hoyle, Gemma L.	2013	Soil warming increases plant species richness but decreases germination from the alpine soil seed bank	Global Change Biology	19	5	1549-1561
51	Huang, Zhenying	2016	The contribution of germination functional traits to population dynamics of a desert plant community	Ecology	97	1	250-261

52	Iogna, Patricia A.	2013	Homeostasis in leaf water potentials on leeward and windward sides of desert shrub crowns: water loss control vs. high hydraulic efficiency	Oecologia	173	3	675-687
53	JI Zijing, 季子敬	2013	Variations in leaf anatomy of Larix gmelinii reflect adaptation of its photosynthetic capacity to climate changes	Acta Ecologica Sinica	33	21	6967-6974
54	Joët, Thierry	2013	Ecological significance of seed desiccation sensitivity ináQuercus ilex	Annals of Botany	111	4	693-701
55	Jung, Vincent	2014	Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events	Journal of Ecology	102	1	45-53
56	Keenan, Trevor F.	2013	Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise	Nature	499	7458	324-327
57	Kerr, K. L.	2015	Expression of functional traits during seedling establishment in two populations of Pinus ponderosa from contrasting climates	Tree Physiology	35	5	535-548
58	Keuper, Frida	2012	A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands	Global Change Biology	18	6	1998-2007
59	Kimball, Sarah	2016	Can functional traits predict plant community response to global change?	Ecosphere	7	12	
60	Klady, Rebecca A.	2011	Changes in high arctic tundra plant reproduction in response to long-term experimental warming	Global Change Biology	17	4	1611-1624
61	Koller, Eva K.	2016	Tight Coupling Between Shoot Level Foliar N and P, Leaf Area, and Shoot Growth in Arctic Dwarf Shrubs Under Simulated Climate Change	Ecosystems	19	2	326-338
62	Kornfeld, Ari	2013	Respiratory flexibility and efficiency are affected by simulated global change in Arctic plants.	New Phytologist	197	4	1161-1172
63	Kremers, Kelseyann S.	2015	Diminished Response of Arctic Plants to Warming over Time	PLOS ONE	10	3	e0116586
64	Kumagai, Tomo'Omi	2012	Strategies of a Bornean tropical rainforest water use as a function of rainfall regime: isohydric or anisohydric?	Plant, Cell & Environment	35	1	61-71
65	Kushwaha, Chandra Prakash	2010	Diversity of deciduousness and phenological traits of key Indian dry tropical forest trees	Annals of Forest Science	67	3	310-310
66	Lazaro-Nogal, A.	2013	Contrasting water strategies of two Mediterranean shrubs of limited distribution: uncertain future under a drier climate	Tree Physiology	33	12	1284-1295
67	Leigh, A.	2012	Do thick leaves avoid thermal damage in critically low wind speeds?	New Phytologist	194	2	477-487
68	Lemke, Isgard H.	2015	Patterns of phenotypic trait variation in two temperate forest herbs along a broad climatic gradient	Plant Ecology	216	11	1523-1536
69	Lewis, J. D.	2011	Leaf photosynthesis, respiration and stomatal conductance in six Eucalyptus species native to mesic and xeric environments growing in a common garden	Tree Physiology	31	9	997-1006
70	Li, Shaowei	2016	Community assembly and functional leaf traits mediate precipitation use efficiency of alpine grasslands along environmental gradients on the Tibetan Plateau	PeerJ	4		e2680
71	Li, Hongbo	2017	Diverse belowground resource strategies underlie plant species coexistence and spatial distribution in three grasslands along a precipitation gradient	New Phytologist	216	4	1140-1150

72	Li, Man	2017	Scaling relationships of twig biomass allocation in Pinus hwangshanensis along an altitudinal gradient	PLOS ONE	12	5	e0178344
73	Limousin, J. M.	2009	Long-term transpiration change with rainfall decline in a MediterraneanáQuercus ilexáforest	Global Change Biology	15	9	2163-2175
74	Limousin, J.-M.	2010	Change in hydraulic traits of MediterraneanáQuercus ilexásubjected to long-term throughfall exclusion	Tree Physiology	30	8	1026-1036
75	Lopez-Iglesias, Bárbara	2014	Functional traits predict drought performance and distribution of Mediterranean woody species	Acta Oecologica	56		10-18
76	Lu, Weizhi	2013	Effects of sea level rise on mangrove Avicennia population growth,colonization and establishment: Evidence from a field survey andgreenhouse manipulation experiment	Acta Oecologica	49		83-91
77	Luo, Wentao	2013	Patterns of Plant Biomass Allocation in Temperate Grasslands across a 2500-km Transect in Northern China	PLoS ONE	8	8	e71749
78	Markesteijn, Lars	2009	Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade tolerance	Journal of Ecology	97	2	311-325
79	Martin-StPaul, Nicolas K.	2013	The temporal response to drought in a Mediterranean evergreen tree: comparing a regional precipitation gradient and a throughfall exclusion experiment	Global Change Biology	19	8	2413-2426
80	Matteodo, Magalì	2013	Elevation gradient of successful plant traits for colonizing alpine summits under climate change	Environmental Research Letters	8	2	024043
81	Mendivelso, Hooz A.	2013	Differential Growth Responses to Water Balance of Coexisting Deciduous Tree Species Are Linked to Wood Density in a Bolivian Tropical Dry Forest	PLoS ONE	8	10	e73855
82	Meyer, Susan E.	2016	Strong genetic differentiation in the invasive annual grass Bromus tectorum across the MojaveûGreat Basin ecological transition zone	Biological Invasions	18	6	1611-1628
83	Mitchell, M. L.	2015	Use of functional traits to identify Australian forage grasses, legumes and shrubs for domestication and use in pastoral areas under a changing climate	Crop and Pasture Science	66	1	71
84	Mu, Junpeng	2013	Divergent seed production responses of white and blue flowers of Gentiana leucomelaena (Gentianaceae) to warming and watering	Plant Ecology & Diversity	6	3-4	495-501
85	Nguyen, Quynh Ngoc	2017	Intraspecific variations in drought response and fitness traits of beech (Fagus sylvatica L.) seedlings from three provenances differing in annual precipitation	Trees	31	4	1215-1225
86	Nunes, Alice	2017	Which plant traits respond to aridity? A critical step to assessfunctional diversity in Mediterranean drylands	Agricultural and Forest Meteorology	239		176-184
87	O'Brien, Michael J.	2014	Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels	Nature Climate Change	4	8	710-714
88	O'Brien, Michael J.	2017	A synthesis of tree functional traits related to drought-induced mortality in forests across climatic-zones	Journal of Applied Ecology	54	6	1669-1686
89	Onstein, Renske E.	2016	Evolutionary radiations of Proteaceae are triggered by the interaction between traits and climates in open habitats	Global Ecology and Biogeography	25	10	1239-1251
90	Osland, Michael J.	2015	Life stage influences the resistence and resilience of black mangrove forests to winter climate extremes	Ecosphere	6	9	art160

91	Ospina, Sonia	2017	Community aggregated traits disclose functional responses to seasonal resource fluctuations and spatial heterogeneity	Journal of Vegetation Science	28	2	291-302
92	Ouédraogo, Dakis-Yaoba	2013	Slow-growing species cope best with drought: evidence from long-term measurements in a tropical semi-deciduous moist forest of Central Africa	Journal of Ecology	101	6	1459-1470
93	Oyarzabal, Mariano	2008	Trait differences between grass species along a climatic gradient in South and North America	Journal of Vegetation Science	19	2	183-192
94	Parolari, Anthony J.	2015	Ecohydrological controls on grass and shrub above-ground net primary productivity in a seasonally dry climate	Ecohydrology	8	8	1572-1583
95	Parra, Antonio	2017	Post-fire environments are favourable for plant functioning ofseeder and resprouter Mediterranean shrubs, even underdrought	New Phytologist	214	3	1118-1131
96	Pasturel, Marine	2016	Grass Physiognomic Trait Variation in African Herbaceous Biomes	Biotropica	48	3	311-320
97	Arrivabene, Hiulana Pereira	2014	Functional traits of selected mangrove species in Brazil as biological indicators of different environmental conditions	Science of The Total Environment	476-477		496-504
98	Pivovaroff, Alexandria L.	2016	Multiple strategies for drought survival among woody plant species	Functional Ecology	30	4	517-526
99	Pohlman, Catherine L.	2008	Effects of Severe Tropical Cyclone Larry on rainforest vegetation and understorey microclimate near a road, powerline and stream	Austral Ecology	33	4	503-515
100	Polley, H. W.	2014	Impacts of climate change drivers on C4 grassland productivity: scaling driver effects through the plant community	Journal of Experimental Botany	65	13	3415-3424
101	Powell, Thomas L.	2017	Differences in xylem and leaf hydraulic traits explain differences in drought tolerance among mature Amazon rainforest trees	Global Change Biology	23	10	4280-4293
102	Ratcliffe, Sophia	2016	Modes of functional biodiversity control on tree productivity across the European continent	Global Ecology and Biogeography	25	3	251-262
103	Ribeiro, Leandro C.	2015	The importance of seed mass for the tolerance to heat shocks of savanna and forest tree species	Journal of Vegetation Science	26	6	1102-1111
104	Ribeiro, Priciane C.	2016	Climate drivers of leaf traits and genetic divergence in the tree Annona crassiflora: a broad spatial survey in the Brazilian savannas	Global Change Biology	22	11	3789-3803
105	Richardson, Sarah J.	2015	Functional and environmental determinants of bark thickness in fire-free temperate rain forest communities	American Journal of Botany	102	10	1590-1598
106	Rosado, Bruno H. P.	2016	Changes in plant functional traits and water use in Atlantic rainforest: evidence of conservative water use in spatio-temporal scales	Trees	30	1	47-61
107	Rueda, Marta	2017	Spatial and evolutionary parallelism between shade and drought tolerance explains the distributions of conifers in the conterminous United States	Global Ecology and Biogeography	26	1	31-42
108	Russell-Smith, Jeremy	2012	Fire persistence traits can be used to predict vegetation response to changing fire regimes at expansive landscape scales – an Australian example	Journal of Biogeography	39	9	1657-1668
109	Sakschewski, Boris	2016	Resilience of Amazon forests emerges from plant trait diversity	Nature Climate Change	6	11	1032-1036
110	Sánchez-Pinillos, Martina	2016	Assessing the persistence capacity of communities facing natural disturbances on the basis of species response traits	Ecological Indicators	66		76-85

111	Sandel, Brody	2012	Climate change and the invasion of California by grasses	Global Change Biology	18	1	277-289
112	Sayer, Emma J.	2017	Links between soil microbial communities and plant traits in a species-rich grassland under long-term climate change	Ecology and Evolution	7	3	855-862
113	Schreiber, Stefan G.	2011	Genetic variation of hydraulic and wood anatomical traits in hybrid poplar and trembling aspen	New Phytologist	190	1	150-160
114	Schreiber, Stefan G.	2015	Variation of xylem vessel diameters across a climate gradient: insight from a reciprocal transplant experiment with a widespread boreal tree	Functional Ecology	29	11	1392-1401
115	Sendall, Kerrie M.	2015	Acclimation of photosynthetic temperature optima of temperate and boreal tree species in response to experimental forest warming	Global Change Biology	21	3	1342-1357
116	Slot, Martijn	2007	Diversity of Tropical Tree Seedling Responses to Drought	Biotropica	39	6	683-690
117	Song, Lu-lu	2012	Adaptive characteristics of grassland community structure and leaf traits along an altitudinal gradient on a subtropical mountain in Chongqing, China	Plant Ecology	213	1	89-101
118	Soudzilovskaia, N. A.	2013	Functional traits predict relationship between plant abundance dynamic and long-term climate warming	Proceedings of the National Academy of Sciences	110	45	18180-18184
119	Stevens, Jens T.	2015	Forest disturbance accelerates thermophilization of understory plant communities	Journal of Ecology	103	5	1253-1263
120	Stromberg, Juliet C.	2016	Riparian plant guilds of ephemeral, intermittent and perennial rivers	Freshwater Biology	61	8	1259-1275
121	Su, Wen-Hua	2015	The role of fire in the Central Yunnan Plateau ecosystem, southwestern China	Forest Ecology and Management	356		22-30
122	Sundqvist, Maja K.	2011	Within- and Across-Species Responses of Plant Traits and Litter Decomposition to Elevation across Contrasting Vegetation Types in Subarctic Tundra	PLoS ONE	6	10	e27056
123	Tardella, Federico M.	2016	Environmental gradients and grassland trait variation: Insight into the effects of climate change	Acta Oecologica	76		47-60
124	Tavşanoğlu, Çağatay	2014	Long-term post-fire dynamics of co-occurring woody species in Pinus brutia forests: the role of regeneration mode	Plant Ecology	215	3	355-365
125	Tian, Y	2014	Effects of morphological adjustment on establishment of Haloxylon ammodendron	Chinese Journal of Ecology	33	5	1164-1169
126	Tian, Miao	2016	Leaf morphological and anatomical traits from tropical to temperate coniferous forests: Mechanisms and influencing factors	Scientific Reports	6	1	19703
127	Uriarte, María	2016	A trait-mediated, neighbourhood approach to quantify climate impacts on successional dynamics of tropical rainforests	Functional Ecology	30	2	157-167
128	van de Weg, Martine J.	2013	Response of dark respiration to temperature in Eriophorum vaginatum from a 30 year old transplant experiment in Alaska	Plant Ecology & Diversity	6	3-4	377-381
129	VanderWeide, Benjamin L.	2014	Belowground bud banks of tallgrass prairie are insensitive to multi-year, growing-season drought	Ecosphere	5	8	art103-art103
130	Vetaas, Ole R.	2012	Vegetation changes in the Red Sea Hills: from mist oasis to arid shrub	Plant Ecology & Diversity	5	4	527-539
131	Vico, Giulia	2017	How competitive is drought deciduousness in tropical forests? A combined eco-hydrological and eco-evolutionary approach	Environmental Research Letters	12	6	065006

132	Villagra, Pablo E	2011	To be a plant in the desert: water use strategies and water stress resistance in the Central Monte desert from Argentina [Ser planta en el desierto: Estrategias de uso de agua y resistencia al estrés hídrico en el Monte Central de Argentina]	Ecologia Austral	21	1	29-42
133	Volaire, Florence	2014	Designing resilient and sustainable grasslands for a drier future: Adaptive strategies, functional traits and biotic interactions	European Journal of Agronomy	52		81-89
134	Wada, Naoya	2008	Ecology of Dryas octopetala sensu lato, a relict plant in the Tateyama Mountains in the North Alps of Japan:Comparison between mid-latitude alpine and arctic tundra populations.	Japanese Journal of Ecology	58	3	205-212
135	Wang, Ruili	2015	Latitudinal variation of leaf stomatal traits from species to community level in forests: linkage with ecosystem productivity	Scientific Reports	5	1	14454
136	Wang, Ruili	2016	Latitudinal patterns and influencing factors of leaf functional traits in Chinese forest ecosystems	Journal of Geographical Sciences	26	1	15-26
137	West, A. G.	2012	Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa	New Phytologist	195	2	396-407
138	Wu, Jianbo	2013	Biomass Partitioning and Its Relationship with the Environmental Factors at the Alpine Steppe in Northern Tibet	PLoS ONE	8	12	e81986
139	Xie, Jiang-Bo	2015	Apparent plasticity in functional traits determining competitive ability and spatial distribution: a case from desert	Scientific Reports	5	1	12174
140	Xu, Gui-Qing	2016	A possible link between life and death of a xeric tree in desert	Journal of Plant Physiology	194		35-44
141	Yang, Haijun	2011	Plant community responses to nitrogen addition and increased precipitation: the importance of water availability and species traits	Global Change Biology	17	9	2936-2944
142	Yang, Yan	2012	Effects of drought and nitrogen addition on photosynthetic characteristics and resource allocation of Abies fabri seedlings in eastern Tibetan Plateau	New Forests	43	4	505-518
143	Yates, Megan J.	2010	Ecophysiological significance of leaf size variation in Proteaceae from the Cape Floristic Region	Functional Ecology	24	3	485-492
144	Yu, Zhen	2017	Global gross primary productivity and water use efficiency changes under drought stress	Environmental Research Letters	12	1	014016
145	Zamin, Tara J.	2014	Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low arctic tundra	Journal of Ecology	102	3	749-766
146	Zhou, Guoyi	2013	A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China	Global Change Biology	19	4	1197-1210
147	Zhu, Qing	2016	Root traits explain observed tundra vegetation nitrogen uptake patterns: Implications for trait-based land models	Journal of Geophysical Research: Biogeosciences	121	12	3101-3112
148	Zwicke, Marine	2015	What functional strategies drive drought survival and recovery of perennialspecies from upland grassland?	Annals of Botany	116	6	1001-1015

Table S2 List of positive plant responses (fitness surrogates) to climate/environmental change mediated by traits that were found in our data-synthesis based on a global systematic review of literature.

fitness category	fitness surrogate
plant survival	delayed mortality
	stress tolerance
	survival
reproductive output	enhanced reproductive effort
	propagule rain
	recruitment
	seed germination
	seed size
vegetative biomass	abundance (community)
	abundance (individuals)
	abundance (population)
	abundance (species)
	biomass (community)
	biomass (individuals)
	community dominant trait
	community mean trait
	community-weighted mean trait
	distribution range
	dominance (individuals)

	growth (based on allometric measurements)
	growth (ecosystem carbon)
	growth (long-term)
	growth (biomass)
	growth (diameter)
	net carbon gain
	nitrogen uptake capacity
	photosynthetic performance
	population mean traits
	primary productivity (ecosystem)
	primary productivity (gross)
	primary productivity (net)
	vegetation cover (community)
	vegetation cover (individuals)
	vegetation cover (spatial)
	vegetation cover (species)
	zone mean trait

Table S3 List of 101 traits found in studies (2007-2017) that are associated with a positive plant response to climate/environmental change. TOP ID from http://top-thesaurus.org/home (Garnier et al. 2017) and "x" indicates the trait is described in Pérez-Harguindeguy et al. (2013).

Group	trait name	short trait name	TOP ID	Perez 2013
whole-plant traits	above ground biomass	AG biomass		
	branching architecture	branching architecture	TOP140	x
	clonality, bud banks and below-ground storage organs	clon bud banks	TOP166	x
	growth form	growth form	TOP136	x
	leaf area : sapwood area ratio	LA sapwood area ratio		x
	leaf area ratio	LA ratio	TOP88	
	life form	life form	TOP210	x
	life history	life cycle		x
	maximum plant lifespan	plant lifespan	TOP255	x
	non-structural carbohydrates	non-struc carboh		
	plant height	height	TOP68	x
	plant summer dormancy	dormancy		
	relative growth rate	growth rate	TOP356	x
	root-mass fraction	root-mass fraction		x
	self-shading	self-shading		
	temperature optimum	opt temp		
	water potential regulation strategy	water pot reg strat		

	water storage capacity	water storage		
	water-use efficiency	WUE		x
leaf traits	area of a leaf	leaf area	TOP25	x
	duration of green foliage	dur. green fol.		x
	leaf area index	LAI		
	leaf area per unit stem area	LA stem area ratio		
	leaf calcium concentration	leaf Ca conc	TOP470	
	leaf carbon (c) concentration	leaf C	TOP471	
	leaf cell soluble sugar content	leaf sol sugar		
	leaf compoundness	leaf compoundness	TOP222	x
	leaf dry-matter content	leaf dry matter	TOP45	x
	leaf hydraulic conductance	leaf hydaul cond		
	leaf lifespan	leaf lifespan	TOP254	x
	leaf magnesium concentration	leaf Mg	TOP476	
	leaf mass ratio	leaf mass ratio	TOP85	
	leaf nitrogen (n) concentration	leaf N	TOP481	x
	leaf nitrogen:phosphorus ratio	leaf N P ratio		x
	leaf palatability as indicated by preference by model herbivores	palatability		x
	leaf phenology	leaf phenol	TOP700	
	leaf phosphorous (p) concentration	leaf P	TOP482	x

	leaf potassium (k) concentration	leaf K	TOP483	x
	leaf proline accumulation	leaf proline		
	leaf shape	leaf shape		
	leaf size	leaf size		
	leaf thickness	leaf thickness	TOP20	x
	leaf vessel diameter	leaf vessel diam		
	leaf water potential as a measure of water status	leaf water pot		x
	light-use efficiency	light-u eff		
	number of leaves	numb leaves		
	palisade-leaf mesophyll thickness ratio	palisade-leaf:mesophyll thickness		
	photosynthetic pathway	photos path		x
	rate of photosynthesis	photosynt rate	TOP357	x
	specific leaf area (area/dry mass)	SLA	TOP50	x
	stomatal conductance	stomatal conduct	TOP367	
	stomatal density	stomatal dens	TOP370	
	stomatal index	stomatal index		
stem traits	bark thickness (and bark quality)	bark thickness	TOP283	x
	photosynthetic stems	photosynt stems	TOP360	
	sapwood area	sapwood area		x
	stem diameter/tree diameter	stem tree diam		
	stem-specific density/wood density	wood density	TOP286	x

	vessel diameter	vessel diam		
	vulnerability to embolism	vuln embolism		x
	xylem/sapwood conductivity	xylem conduct		x
below-ground traits	below-ground biomass	BG biomass		
	fine root system	fine roots		
	lateral root length	lat root length		
	nutrient-uptake strategy	nutrient uptake		x
	rhizosheath development	rhizosheath		
	root branching intensity	root branching		
	root density	root density		
	root diameter	root diam	TOP944	x
	root dry matter content	RDMC		
	root lateral extent	root lat extent		x
	root lifespan	root lifespan		
	root nitrogen concentration	root N		
	root tissue density	RTD		x
	root water content	root water		
	root:shoot ratio	root shoot ratio		
	rooting depth	root depth		x
	specific root length (root length/dry mass of fine roots)	SRL	TOP935	x
regenerative traits	dispersal potential	disp potential		x
	dispersal syndrome	disp syndrome	TOP346	x
	dispersule size	disp size	TOP102	x
	neonatal biomass	neonatal biomass		
	resprouting capacity after major disturbance	resprouting		x
	seed appendages/morphology	seed append		

	seed banks	seed banks		
	seed germination	seed germ		
	seed mass	seed mass	TOP103	x
	seed water content	seed water content		
	serotiny	serotiny		
flowering traits	bud number	bud number		
	flower colour	flower colour	TOP242	
	flower pollination syndrom	pollination synd.	TOP333	x
	flowering duration	flowering duration		
	inflorescence type	inflor type		
	onset of flowering	onset flower		
	vernalization	vernalization		
other traits	acclimation of photosynthesis temperature optimum	acclimation photosynthesis		
	cytochrome pathway activity	cytochrome pathway		
	photosynthetic nitrogen-use efficiency	N use efficiency		
	saturated osmotic potential	sat osm pot		
	shade tolerance	shade tol		

Table S4: Proportion of positive records out of the total number of records (positive + null) for each trait group considered in the data-synthesis based on the global systematic literature review identifying traits that mediate positive responses to climate change.

trait group	% positive records	total number records
leaf	67	247
whole-plant	82	134
below-ground	83	76
regenerative	84	56
stem	73	56
flower	63	16
other	69	13

Table S5: Trait scoring calculated from the proportion of biomes (n=12) and climate/environmental changes (n=6) where a trait was associated with a positive plant response, weighted by the proportion of positive records out of total records (positive + null).

trait group	trait	score	proportion positive records	proportion biomes	proportion environmental drivers
leaf	Specific leaf area (area/dry mass)	0.78	0.78	1	1
whole-plant	Plant height	0.606	0.73	0.83	0.83
whole-plant	water-use efficiency	0.606	0.91	0.83	0.5
regenerative	Resprouting capacity after major disturbance	0.583	1	0.5	0.67
whole-plant	Relative growth rate	0.583	1	0.67	0.5
whole-plant	Clonality, bud banks and below-ground storage organs	0.576	0.81	0.58	0.83

stem	Stem-specific density/wood density	0.571	0.86	0.67	0.67
below-ground	rooting depth	0.567	0.8	0.58	0.83
regenerative	Dispersule size	0.417	1	0.33	0.5
leaf	Leaf dry-matter content	0.409	0.82	0.67	0.33
below-ground	root:shoot ratio	0.4	0.8	0.5	0.5
leaf	duration of green foliage	0.37	0.89	0.5	0.33
regenerative	seed banks	0.344	0.75	0.25	0.67
leaf	Leaf size	0.333	0.67	0.5	0.5
whole-plant	Life form	0.328	0.88	0.25	0.5
leaf	Leaf thickness	0.327	0.79	0.5	0.33
leaf	stomatal conductance	0.321	0.77	0.5	0.33
leaf	Leaf nitrogen (N) concentration	0.303	0.52	0.67	0.5
stem	Bark thickness (and bark quality)	0.292	1	0.25	0.33
leaf	Area of a leaf	0.289	0.53	0.58	0.5
stem	Vulnerability to embolism	0.267	0.8	0.5	0.17
below-ground	Specific root length (root length/dry mass of fine roots)	0.265	0.91	0.25	0.33
leaf	Leaf water potential as a measure of water status	0.259	0.78	0.5	0.17
other	acclimation of photosynthesis temperature optimum	0.25	1	0.17	0.33
whole-plant	leaf area ratio	0.25	1	0.17	0.33

below-ground	root density	0.25	1	0.17	0.33
leaf	leaf calcium concentration	0.25	1	0.17	0.33
leaf	leaf vessel diameter	0.25	1	0.17	0.33
leaf	number of leaves	0.25	1	0.17	0.33
leaf	rate of photosynthesis	0.25	1	0.17	0.33
regenerative	neonatal biomass	0.25	1	0.17	0.33
stem	stem diameter/tree diameter	0.25	1	0.17	0.33
whole-plant	life history	0.25	1	0.17	0.33
regenerative	Dispersal syndrome	0.233	0.8	0.25	0.33
whole-plant	Root-mass fraction	0.233	0.8	0.25	0.33
whole-plant	water storage capacity	0.208	0.83	0.33	0.17
regenerative	serotiny	0.208	1	0.25	0.17
whole-plant	water potential regulation strategy	0.208	1	0.25	0.17
below-ground	root branching intensity	0.208	1	0.25	0.17
other	photosynthetic nitrogen-use efficiency	0.208	1	0.25	0.17
whole-plant	Growth form	0.2	0.8	0.17	0.33
leaf	leaf phenology	0.188	0.75	0.17	0.33
whole-plant	Maximum plant lifespan	0.188	0.75	0.17	0.33
leaf	leaf phosphorous (P) concentration	0.175	0.6	0.25	0.33

below-ground	root water content	0.167	1	0.17	0.17
below-ground	lateral root length	0.167	1	0.17	0.17
leaf	leaf nitrogen:phosphorus ratio	0.167	1	0.17	0.17
whole-plant	Branching architecture	0.167	1	0.17	0.17
leaf	leaf area index	0.167	0.67	0.17	0.33
leaf	Leaf potassium (K) concentration	0.167	0.67	0.17	0.33
regenerative	Seed mass	0.146	0.5	0.25	0.33
flowering	Onset of flowering	0.146	0.5	0.25	0.33
whole-plant	non-structural carbohydrates	0.139	0.67	0.08	0.33
below-ground	fine root system	0.125	0.75	0.17	0.17
leaf	leaf mass ratio	0.125	1	0.08	0.17
whole-plant	plant summer dormancy	0.125	1	0.08	0.17
leaf	Leaf lifespan	0.125	0.5	0.17	0.33
below-ground	below-ground biomass	0.125	1	0.08	0.17
below-ground	Nutrient-uptake strategy	0.125	1	0.08	0.17
below-ground	rhizosheath development	0.125	1	0.08	0.17
below-ground	root dry matter content	0.125	1	0.08	0.17
below-ground	root lateral extent	0.125	1	0.08	0.17
below-ground	root lifespan	0.125	1	0.08	0.17

below-ground	root tissue density	0.125	1	0.08	0.17
flowering	Bud number	0.125	1	0.08	0.17
flowering	Flower colour	0.125	1	0.08	0.17
flowering	Inflorescence type	0.125	1	0.08	0.17
flowering	vernalization	0.125	1	0.08	0.17
leaf	leaf area per unit stem area	0.125	1	0.08	0.17
leaf	leaf cell soluble sugar content	0.125	1	0.08	0.17
leaf	leaf compoundness	0.125	1	0.08	0.17
leaf	leaf proline accumulation	0.125	1	0.08	0.17
leaf	leaf shape	0.125	1	0.08	0.17
leaf	light-use efficiency	0.125	1	0.08	0.17
other	Cytochrome pathway activity	0.125	1	0.08	0.17
other	saturated osmotic potential	0.125	1	0.08	0.17
other	shade tolerance	0.125	1	0.08	0.17
regenerative	seed appendages/morphology	0.125	1	0.08	0.17
regenerative	seed germination	0.125	1	0.08	0.17
regenerative	seed water content	0.125	1	0.08	0.17
stem	photosynthetic stems	0.125	1	0.08	0.17
stem	sapwood area	0.125	1	0.08	0.17

whole-plant	self-shading	0.125	1	0.08	0.17
whole-plant	temperature optimum	0.125	1	0.08	0.17
leaf	Leaf carbon (C) concentration	0.125	0.6	0.25	0.17
leaf	leaf hydraulic conductance	0.125	0.43	0.25	0.33
stem	Xylem/sapwood conductivity	0.111	0.44	0.33	0.17
leaf	Photosynthetic pathway	0.104	0.5	0.08	0.33
below-ground	root diameter	0.083	0.67	0.08	0.17
flowering	Flowering duration	0.083	0.5	0.17	0.17
below-ground	root nitrogen concentration	0.063	0.5	0.08	0.17
flowering	flower pollination syndrom	0.063	0.5	0.08	0.17
leaf	leaf magnesium concentration	0.063	0.5	0.08	0.17
leaf	Leaf palatability as indicated by preference by model herbivores	0.063	0.5	0.08	0.17
leaf	palisade-leaf mesophyll thickness ratio	0.063	0.5	0.08	0.17
regenerative	Dispersal potential	0.063	0.5	0.08	0.17
whole-plant	Above ground biomass	0.063	0.5	0.08	0.17
leaf	stomatal index	0.042	0.33	0.08	0.17
whole-plant	Leaf area : sapwood area ratio	0.042	0.33	0.08	0.17
leaf	stomatal density	0.031	0.25	0.08	0.17
stem	vessel diameter	0.031	0.25	0.08	0.17

Table S6: Global trait observations and ranking of our top 8 traits in terms of total trait observations and number of species with trait observations. Two of our 8 top traits are considered within the top 10 traits collected out of 2087 traits in the TRY database (Kattge et al. 2011).

Trait	TRY rank (trait observations)	TRY Trait observations	TRY rank (number of species with trait observations)	TRY species with trait observations
specific leaf area	15	146 315	24	13 101
plant height	4	249 551	9	28 944
wood density	5	231 503	4	79 298
rooting depth	157	10 106	95	3 886
Water-use-efficiency	445	1516	520	217
resprouting capacity	99	18674	17	15 997
clonality, bud banks and belowground storage (Plant vegetative reproduction)	363	2545	218	1 822
relative growth rate	230	5772	299	879

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CHAPTER 5 (RESEARCH PAPER 2): DEEPER ROOT TO SURVIVE DRIER CLIMATES? A CASE STUDY IN THE CAPE FLORISTIC REGION

By Nicola Kühn, Carolina Tovar, Kathy Willis, and Marc Macias-Fauria


Photo: Nicola Kühn

Linking statement: The research approach of the second paper of this thesis (**Chapter 5 (Research Paper 2)**) was inspired by the lack of root-focused studies despite the observed importance of root traits in determining response to climate change identified in the first paper of this research (**Chapter 4 (Research Paper 1)**). This was particularly evident for African drylands. The following chapter therefore presents results from a field study that collected root (and aboveground) trait data to analyse how traits vary across multiple scales pertaining to water limitation (including across a regional precipitation gradient and along local topography) in the semi-arid Fynbos biome of South Africa. The research presented in this chapter has been submitted to the *Journal of Vegetation Science*.

Author contribution statement: NK and MM-F conceptualised the research and designed the approach with comments from CT and KJW. NK conducted the fieldwork to collect the data. NK analysed the data with assistance from MMF and CT. NK wrote the manuscript with significant contributions from all authors (MM-F, CT, KJW).

ABSTRACT

1. Roots are responsible for essential plant functions including water uptake. However, the extent to which root traits (size and structure) determine plant presence in water-limited environments is still poorly understood. Here we analysed root variation across water availability gradients within a dry South African biome.
2. We measured 6 belowground (root) and 8 aboveground (leaf+stem) traits of 124 individuals of nine dominant woody shrub species from wetter and drier sites (600-700 *vs.* 250-300mm annual precipitation) in the Fynbos biome of the Cape Floristic Region. Within sites, we sampled from recently burnt and unburnt/more mature vegetation and at three locations along topographical gradients.
3. Drier regions showed greater maximum rooting depth, length, root dry matter content and root:shoot ratio. These trait patterns were consistent at an intraspecific level, along locally drier topographical locations and in post-fire environments.
4. Roots accounted for significant whole-plant trait variation and significantly, in drier conditions, increased root allocation (at the expense of shoot allocation) deviated from expected global allometric relationships.
5. Our study also demonstrates that the combination of fire and drought on root systems in the drier site results in poor vegetation recovery in terms of plant size and cover – a finding that raises concern for future Fynbos resilience, particularly at its arid limits.
6. *Synthesis:* Our results reveal that at drier sites within a biome, roots are not only deeper, but also longer, thicker, and more invested-in as compared with shoots. This is consistent across scales of water availability generated by regional precipitation gradients and local topographical gradients, as well as in post-fire conditions and within individuals of the same species. Our research suggests that root investment will be especially crucial for survival in a drier and warmer future and should be a focus of more research for global drylands.

Key words: biomass allocation, environmental gradient, Fynbos, Mediterranean, plant strategies, roots, plant functional traits, water-limited

5.1 INTRODUCTION

It has long been recognised that specific root traits such as rooting-depth, may be critical to the survival of plants in water-stressed environments. Roots play a vital role in plant functioning, including water and nutrient uptake, resprouting capacity, and anchorage (Jackson *et al.*, 1999; Pérez-Harguindeguy *et al.*, 2013). They also contribute substantially to nutrient, carbon and water dynamics (Bardgett *et al.*, 2014) and are essential in the maintenance of ecosystem function under decreasing or variable precipitation conditions (Jackson *et al.*, 1996; Maeght *et al.*, 2013).

Although there have been some recent efforts to address root-trait-environment relationships through collation and expansion of root trait data (Kattge *et al.*, 2011; Iversen *et al.*, 2017; Laliberté, 2017; Guerrero-Ramírez *et al.*, 2021), a significant gap remains in terms of understanding how roots vary along climatic and environmental gradients and how root trait variation influences performance in water-limited environments (Funk *et al.*, 2021). This is in direct contrast to aboveground traits – where trait variation has been studied at global to local scale (Díaz *et al.*, 2016), in dry environments (Le Bagousse-Pinguet *et al.*, 2017), along water and/or other environmental gradients (Ackerly, 2004; Thuiller *et al.*, 2004) and at the intraspecific level (Carlson *et al.*, 2016). This knowledge gap associated with root traits is largely due to the difficulty in measuring them (Iversen *et al.*, 2017; Laliberté, 2017) which normally involves labour and time-intensive excavation of root systems.

At a global scale, it has been demonstrated that plants in semi-arid ecosystems tend to have deeper roots (Schenk & Jackson, 2002a, 2005), reflecting a tendency in water-limited ecosystems for plants to access water that was stored at depth during occasional or seasonal wet periods (Schenk & Jackson, 2002a; Fort *et al.*, 2017). However, what is still not well understood is whether trait variation occurs across a water availability gradient within a dry biome. Further, topography can alter moisture availability within a landscape, potentially compounding or cancelling larger scale (regional) water availability effects. For example, does growing at a wetter location of a drier site (i.e., a valley) cancel out the effects of being in drier conditions generally and vice versa in a drier (upper slope) location of a wetter site? Topography has indeed been linked to changes in rooting depth at a global scale (Fan *et al.*, 2017), however it is seldom explicitly considered in regional or local gradient studies.

Disturbances such as fire are also known to influence trait values in a region/landscape (Díaz *et al.*, 1999; McIntyre *et al.*, 1999). Fire-prone biomes tend to have a suite of fire trait attributes adapted to cope with this disturbance, including: deeper roots (Hollingsworth *et al.*, 2013; Aubin *et al.*, 2016), greater resprouting capacity (Clarke *et al.*, 2013, 2015; Hollingsworth *et al.*, 2013; Tavşanoğlu & Gürkan, 2014), greater bark thickness (Aubin *et al.*, 2016), and greater seed storage abilities – in the canopy via serotiny (Buma *et al.*, 2013; Sánchez-Pinillos *et al.*, 2016) or in soil-stored seed banks (Hollingsworth *et al.*, 2013; Tavşanoğlu & Gürkan, 2014). However, another knowledge gap remains: how does the interaction of fire and water availability in fire-prone and dry biomes affect root-traits? This is of particular importance because, as highlighted by Enright et al. (2014), it is becoming increasingly clear that the resistance and resilience of plants to increased aridity and changes in fire regime will depend on their functional traits.

There has been some recent synthesizing work (Weigelt *et al.*, 2021) to indicate that root traits play a unique role in plant form and function globally by contributing to a size gradient where root depth characterises a unique axis of variation. We do not yet know however, whether this varies according to water availability and further, whether this alters root biomass allocation patterns in drier conditions. To address these gaps, our research study focused on the nutrient-poor, drought- and fire-adapted Fynbos biome of South Africa where we explored below and aboveground trait variation across water availability locally within a dry biome (**Fig. 5.1**). We collected trait data for 124 woody Fynbos shrubs across a regional precipitation gradient, a local topographical gradient, and in both recently burnt and older/unburnt sites. We tested the following hypotheses:

> H1. Trait variation (including intraspecific variation) exists across water availability gradients within a biome: specifically, greater root investment is more prevalent in drier conditions along gradients.
>
> H2. Dominant traits in recently burnt/younger vegetation differ from unburnt/more mature vegetation.

H3. Roots account for a significant portion of whole-plant trait variation in our study system.

H4. Belowground *vs.* aboveground investment by plants is higher in drier sites.

This paper presents the results of our study where we predicted that regional and local water availability would influence belowground traits (**Fig. 5.1**). We discuss the findings in the context of whether plants prioritize root investment over aboveground plant parts in drier conditions and what implications these results may have for a drier future predicted for the Cape Floristic Region.

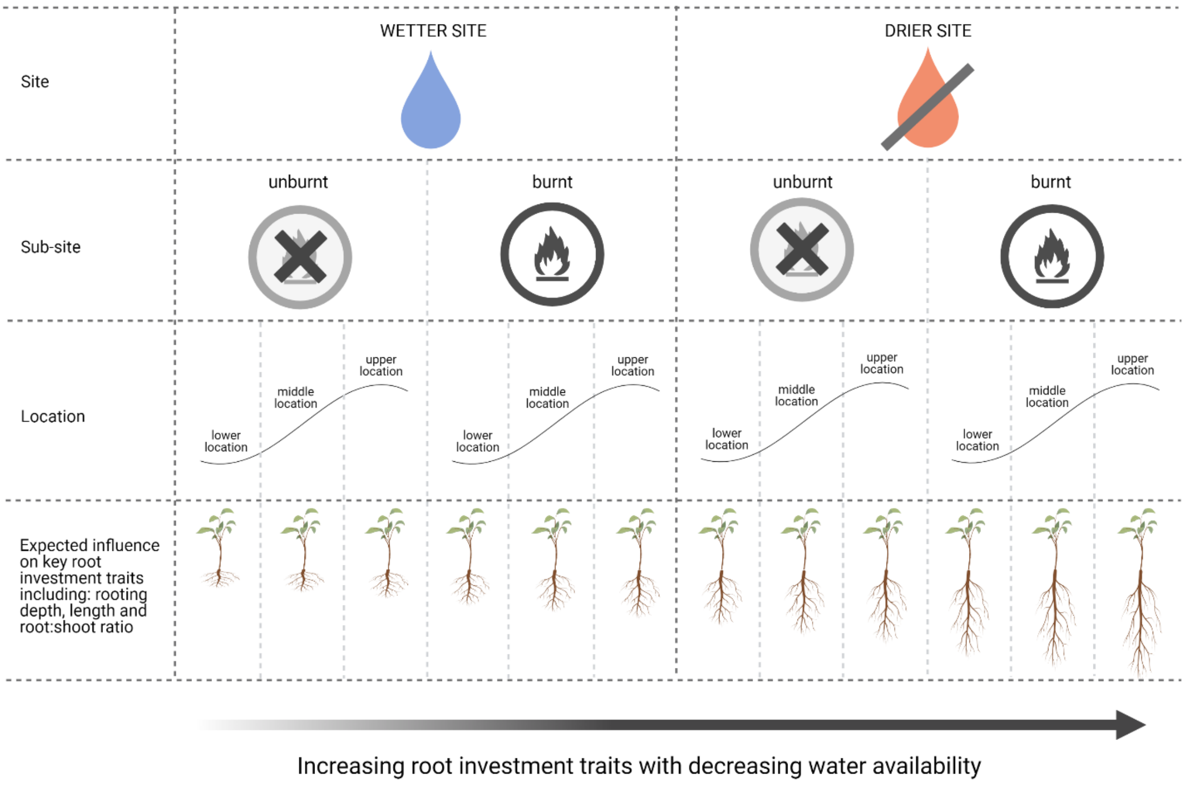

Figure 5.1: Predictive framework summarizing the expected influence of regional and local water availability gradients on root investment-related traits in Fynbos shrubs of the CFR in South Africa Source: designed in BioRender by Nicola Kühn.

5.2 METHODS

5.2.1 STUDY SITE

This study was conducted in the Fynbos biome, which falls within a temperate climatic zone and experiences a Mediterranean-type climate of cool wet winters and hot dry summers with periodic droughts and frequent fires. The vegetation is characterised by small woody shrubs (predominantly Proteaceae, Ericaceae and Restionaceae). Most of the Fynbos biome receives annual precipitation between 300mm and 2000mm. Soils in the Fynbos biome are typically acidic and nutrient poor. We sampled at two main sites along a water availability gradient (**Fig. 5.1, 5.2**).

The drier site is located at the extreme of the Fynbos biome extent, in the northern central part of the Western Cape, and borders the Nama-Karoo biome (33° 20′ 13′′ S, 20° 23′ 35′′ E). This is a high-lying region (1175–1200 m above sea level), experiencing hot, dry summers and cold (nights frequently below freezing), dry winters, with a mean annual precipitation of 250-300 mm (CapeFarmMapper v. 2.3.2.5). The Köppen-Geiger climate classification for the site is BWk (cold desert climate). Soils at this site are rocky, less than 450mm deep with less than 15% clay (CapeFarmMapper v. 2.3.2.5). The site is dominated by renosterbos or rhinoceros bush (*Dicerothamnus rhinocerotis* (L.f.) Koekemoer*,* Asteraceae family).

The wetter site, called Klapmutskop, is in the middle of the Western Cape near Stellenbosch. This lower-lying region (300 - 500m a.s.l.), experiences hot, dry summers and cool, wet winters, with mean annual precipitation of 600-700mm. The Köppen-Geiger classification for the site is CSa (hot summer Mediterranean climate). Soils at this site have a strong texture contrast, with less than 15% clay and depth between 450mm and 750mm (CapeFarmMapper v. 2.3.2.5). This site is dominated by *Seriphium plumosum L.* (Asteraceae family) and is surrounded by vineyards.

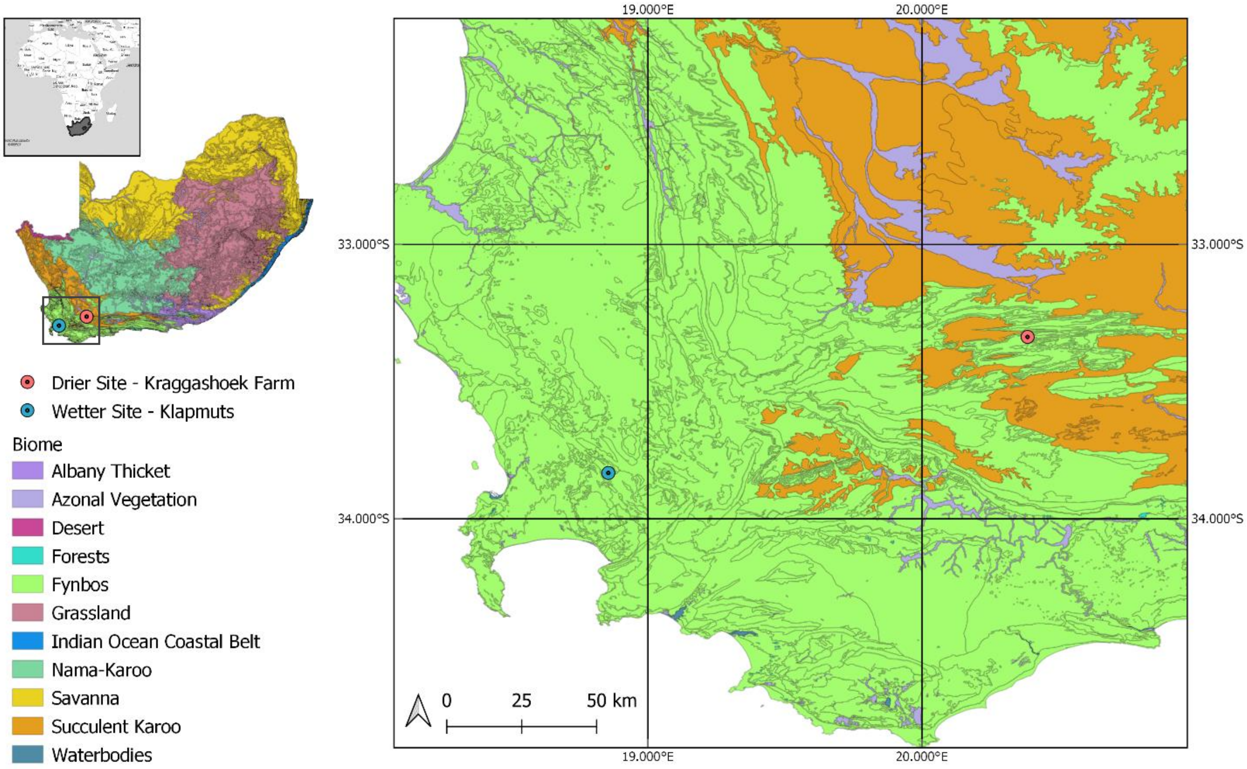

Figure 5.2: Study site location in Fynbos biome, Western Cape, South Africa.

5.2.2 SAMPLING DESIGN: SITE, SUB-SITE, AND LOCATION SELECTION

The two sites selected for this study were chosen due to their difference in rainfall. Both sites had fires in January 2016, leaving patches of *burnt* vegetation with an aboveground age of 3-4 years, and included both seedlings and resprouters. On this landscape there are also patches of vegetation burnt from previous burning episodes which consist of more mature vegetation – i.e., 8-10+ years old aboveground, referred to as *unburnt* here. The wetter site's unburnt sub-site was confirmed to be 8 years old at the time (according to the conservancy's management records), whereas the drier site had no exact fire records excepting confirmation from the landowner and surrounding farmers, that this site had not been burnt for at least the last 10 years. At both sites, we sampled in both the recently burnt and unburnt patches, and therefore ended up with four sub-sites (see **Fig. 5.1**). Within each sub-site, we sampled at three locations along a topographical gradient that were designated as upper, middle, and lower locations along a slope and were approximately 50-100 m in elevation from each other.

5.2.3 FIELD DATA COLLECTION

Fieldwork was conducted over four fieldtrips in November 2018 (late Spring-Summer), March 2019 (Summer), August 2019 (Winter) and November 2019 (late Spring-Summer).

Species Dominance survey

At each location of each sub-site, we conducted a line-intercept vegetation survey to establish the dominant species. This involved demarcating two parallel 20m line transects, 4 metres apart, to obtain a representative sample of the vegetation and reduce patch effects. Each individual plant intersecting the line was identified and the canopy width and height measured. Species canopy cover and count estimates were then calculated for each location by summing the data from the two lines per location.

Trait data collection

At each location, at least 5 individuals of the dominant species (those making up more than 70% shrub cover out of the total line transect length) were selected for sampling. In total, we excavated 124 individual plants. This was made up of ~10 individuals per location, ~30 individuals per sub-site and ~60 individuals per site. We collected 5 root traits, 1 stem trait, 1 whole plant trait, 5 leaf traits and 5 traits that comprise allocation components (**Table 5.1**). Traits were collected due to their perceived importance for coping with dry conditions, their role in determining global plant strategies (Díaz *et al.*, 2016), and their relative ease of collection.

Table 5.1: Traits selected for this study and motivation for selection

Trait chosen	Calculation if applicable	Unit	Motivation for selection	Source
Maximum rooting depth	-	cm	Established importance in drylands.	(Fort *et al.*, 2017); (Kühn et al. 2021)
Maximum root length	-	cm	To account for plants that invest in roots but not solely in terms of vertical depth.	(Fort *et al.*, 2017)
Maximum lateral root extent	-	cm	Trade-offs involving this trait proposed to optimize water acquisition and importance in dry environments.	(Schenk & Jackson, 2002b; Lynch, 2013; Li *et al.*, 2017)
Root dry matter content (RDMC)	Dry mass root / fresh mass root	g	Representation of root construction costs; it is a good proxy for root tissue density	(Birouste *et al.*, 2013)
Root diameter at origin	-	mm	Indication of size; it influences species ability to reach deeper soil layers.	(Fort *et al.*, 2017)
Stem-specific density (SSD) (also referred to as wood density)	dry mass / volume	$g.cm^{-3}$	Links with drought tolerance/avoidance strategies, and thus integral part of the Wood Economics Spectrum. Also considered a good, easily measurable proxy for other hydraulic traits.	(Chave *et al.*, 2009); (Kühn et al. 2021)
Plant height	-	cm	Established importance for plant form and function. Established importance under aridification in dry biomes.	(Díaz *et al.*, 2016); (Kühn et al. 2021)
Specific leaf area (SLA)	Leaf area / dry mass	$mm^2.mg^{-1}$ or $m^2.kg^{-1}$	Essential component of the Leaf Economics Spectrum and global spectrum of plant form and function. Established importance under aridification across biomes.	(Wright *et al.*, 2004, 2017; Díaz *et al.*, 2016); (Kühn et al. 2021)
Leaf area	Leaf length x leaf width	mm^2	Established importance for plant form and function. Established importance in dry regions.	(Wright *et al.*, 2004, 2017; Díaz *et al.*, 2016)
Leaf dimensions (length and width)	-	mm	Components of leaf area.	(Wright *et al.*, 2017)

Leaf dry matter content (LDMC)	Dry leaf mass / fresh leaf mass	g.g^{-1}	Representative of leaf construction costs and thus essential component of leaf economics spectrum.	(Garnier *et al.*, 2016)
Leaf water content (LWC)	1-LDMC	g.g^{-1}	Greater leaf water storage capacity is linked to drought tolerance.	(Vendramini *et al.*, 2002)
Leaf succulence	(Fresh mass-dry mass)/ leaf area	g.m^{-2}	Linked to drought tolerance through enhanced water storage and reduced transpiration.	(Mantovani, 1999)
Root/belowground dry mass (BGM)	-	g	For allometric analyses. Greater investment in roots supports drought tolerance.	(Markesteijn & Poorter, 2009)
Leaves dry mass	-	g		
Stems dry mass	-	g		
Aboveground mass (AGM)	Stems mass + leaves mass	g		
Aboveground volume (AGV)	(4π x canopy radius 1 x canopy radius 2 x plant height)/3	m^3		

Prior to excavation, plant height and canopy width (one perpendicular to the other) of individuals were measured. To collect sufficient trait data, individual entire plants were excavated. This involved careful attention to the root systems: the primary root system was prioritized, but the majority of the secondary systems were excavated in most cases too. Once the end of the primary root system was found, and before complete removal of the plant, soil depth, maximum rooting depth and maximum lateral rooting extent were measured.

Once excavated, a scaled photograph was taken of the whole plant including the root system. Root diameter at the origin of the root (as close as possible to the root collar), maximum primary root length and maximum root length of longest root (if different) were measured. The whole root system was refrigerated until fresh mass could be recorded. Following the methods specified by Pérez-Harguindeguy et al. (2013), one to two stem sections were collected from the base of stems where there was a relatively continuous/straight stem segment and kept refrigerated until fresh dimensions (length, diameter at three places along length of section) and fresh mass were collected. Leaf samples were collected and kept refrigerated until fresh leaf dimensions (length, width) and fresh mass were measured from five individual leaves from each of 5 branches (25 leaves per individual plant). The root system, stem sections, leaf samples and remaining aboveground material were oven-dried at 70^{o} C for 72 hours (Pérez-Harguindeguy *et al.*, 2013), after which dry mass measurements were made for leaf samples, stem sections, roots, and separately for remaining aboveground leaves and stems.

5.2.4 STATISTICAL ANALYSIS

We conducted trait-to-trait Pearson correlations (**Fig. S5.1**) to establish a subset of traits that represented unique trait variation within plant parts (roots, stems, leaves) with minimal collinearity. This resulted in inclusion of maximum root depth, root dry matter content, stem-specific density, plant height, specific leaf area and leaf dry matter content in the analysis of individual traits.

Traits across sites were compared using Welch's Two Sample t-tests which account for unequal variances. Traits across sub-sites were compared with Analysis of Variance tests and post-hoc Tukey tests.

We conducted intraspecific trait analysis on *Dicerothamnus rhinocerotis* individuals in the sub-sites where they were dominant and had the same age to account for age-related effects (wetter+burnt, drier+burnt).

To analyse whole plant trait variation, we performed a Principal Component Analysis (PCA) using the same traits selected after the correlation analysis, except for root dry matter content (RDMC), as this trait was not measured in all sub-sites. However, RDMC appears not to add significantly more variation than that already explained by SSD and LDMC (**Fig. S5.2**) for the sites in which we did have RDMC measurements. To analyse biomass allocation, linear regressions of root dry mass to aboveground dry mass (from two sub-sites) and root dry mass to aboveground volume (from three sub-sites) were run comparing the wetter and drier sites.

All analyses were run in R using base stats (R Core Team, 2013), ggbiplot (Vincent, 2019) and ggplot2 (Wickham, 2016) packages.

5.3 RESULTS

5.3.1 SPECIES DIVERSITY AND DOMINANCE

Results from the line intercept vegetation survey indicate that the greatest number of species was found in the wetter+unburnt sub-site (25 sp.), followed by the drier+burnt sub-site (21), the drier+unburnt sub-site (19) and then the wetter+burnt sub-site (9) (**Table S5.1**). Mean plant height at the drier+burnt sub-site (16.4cm) was the lowest of all sites – less than half the height of the plants in the second shortest sub-site, wetter+burnt (36.8cm), and four times shorter than the tallest sub-site, wet+unburnt (65.4cm). In the drier site, two resprouter species were overwhelmingly dominant in the middle and upper locations of the burnt sub-sites (e.g., *Aspalathus subtingens* – 79%, and *Aspalathus nigra* – 91% of total shrub cover, respectively – see **Table S5.2**), with slightly more diversity in shrub cover in the lower location. In the unburnt sub-sites and across locations, the shrub cover was dominated by the reseeder *Dicerothamnus rhinocerotis*, with a non-negligible share of resprouters (*Aspalathus spp.* and *Ruschia multiflora*).

5.3.2 TRAITS ALONG ENVIRONMENTAL GRADIENTS

Inter-site variability

All below- and aboveground traits showed significant differences between the wetter and drier sites (**Fig. 5.3**). In terms of belowground traits, maximum rooting depth, maximum rooting length and RDMC were significantly greater at the drier than at the wetter site ($p<0.01$). For aboveground traits, SLA and plant height were significantly lower and LDMC and SSD were significantly greater at the drier than at the wetter site (all $p<0.01$). Root length to shoot height ratios were significantly greater at the drier sites ($p<0.01$). All statistical results reported in **Table S5.3**.

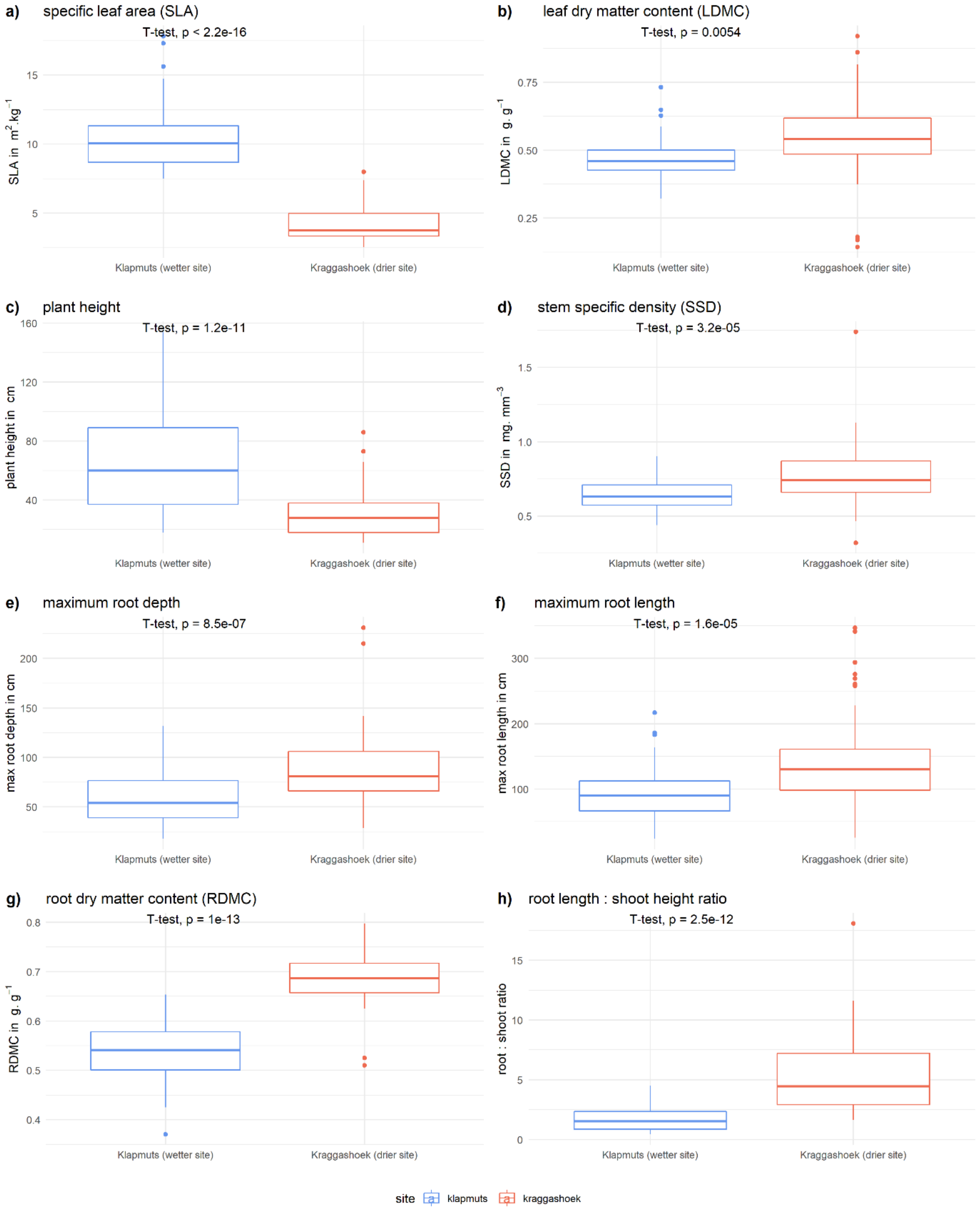

Figure 5.3: Above- and Belowground traits across the wetter (Klapmuts) and drier site (Kraggashoek). See supplementary Fig. S3 for all other traits. Significant differences were tested using Welch's Two Sample t-tests (see Table S5.3 for details).

Intraspecific variation in wetter vs drier sites

Individuals of *Dicerothamnus rhinocerotis* also showed significant differences in trait values between wetter and drier sites for four out of six measured traits (in burnt sites, see methods) (**Fig. 5.4**). With respect to belowground traits, root depth to shoot height ratio and RDMC were found to be significantly greater at the drier site, whereas maximum root depth and maximum root length showed no significant differences. In terms of aboveground traits, SLA and plant height were significantly lower, and LDMC and leaf area significantly greater, at the drier site. SSD was not found to differ significantly across any sub-site.

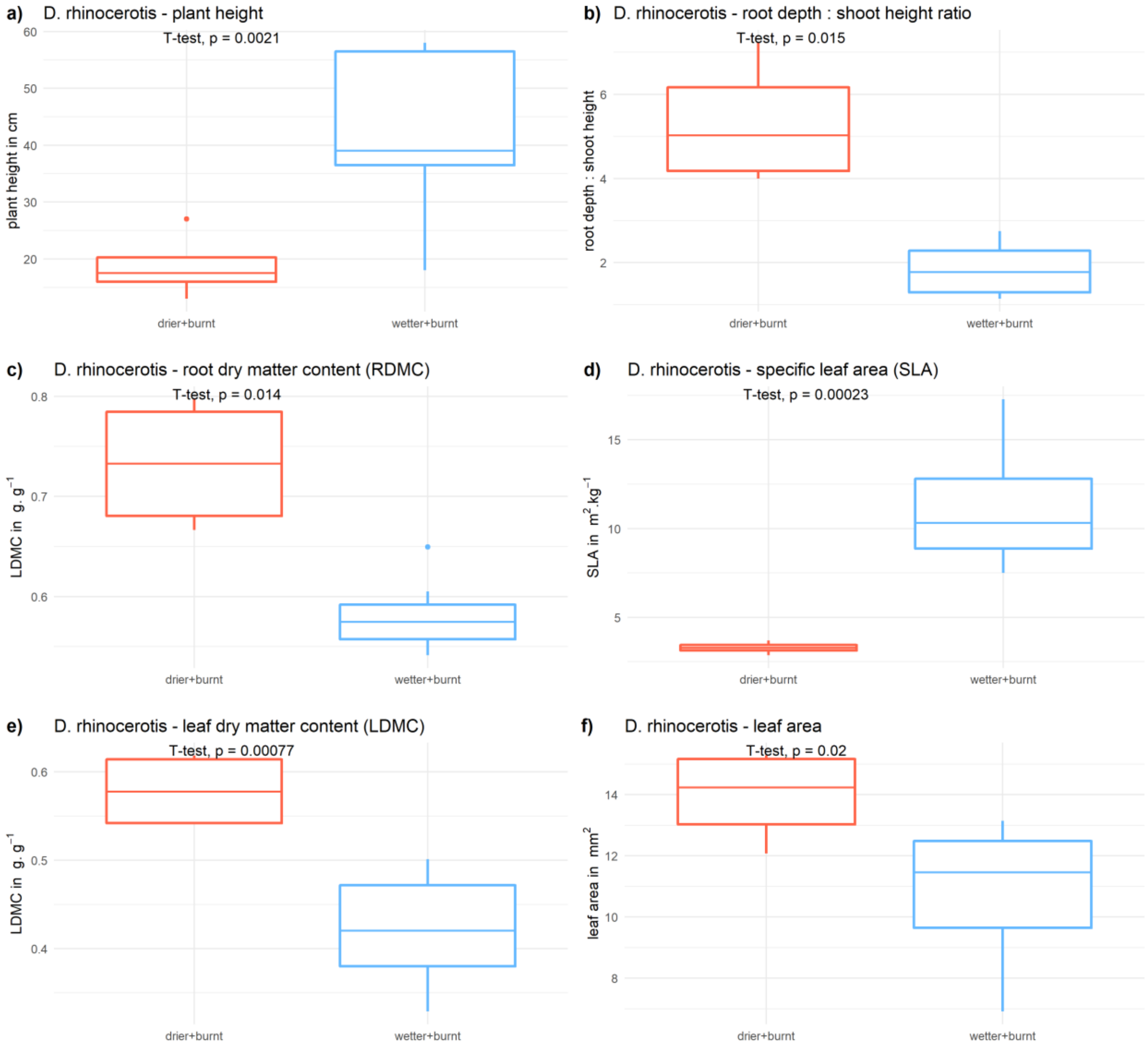

Figure 5.4: Intraspecific variation in traits across drier+burnt and wetter+burnt sites of Dicerothamnus rhinocerotis. See supplementary Fig. S5.4 for additional information. Differences were tested using Welch's two sample t-test.

Intra-site variability across a topographical gradient (upper, middle, lower locations)

Significant differences across the topographical gradient were observed for metrics of root:shoot ratio ($p<0.001$); the upper locations (driest location) showed greater values (i.e., greater relative investment in roots than in aboveground biomass) than both the middle and lower sub-sites ($p<0.01$). However, this relationship appears relative to aboveground size, with no significant differences in maximum root depth and length found. For the aboveground traits, specific leaf area was found to be significantly smaller at the upper than the middle locations ($p<0.01$), and LDMC and SSD were found to be significantly greater at both the upper and middle locations than at the lower locations ($p<0.001$ and $p<0.01$ respectively) (**Fig. S5.5**).

Separate analysis of the wetter and drier sites showed different trends across the topographic gradient (**Fig. 5.5**). At the drier site, the upper (driest) location had significantly greater root: shoot ratio (depth *vs.* height) than the lower location ($p<0.01$) (**Fig. 5.5c**). However, at the wetter site, the upper location (driest) had significantly smaller maximum rooting depth and root:shoot ratio (depth *vs.* height) than the middle locations ($p<0.05$ and $p<0.05$ respectively) and the lower locations ($p<0.005$ and $p<0.01$ respectively) (**Fig. 5.5b, d**). All statistical results reported in **Table S5.4.**

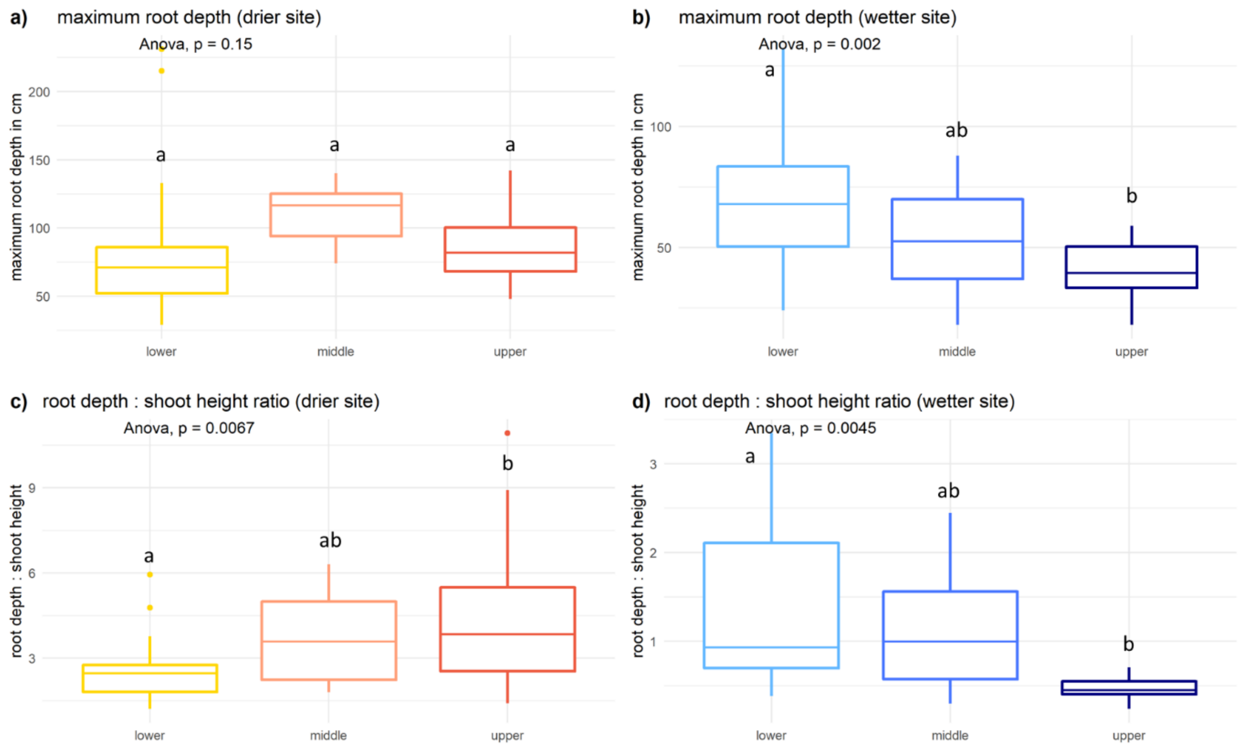

Figure 5.5: Maximum root depth in a) the drier site and b) the wetter site. Root depth to shoot height ratio in c) the drier site and d) the wetter site. Post-hoc Tukey results significant to p<0.01 are designated with a, b. NOTE the absolute differences along the y-axis in c) and d).

Intra-site variability across sub-sites of burnt and unburnt patches

Trait patterns in the recently burnt patches across wetter and drier sites (**Fig. 5.6**) showed a similar pattern. Smaller values of root length, root:shoot ratios, plant height, SSD, SLA, leaf area and LDMC were found at the drier site at the younger/recently burnt site compared with the unburnt mature vegetation (all p<0.01). However, in the wetter site only root:shoot ratio, RDMC, plant height and SSD were significantly lower at the burnt/younger sub-site (p<0.01). All statistical results reported in **Table S5.5**.

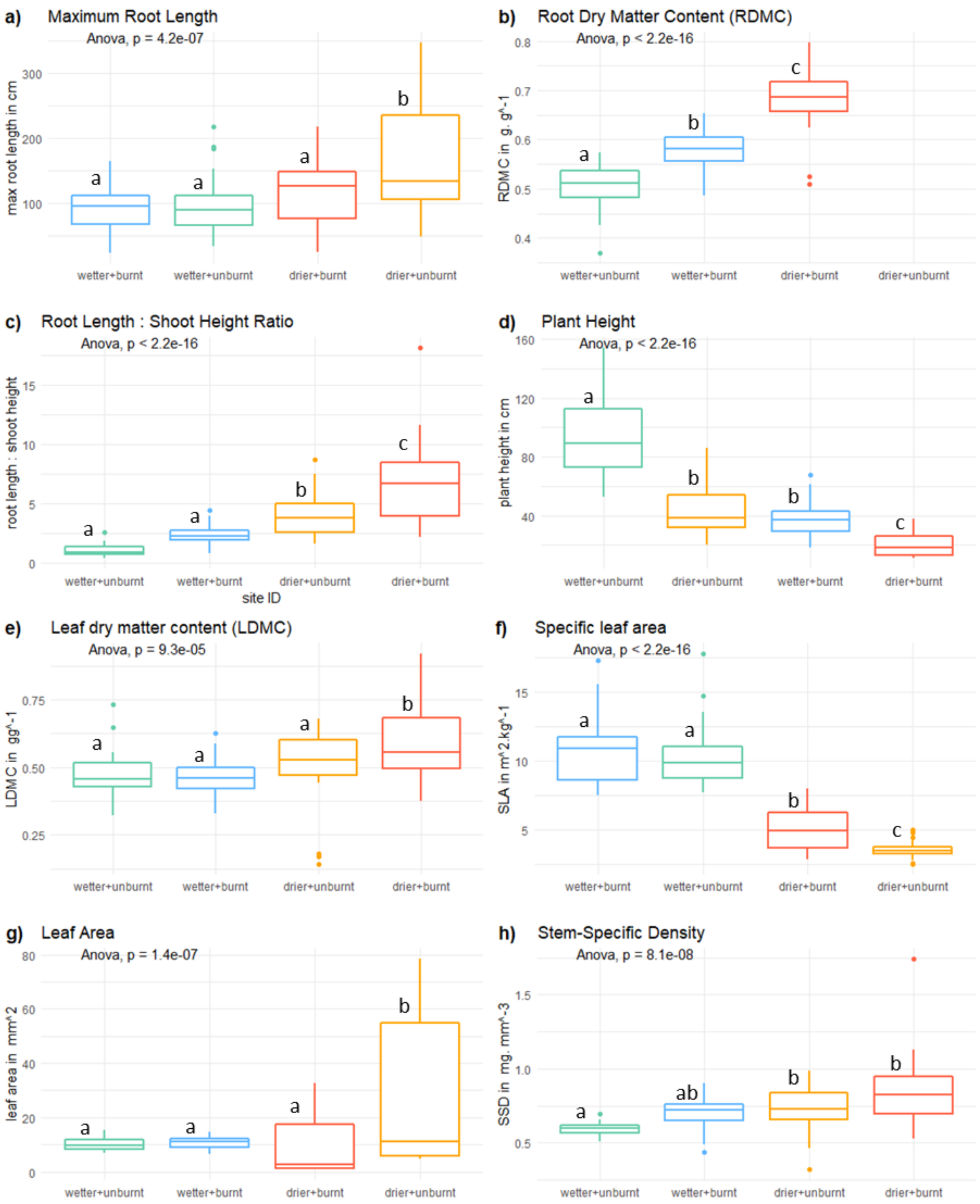

Figure 5.6: Traits across sub-sites. Green and blue are wet site. Red and orange are drier site. Post-hoc Tukey results significant to p<0.01 are designated with a, b, c.

5.3.3 WHOLE PLANT PERSPECTIVE / TRAIT SPACE

PCA: Fynbos shrub trait-space

Whole-plant trait variation of five key traits (most statistically independent and ecologically important) as detected using PCA captured 66.5% of the total variance in the first two axes (**Fig. 5.7**, PC 1 36.6% and PC 2 29.9%, group ellipses represent confidence intervals of 68%). PC 1 was mainly positively correlated with SLA and plant height, and negatively related to SSD, LDMC and maximum rooting depth and thus, discriminated between wetter and drier sites. The second axis was mostly negatively related to maximum rooting depth and root diameter. PC 2 did not discriminate between sites, but within the drier site there was more variation across PC2, which is likely explained by the intraspecific variation in traits observed for *Dicerothamnus rhinocerotis* at the drier site (**Fig. S5.6a**).

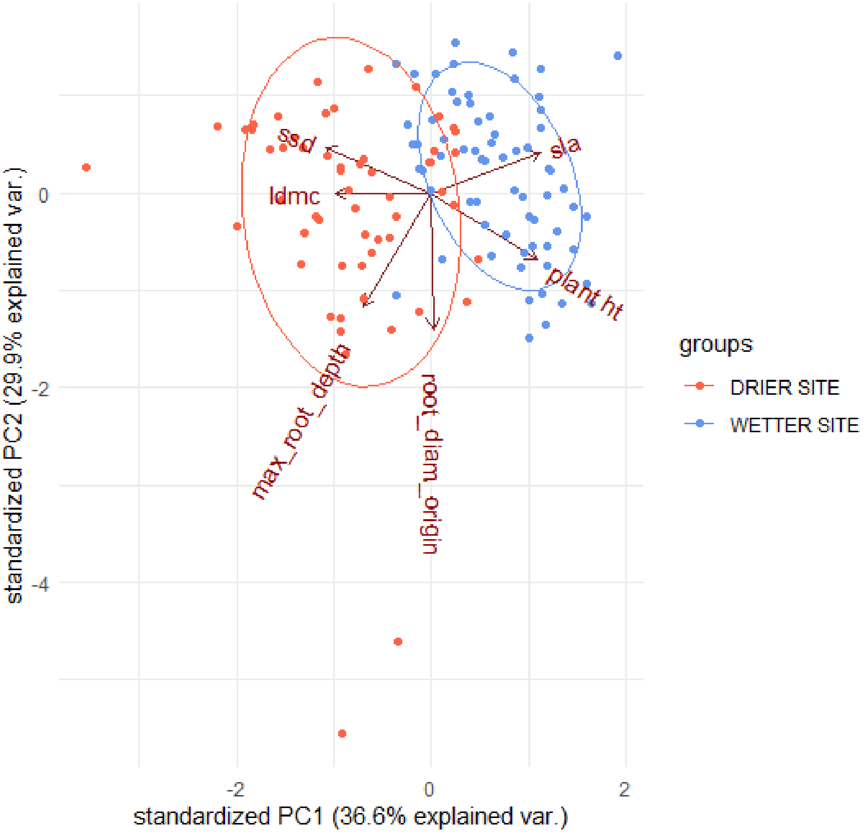

Figure 5.7: PCA of selected traits across sites where PC 1 represents resource economics and PC 2 represents belowground investment. Wetter site points aggregate on the positive end of PC1 and drier site on negative side. See supplementary Fig. S6a-d for categorisation by species, sub-sites, and topography. Trait acronyms: sla= specific leaf area, plant ht= plant height, root_diam_origin= root diameter at origin, max_root_depth=maximimum root depth, ldmc=leaf dry matter content, ssd=stem-specific density.

Biomass allocation

The relationships between the root:shoot mass ratio (**Fig. 5.8a**) and root mass:shoot volume ratio (**Fig. 5.8b**) indicated a difference in allocation patterns between the wetter and the drier sites, with more allocation to roots in the drier site as compared with the wetter site. Comparing slope regressions, or scaling exponents (**Table 5.2**), the drier site showed lower allocation to shoots (leaves and stems) in relation to roots than was expected from isometric scaling theory and global observations (Enquist & Niklas, 2002).

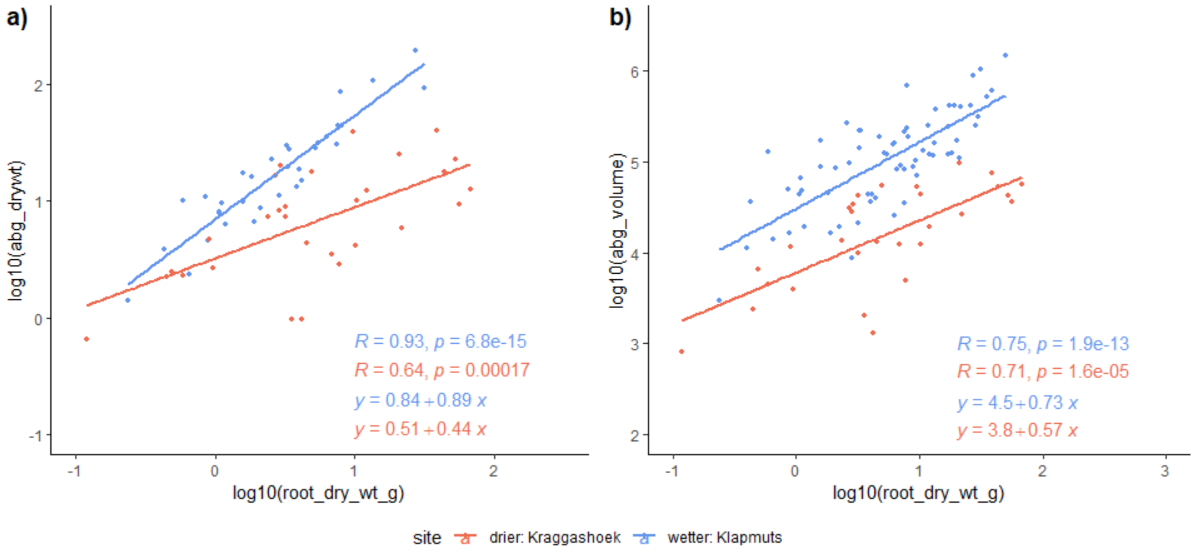

Figure 5.8: Root to shoot linear regression plots with log transformed data of a) root dry weight (x-axis) to shoot dry weight (y-axis) ratio for n=2 sub-sites, b) root dry weight (x-axis) to shoot volume (y-axis) for n=3 sub-sites.

Table 5.2: Scaling exponents compared between the sites of this study and that of the expected and observed global isometric scaling relationships from (Enquist & Niklas, 2002).

	Scaling exponent				
	This study			**Enquist & Niklas (2002)**	
Dry weight relationships	**Wetter site**	**Drier site**	**Both sites**	**Expected relationship from theory**	**Observed global dataset**
Leaves: stems	0.8	0.69	0.8	0.75	0.75
Leaves: roots	0.87	**0.28**	**0.38**	0.75	0.79
Stems: roots	0.91	**0.58**	**0.59**	1	1.09
Aboveground (leaves+stems) : roots	0.89	**0.44**	**0.49**	1	0.98

5.4 DISCUSSION

5.4.1 ABOVE- AND BELOWGROUND TRAIT VARIATION ACROSS ENVIRONMENTAL GRADIENTS

This study set out to understand trait variation across water availability gradients of woody shrubs in the Fynbos biome: a fire-prone, Mediterranean-type climate with frequent and intense droughts. Our results show that trait values vary locally across water availability gradients including a) within a biome, across sites characterised by higher and lower rainfall (**Figs. 5.3, 5.4**) and b) within a community, across lower (topographically wetter), middle and upper (topographically drier) locations (**Fig. 5.5**) (H1). Furthermore, these trends were consistent in a) post-fire categories comparing younger (3-4 yrs) to mature (10+ yrs) vegetation (**Fig. 5.6**) and b) within individuals of the same species (*Dicerothamnus rhinocerotis* – **Fig. 5.4**) (H2). Our analysis therefore provides important additional information on both above and belowground traits in response water availability and burning in a Mediterranean-type biome, where previous studies have predominantly focused on aboveground traits (Fonseca *et al.*, 2000; Ackerly, 2004; Thuiller *et al.*, 2004; Ordoñez *et al.*, 2010; Lázaro-Nogal *et al.*, 2013; Nunes *et al.*, 2017), but see (Schenk & Jackson, 2002b; Volaire, 2008; de la Riva *et al.*, 2018).

Water availability gradient (wetter vs. drier climate and topography gradients)

The greater root depth and length observed at the drier sites in our study suggest that deep vertical exploration of the root profile in search of deeper water resources is prioritised as compared with the wetter sites. Although reflected globally for drier biomes (Schenk & Jackson, 2002a), our results indicate that this pattern holds true at a local scale within a dry biome, with mean root depths of 88.54cm *vs.* 57.67cm, and mean root lengths of 142.63cm *vs.* 93.66cm at the drier (200-300mm precipitation) and wetter site (600-700mm annual precipitation), respectively. This highlights the importance of considering root variation when investigating vegetation’s contribution to water dynamics and associated ecosystem processes. The greater RDMC observed in the drier site implies greater construction costs invested in roots and thus in the longevity of root systems. Linked to this, we observed qualitatively from scaled photographs and field observation that there were fewer fine roots, typically associated with shorter lifespan and which are often seasonal, in the drier as compared with the wetter sites (**Fig. S5.7**, **S5.8**). A potential explanation for this is that shrub strategy in the drier site is to root deeper as water is the priority, whereas in the wetter site there is more often sufficient water available and therefore root depth can be sacrificed in favour of enhancing the shallow fine root systems to prioritize nutrient uptake. A complementary explanation, relevant for nutrient-poor fynbos soils, could be that the greater abundance of finer root systems in the wetter sites is due to the wetter soil having more competition for nutrients, which become a more important limiting factor than water does.

The expectation that roots will be deeper at middle and upper locations of the topographical gradient due to the further relative distance to the ground water table at these locations (Fan *et al.*, 2017) held true for the drier site when accounting for shoot height (i.e., in terms relative to aboveground biomass only). In the wetter site however, deeper roots (independently and in relation to shoot height) are more prevalent in the lower locations where water is more available, suggesting that Fan et al.'s (2017) hypothesis might hold especially true in drier sites within already dry biomes.

We observed a general conservative plant strategy in drier conditions, with higher stem-specific density, LDMC and RDMC at the drier site overall and at drier locations of both sites and lower SLA at the drier site (**Fig. 5.3, S5.5**), which is consistent with the wood (Chave et al. 2009), leaf (Wright et al. 2004), root (Roumet *et al.*, 2016) and whole-plant economic spectra (Reich, 2014).

Burnt vs. unburnt

An added consideration in fire-driven ecosystems is whether younger shrubs (developed shortly after burning) have a specific suite of traits that prioritise different strategies as compared with more mature shrubs. Additionally, understanding whether traits are uniquely influenced by the interaction between fire and drier conditions is important. The burnt *vs.* unburnt sampling results present two key points. The first is that that burnt vegetation was significantly different to unburnt vegetation in the drier site (6/8 traits measured) but less so in the wet site (2/8 traits measured) (**Fig. 5.6**). The observed trend could be reflecting greater overall diversity of trait attributes, and thus plant strategies, present in the drier site to cope with the extreme edge of the aridity gradient (Fynbos rarely grows below 275mm precipitation (Allsopp *et al.*, 2014). This is in line with previous findings suggesting that in drier conditions greater trait variation can be a signal of the co-existence of species with either stress-avoidant or stress-tolerant strategies where facilitation and competition between species can also exist (Gross *et al.*, 2013; Le Bagousse-Pinguet *et al.*, 2017; Mitchell *et al.*, 2017a).

The second key finding is that at the drier site we see evidence of poorer post-fire recovery than in the wetter site, in the form of lower mean individual plant heights (drier site less than half the wetter site), relative vegetation cover (less than half the relative canopy cover), relative individual plant counts along the sampling transects (**Table S5.1**), and lower diversity in regenerative strategy (i.e., dominance of resprouters in upper and middle locations – see **Table S5.2**). This suggests that the combination of the fire in 2016 and drought between 2015-2017 (Naik & Abiodun, 2019) might have limited the number of plants, overall vegetation cover, and regeneration strategies that were able to persist in the drier+burnt sub-site.

It can be argued that the driest environmental space would be found in the drier+burnt sub-site due to the switch from a facilitating effect of water retention by surrounding plants (as predicted by the stress-gradient hypothesis (Bertness & Callaway, 1994)) to competition under severe resource limitation (O'Brien *et al.*, 2017). Furthermore, the drought coincided with the immediate time post-fire, so the growing conditions of the plants at the drier+burnt sub-site would have experienced the driest conditions. Measured trait values support this idea, since those values expected in dry conditions were found in these sub-sites, which include: greater root:shoot ratio, greater RDMC, greater LDMC, greater SSD and smaller plant height (**Fig. 5.6**). At a smaller scale, the drier+burnt+upper locations would represent the driest environmental space. Traits supporting this include: greater root:shoot ratio, greater RDMC, greater LDMC and greater SSD. This indicates that not only root traits signal a topographical pattern along the water availability gradient with trait values expected at driest conditions at the upper site, but some aboveground traits associated with plant construction (e.g. LDMC, SSD) show a similar pattern too.

Intraspecific trait variation

Reflecting patterns at the inter-site level, we found intraspecific trait variation of individuals of the same species across our water availability gradient, for a species which is present at both the wetter and drier sites: *Dicerothamnus rhinocerotis* (Rhino bush). Smaller plant height, greater root depth to shoot height ratios (see more below), lower SLA, higher LDMC and RDMC were measured at the drier site for this species (**Fig. 5.4**). Despite the lower SLA observed, leaf area was larger in the drier site as opposed to the wetter site, which supports the variable nature of leaf area as found in other studies (Oyarzabal *et al.*, 2008; Baruch *et al.*, 2017) and suggests multi-trait feedbacks at play which influence leaf area. The only relatively conserved trait (i.e., less variation within the species) was stem specific density, which did not show significant differences across all sampled populations (**Fig. S5.4.1**). The widespread distribution and common nature of *Dicerothamnus rhinocerotis* across the Fynbos biome might be caused by the high overall trait variation we observe within this species, in alignment with the idea that successful species can be phenotypic generalists and showcase trait plasticity to cope with a varied environment (Siefert *et al.*, 2015; Mitchell *et al.*, 2017b). Understanding the trait-climate relationships of this species (which has historically been dismissed as a shrub typical of a degraded landscape (Levyns, 1926) and thus rarely studied), is particularly important in this region, as it likely plays a disproportionate role in ecosystem processes and functioning due to its relative dominance. Overall, the observation in our study of significant intraspecific root variation, contradicts other research in Mediterranean and Temperate ecosystems (Funk *et al.*, 2021; Weemstra *et al.*, 2021), suggesting that perhaps at drier limits of biomes intraspecific root variation becomes even more important.

5.4.2 WHOLE-PLANT TRAIT SPACE ACROSS A WATER AVAILABILITY GRADIENT

To cope with different environmental conditions, plants employ various strategies underpinned by different traits and often combinations of traits as opposed to singular traits (Fonseca *et al.*, 2000), aligning with Reich's notion of an integrated whole-plant economics spectrum (Reich, 2014). We see evidence for this in our study, with consistently resource-conservative or "slower" type traits (Reich, 2014) co-occurring in the drier site. However, we also see that when considering root traits alongside other traits, an approach often missing from global and local analyses, roots play a unique role in explaining overall trait variation (H3) which is supported by recent literature emphasizing that the multidimensionality of root trait variation (Weemstra *et al.*, 2016; Bergmann *et al.*, 2020) is responsible for the multidimensional nature of whole plant trait variation (Weigelt *et al.*, 2021).

Plant strategies in Fynbos

Our results show that the trait space of a subset of unique traits in Fynbos plants has two main axes of variation (**Fig. 5.7**). The first axis represents variation along a resource economics axis, explaining 36.6 % of total trait variation, with LDMC, SSD, SLA and plant height loading the highest on this axis (**Fig. S5.9**). The second axis represents belowground size/investment variation and explains 29.9% of total variation, with maximum rooting depth and root diameter loading the highest on this axis (**Fig. S5.9**).

Our results from Fynbos shrubs differ from Diaz et al.'s global analysis of trait variation (2016) in two ways. First, the resource economics axis is the first axis of variation as opposed to plant size being the first in the global analysis. This indicates that resource economics is probably a more significant driver of plant form and function than size in Fynbos shrubs. This finding is also observed in other extreme environments like the tundra (Thomas *et al.*, 2020). Second, our study highlights the importance of root investment (depth and diameter) for Fynbos woody shrubs, supporting the recently proposed integrated framework of plant form and function which indicates that root depth may present an additional axis of variation (Weigelt *et al.*, 2021) and echoing work on the role of these traits in other Mediterranean ecosystems (Fort *et al.*, 2017) and globally in dry environments (Ottaviani *et al.*, 2020).

Interspecific and intraspecific variation in plant strategies across sites

Species found at the drier sites show more variation of trait values as compared with each other (interspecific variation) and within themselves (intraspecific variation) than those species at the wetter sites (**Fig. S5.6a**). Two drier site species, *Osteospermum polygaloides* and *Ruschia multiflora*, lie between the wetter and drier site groupings. This is probably due to two reasons: 1) these two species are very different in terms of typical growth form as compared with other dominant plants in the area. *Osteospermum polygaloides* is a rhizome with semi-succulent leaves, and *R. multiflora* has fully-succulent leaves (see also **Fig. S5.10**), and 2) they are both dominant at the (wetter) lower locations within the drier site and would therefore be expected to experience conditions closer to the wetter site grouping than the other drier site species would.

Overall, these results suggest that at the drier site there is more variability in plant strategies, underpinned by traits, as well as more within-species flexibility of trait values. This agrees with work from the tundra that indicates that differences in trait expression (Thomas *et al.*, 2020) and phenotypic plasticity (Pérez-Ramos *et al.*, 2019) encourage coexistence of species in resource limited ecosystems as opposed to the notion that stress-tolerant species are thought to be less phenotypically variable (Grime, 1979) and thus would not show high intraspecific variation.

5.4.3 DO PLANTS PRIORITIZE ROOT INVESTMENT OVER ABOVEGROUND PLANT PARTS IN DRIER CONDITIONS?

It has been predicted that plants have greater root:shoot ratios in dry environments generally (Chapin *et al.*, 1993), but differences (including intraspecific ones) across a water availability gradient have generally remained unstudied within biomes. Beyond the variation in root traits across the water availability gradient, our study asked whether there was preferential allocation to roots in relation to aboveground systems in drier environments. The greater biomass allocation to roots *vs.* shoots (stems + leaves) at the drier site as compared with the wetter site (**Fig. 5.8**, **Table 5.2**) suggests that root investment is indeed prioritized for drier site shrubs (H4), with mean root depth to shoot height ratios being 3.5 in the drier site *vs.* 1.1 in the wetter site. This pattern is reflected at the intraspecific level too for *D. rhinocerotis* (2.6 in drier site *vs.* 1.3 in wetter site) suggesting additionally that this preferential investment to the root systems appears to be determined at an early age because these were results from individuals in the burnt patches (thus 1-4 years old). In terms of topography, the opposite trend was observed in the wetter *vs.* drier sites, i.e., greater root:shoot ratio at upper locations in drier site *vs.* greater root:shoot ratio at lower locations in wetter site. This may further support our hypothesis that drier conditions select for greater allocation to root systems.

Furthermore, the finding that in drier conditions, increased root allocation deviated from expected allometric relationships whereas this was not apparent in wetter conditions (**Table 5.2**), suggests that allocation theory relationships might need to be revisited for especially dry environments.

5.4.4 IMPLICATIONS FOR A DRIER FUTURE

A question that this research raises is whether in predicted drier future conditions, the increased allocation to belowground resources will affect other resource allocation, additional to aboveground biomass, such as regenerative resources. In turn this raises questions on whether recruitment would still be prioritized when conditions become drier, which could ultimately influence species persistence in a landscape. Furthermore, the finding that post-fire+drought recovery appeared to be much poorer in the drier site suggests that in the dry extremes of fynbos distribution, the combination of fire and drought may significantly change the species composition due to there being a limited set of traits that will allow plants to survive (in this case probably the ability to resprout).

5.4.5 LIMITATIONS OF THIS WORK AND FUTURE OPPORTUNITIES

This study only included woody Fynbos shrubs, whereas these landscapes have significant proportions of grasses and restios. Considering these other growth forms, with potentially quite different rooting strategies (West *et al.*, 2012), will be important if we want to scale up the interpretation of how traits influence ecosystem processes in this biome. Relatedly, it appears that succulence may present another important adaptation to drier conditions – an additional axis of trait variation was characterised by succulence (**Fig. S5.10**). This result was however based on one species in one location and therefore requires further testing. Our study highlighted the key role roots play in defining plant strategies, encouraging further exploration of root trait gradients (Weigelt *et al.*, 2021) including the “collaboration” gradient defined by the presence/lack of mycorrhizal associations (Bergmann *et al.*, 2020) which was out of the scope of this study. Our results show that allocation patterns differ across environmental gradients: this suggests that allometric relationships should be applied with caution and that field data, such as collected in this study, are extremely valuable and in demand to advance theory. Finally, this study did not produce evidence of where in the soil depth plants obtain water from, which would benefit from an isotopic analysis in future work.

5.4.6 CONCLUSION

Our study uniquely shows the contribution of root traits to overall trait variation across water availability gradients (including a regional precipitation and topographical gradient) of woody shrubs within the

Fynbos biome of South Africa. Our findings indicate preferential allocation to root investment in drier conditions, implying the importance of roots in determining whether plants can persist in a dry, drought- and fire-prone biome such as Fynbos. They also show that in some of the dominant species (e.g., *Dicerothamnus rhinocerotis*) trait responses were reflected intraspecifically. Our work thus indicates that inclusion of field collected root trait data in trait-environment studies is essential to fully appreciate the response of vegetation in dry biomes to climate change; a sentiment recently echoed at a global scale (Ottaviani *et al.*, 2020). Trait measurements from our study also indicated that the negative influence of the combination of fire and drought was more apparent at the drier site, raising concern for future Fynbos resilience in the arid limits of these already dry landscapes.

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AUTHOR CONTRIBUTIONS:

NK and MM-F designed the study with comments from CT and KJW. NK conducted the fieldwork to collect the data. NK analysed the data with assistance from MMF and CT. NK wrote the manuscript with significant contributions from all authors.

DATA AVAILABILITY

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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SUPPLEMENTARY MATERIAL

Supplementary tables

Table S5.1: Individual plant counts, relative individual counts (to the number of locations sampled at each sub-site), sum of the canopy cover, percentage of the relative canopy cover in relation to total ground cover, mean plant height (and standard deviation), mean canopy cover (and standard deviation) of each sub-site.

Sub-site	No. of species	Individuals	rel. count individuals	Sum of canopy	% rel. canopy cover	Mean plant height	StdDev plant height	Mean canopy	StdDev canopy
Dry + burnt	21	153	51	2764	**23.03**	16.4	7.4	18.1	14.0
Dry + unburnt	19.0	282	94	8610	**71.75**	39.4	22.0	30.5	26.2
Wet + burnt	9	202*	101	3966	**49.58**	36.8	16.7	19.6	12.9
Wet + unburnt	25.0	231	77	8005	**66.71**	65.4	32.5	34.7	36.0

Table S5.2: Dominant species at each location across site types and the number of individuals, sum of canopy cover for each species and the % of total shrub cover at each location.

site	location	species	regeneration strategy	individuals	sum canopy cover	% of total shrub cover at location
Dry + burnt	lower	*Dicerothamnus rhinocerotis*	Reseeder	13	188	**23.5**
Dry + burnt	lower	Osteospermum polygaloides	Rhizome – vegetative reproducer	23	402	**50.3**
Dry + burnt	middle	Aspalathus subtingens	Resprouter	20	359	**79.4**
Dry + burnt	upper	*Aspalathus* nigra	Resprouter	12	365	**91.0**
Dry + unburnt	lower	*Dicerothamnus rhinocerotis*	Reseeder	45	2065	**72.4**
Dry + unburnt	lower	Ruschia multiflora	? both	5	307	**10.8**
Dry + unburnt	middle	*Dicerothamnus rhinocerotis*	Reseeder	18	427	**60.6**
Dry + unburnt	upper	*Dicerothamnus rhinocerotis*	Reseeder	44	1498	**71.6**
Dry + unburnt	upper	*Aspalathus* nigra	Resprouter	10	478	**22.8**
Wet + burnt	lower	*Dicerothamnus rhinocerotis*	Reseeder	37	506	**24.3**
Wet + burnt	lower	*Stoebe plumosa*	? both	50	1006	**48.4**
Wet + burnt	middle	*Dicerothamnus rhinocerotis*	Reseeder	16	160	**8.9**

Wet + burnt	middle	*Stoebe plumosa*	? both	59	1546	**85.7**
Wet + unburnt	lower	*Anthospermum aethiopicum*	Reseeder	4	33	**10.8**
Wet + unburnt	lower	*Anthospermum spathulatum*	Reseeder	13	245	**80.3**
Wet + unburnt	middle	*Anthospermum aethiopicum*	Reseeder	14	321	**37.3**
Wet + unburnt	middle	*Anthospermum spathulatum*	Reseeder	16	318	**36.9**
Wet + unburnt	upper	*Anthospermum aethiopicum*	Reseeder	40	672	**43.0**
Wet + unburnt	upper	*Anthospermum spathulatum*	Reseeder	13	278	**17.8**

Note: The upper location was not sampled in the wet + burnt sub-site due to sampling difficulty. On the accessible parts of this location a thicket patch growing covered the rocky outcrop which acted as a small-scale catchment and increased water availability, fundamentally altering the expected higher dryness at this location of the topographical gradient.

Table S5.3: Statistical test results of Welch’s Two Sample T-test comparing trait values between the wetter and drier site.

Trait	**Mean wetter site**	**Mean drier site**	**T value**	**P value**	**df**	**significance codes (0 =‘***’ 0.001= ‘**’ 0.01 =‘*’)**
Max root depth	57.67	88.54	-5.2758	8.5E-07	93.74	***
Max root length	93.66	142.63	-4.5803	1.6E-05	82.51	***
Max lateral extent	38.47	44.67		not significant		NS
RDMC	0.54	0.68	-10.3140	1.0E-13	47.64	***
Root length: shoot height	1.71	5.39	-8.6126	2.5E-12	64.73	***
root diameter	10.76	13.03		not significant		NS
SLA	10.47	4.31	18.8100	2.2E-16	109.4	***
LDMC	0.47	0.54	-2.8660	5.4E-03	75.1	**
Leaf area	10.35	20.48	-3.1830	2.4E-03	56.76	**
leaf succulence	118.46	316.32	-3.9754	2.0E-04	56.64	***
Leaf water content	0.53	0.46	2.8660	5.4E-03	75.1	**
Plant height	66.99	31.10	7.6552	1.2E-11	100.7	***
Stem specific density	0.65	0.78	-4.4199	3.2E-05	76.21	***

Table S5.4: Statistical test results of ANOVA comparing trait values across topographical locations (lower, middle, upper).

Trait	F value	p value	df	significance codes (0 =‘***’ 0.001= ‘**’ 0.01 =‘*’)
Max root depth		not significant		
Max root length		not significant		
Max lateral extent	4.509	1.42E-02	2	*
RDMC	4.192	1.81E-02	2	*
Root length : shoot height	8.629	3.14E-04	2	***
root diameter		not significant		
SLA	6.363	2.36E-03	2	**
LDMC	19.81	3.62E-08	2	***
Leaf area	6.697	1.74E-03	2	**
leaf succulence	6.689	1.76E-03	2	**
Leaf water content	19.81	3.62E-08	2	***
Plant height		not significant		
Stem specific density	7.2	1.11E-03	2	**

Table S5.5: Statistical test results of ANOVA comparing trait values across sub-sites (wetter+burnt, wetter+unburnt, drier+burnt, drier+unburnt).

Trait	F value	p value	df	significance codes (0 =‘***’ 0.001= ‘**’ 0.01 =‘*’)
Max root depth	13.240	1.6E-07	3	***
Max root length	12.360	4.2E-07	3	***
Max lateral extent	5.077	8.6E-03	3	**
RDMC	98.780	2.0E-16	3	***
Root length: shoot height	47.360	2.0E-16	3	***
root diameter	11.360	1.3E-06	3	***
SLA	119.000	2.0E-16	3	***
LDMC	7.719	9.3E-05	3	***
Leaf area	13.390	1.4E-07	3	***
leaf succulence	16.180	6.8E-09	3	***
Leaf water content	7.719	9.3E-05	3	***
Plant height	115.200	2.0E-16	3	***
Stem specific density	13.86	8.1E-08	3	***

SUPPLEMENTARY FIGURES

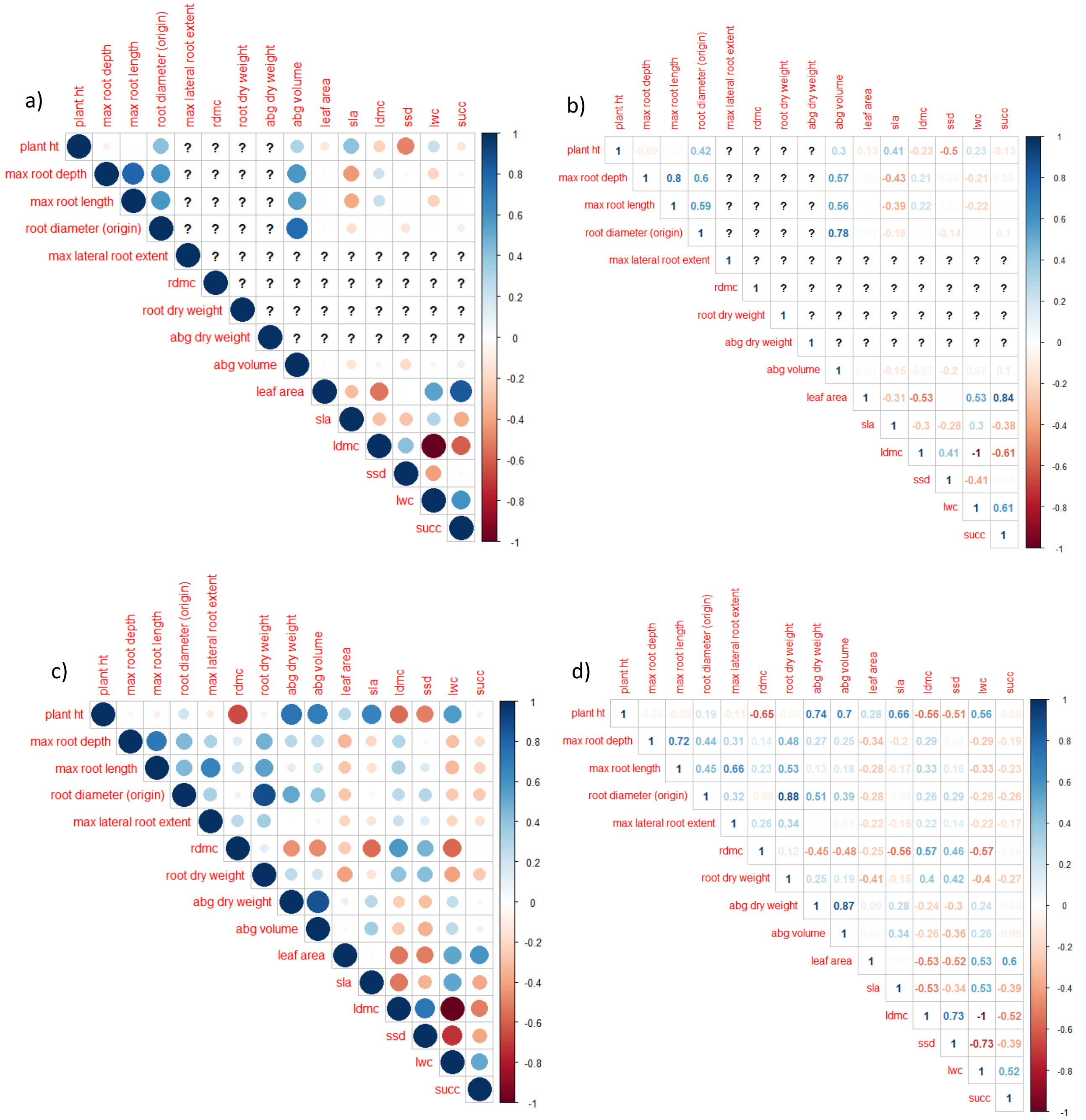


Figure S5.1: Correlation matrices of measured traits. a) Graphical representation of correlation for all data n=124 and b) correlation coefficient for all data n=124. The question marks indicate traits that did not have values for all individuals and thus could not be correlated. C) Graphical representation of correlation for a subset of data where all traits had values for an individual n=52. D) Correlation coefficients of subset of data where all traits had values for an individual n=52)

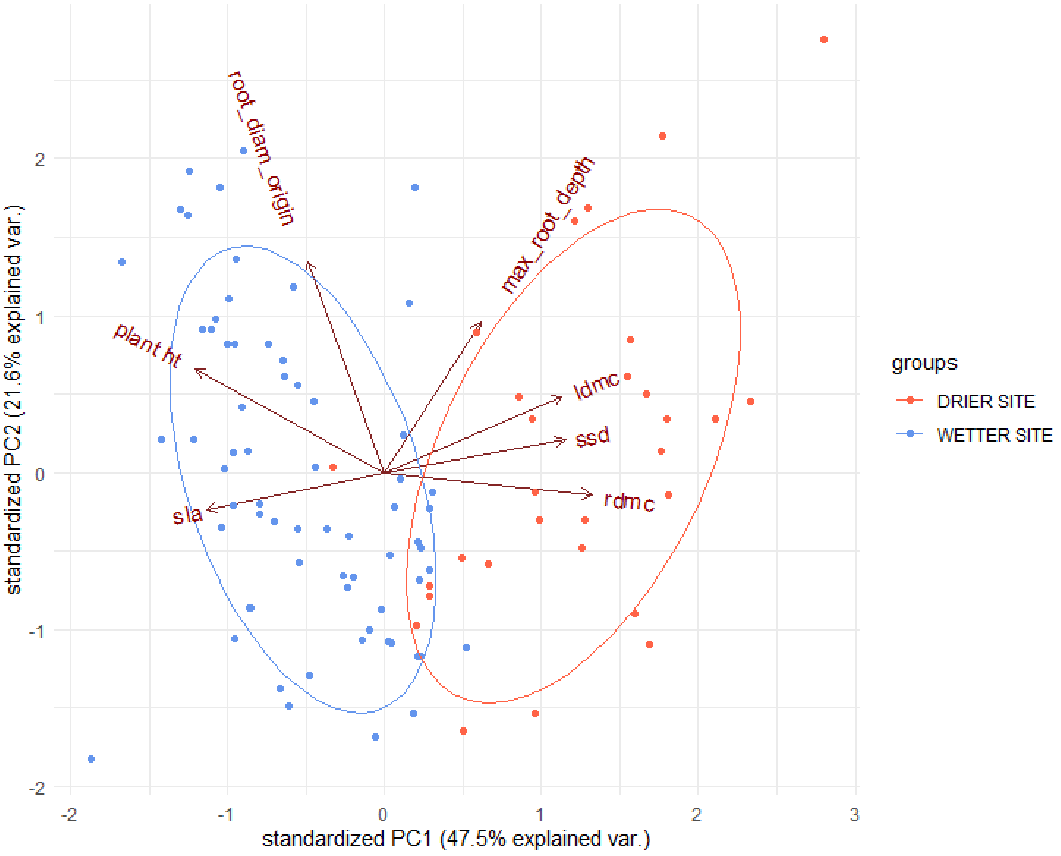


Figure S5.2: PCA showing sites where RDMC measures are available (dry + burnt and wet + burnt) to show how RDMC has a high correlation with LDMC and SSD. Principal components (although switched) are similar in terms of PC 1 being resource economics and PC 2 being belowground investment. RDMC loads more on the resource economics axis than the belowground investment axis. Ellipses are groupings at a 68% confidence interval.

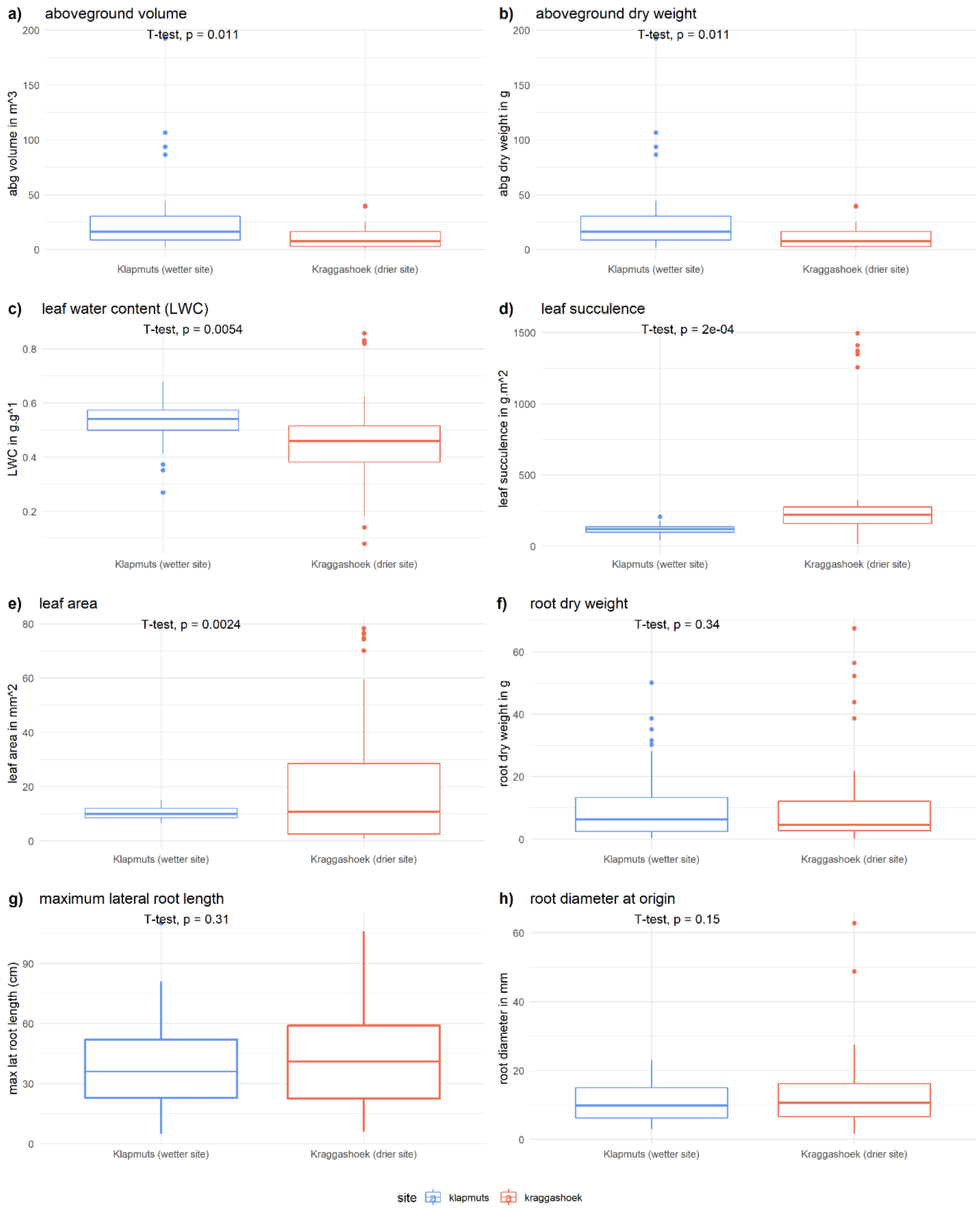


Figure S5.3: Remaining Above- and Belowground traits across the wetter (Klapmuts) and drier site (Kraggashoek). Significant differences were tested using Welch's Two Sample t-tests (see Table S5.3 for details).

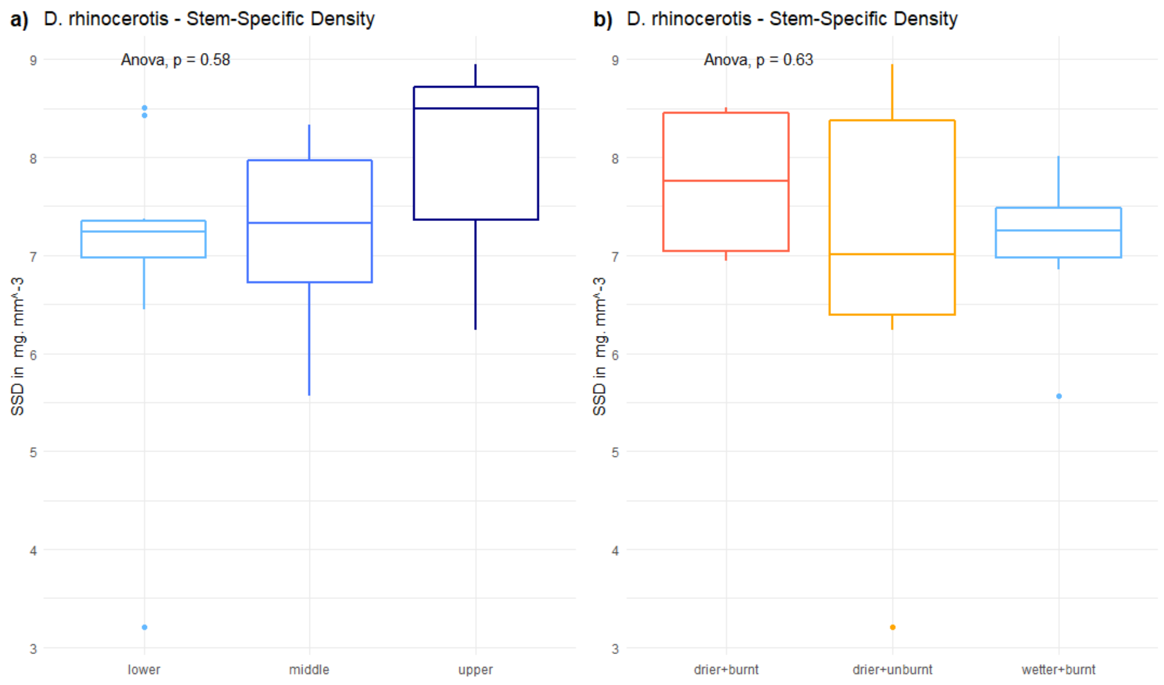


Figure S5.4.1: Stem specific density of *Dicerothamnus rhinocerotis* a) across topographical gradients and b) across sub-sites where this species is present. Individuals at the drier+unburnt sub-site are more than 10 years old whereas at drier+burnt and wetter+burnt individuals are 1-4 years old. This suggests that stem specific density is not plastic in this species across age or environmental gradient.

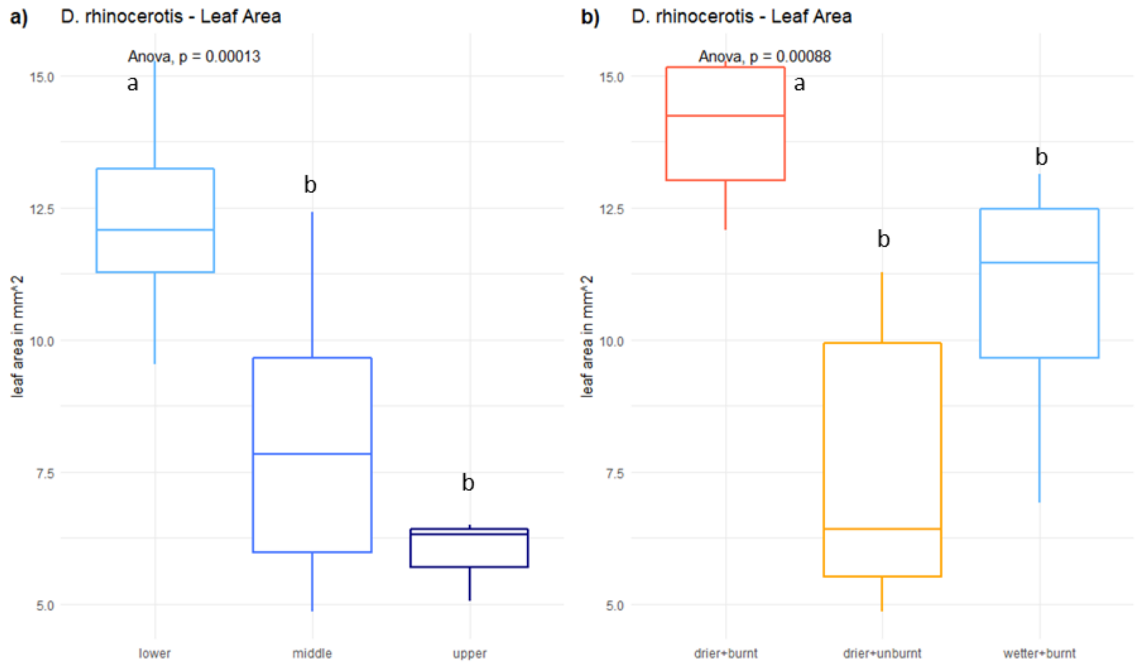


Figure S5.4.2: Variation in leaf area of *Dicerothamnus rhinocerotis* across a) topographical locations and b) sub-sites. Significant differences denoted by a, b and significant at the p<0.05 level.

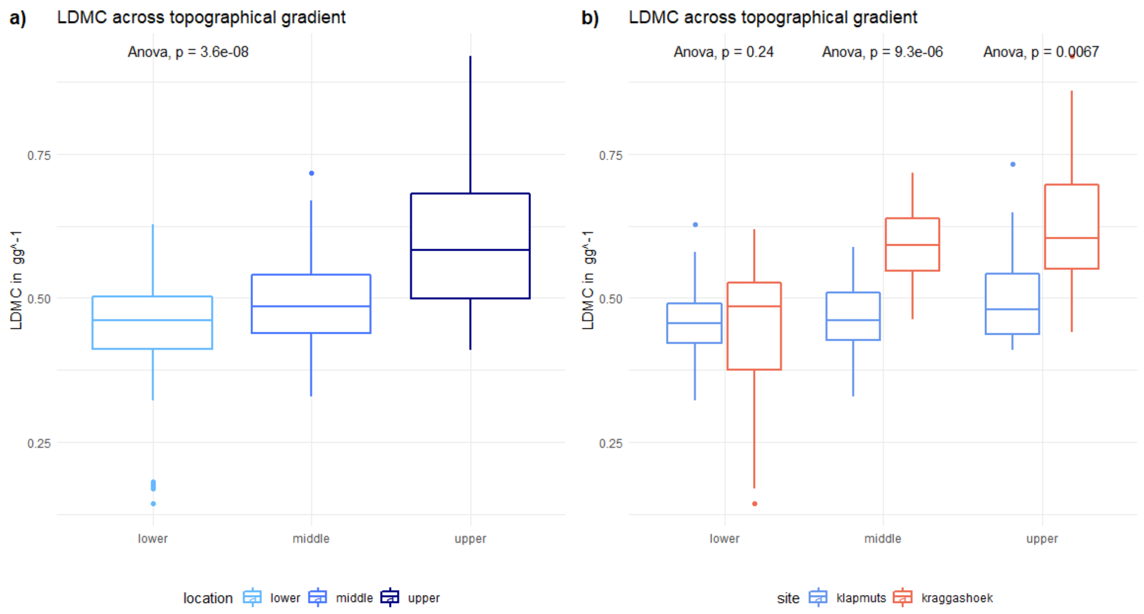


Figure S5.5.1: Leaf dry matter content (LDMC) along a topographical gradient for a) across sites, b) wetter and drier sites separated. For a) significant differences between upper-lower (p<0.001). Significant differences were tested using Anovas (see Table S5.4 for details on location analysis).

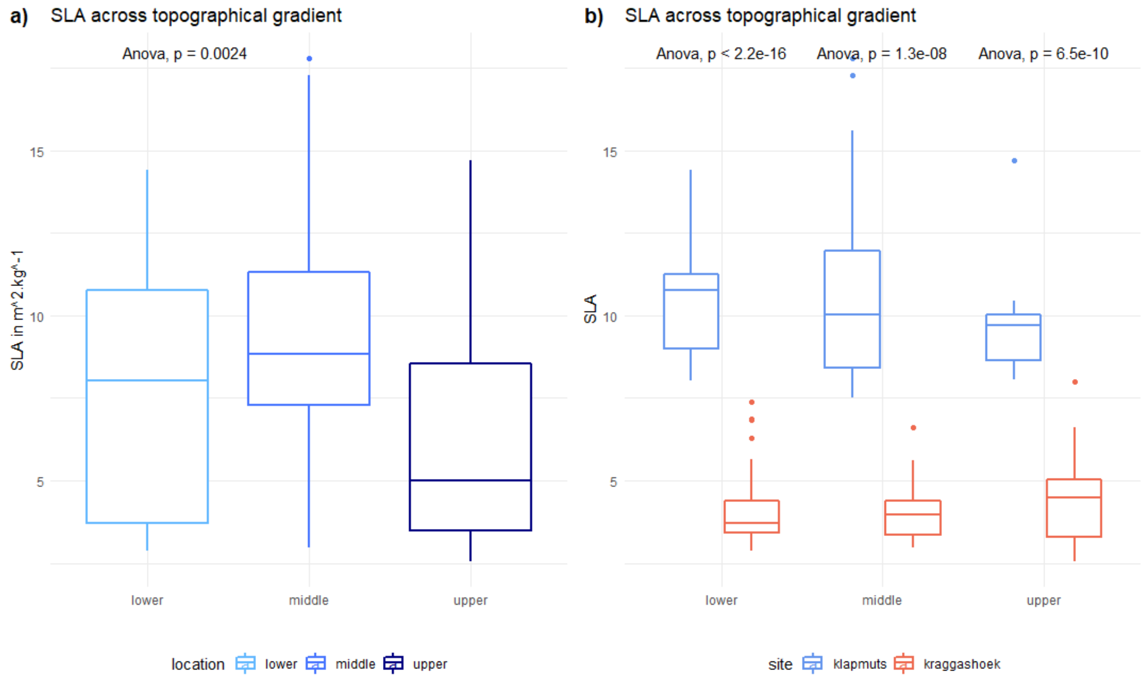


Figure S5.5.2: Specific leaf area (SLA) along a topographical gradient for a) across locations, b) wetter and drier sites separated (red=drier site, blue=wetter site). For a) significant differences between upper-middle (p <0.01). Significant differences were tested using Anovas (see Table S5.4 for details on location analysis).

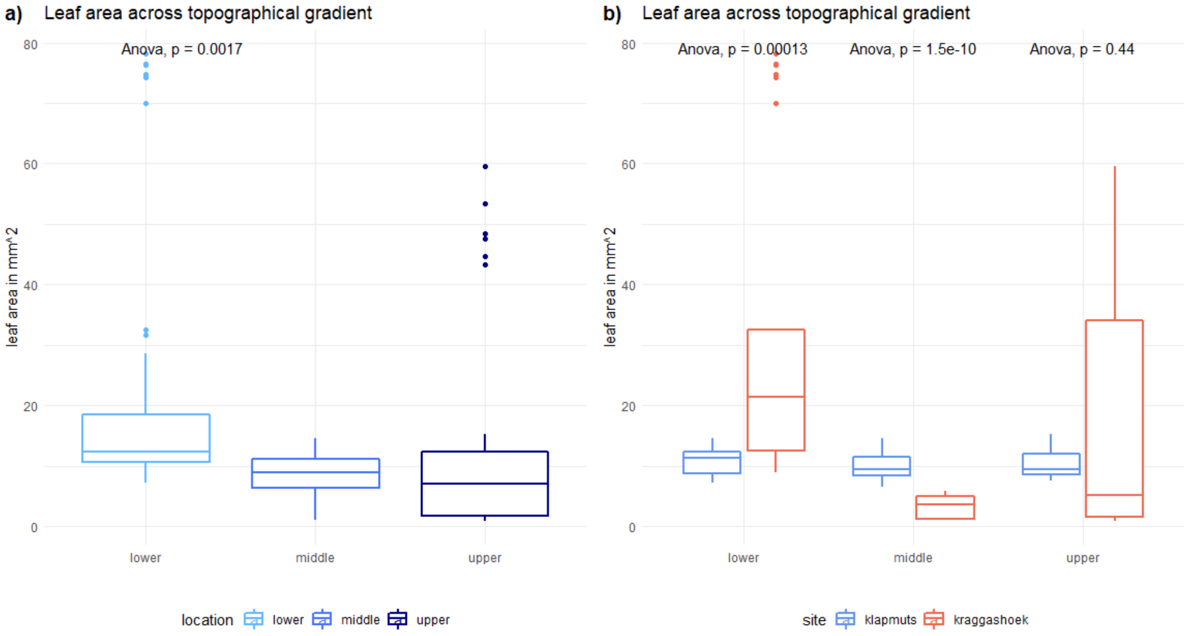


Figure S5.5.3: Leaf area along a topographical gradient for a) across locations, b) wetter and drier sites separated. For a) significant differences between middle-lower ($p<0.01$). Significant differences were tested using Anovas (see Table S5.4 for details on location analysis).

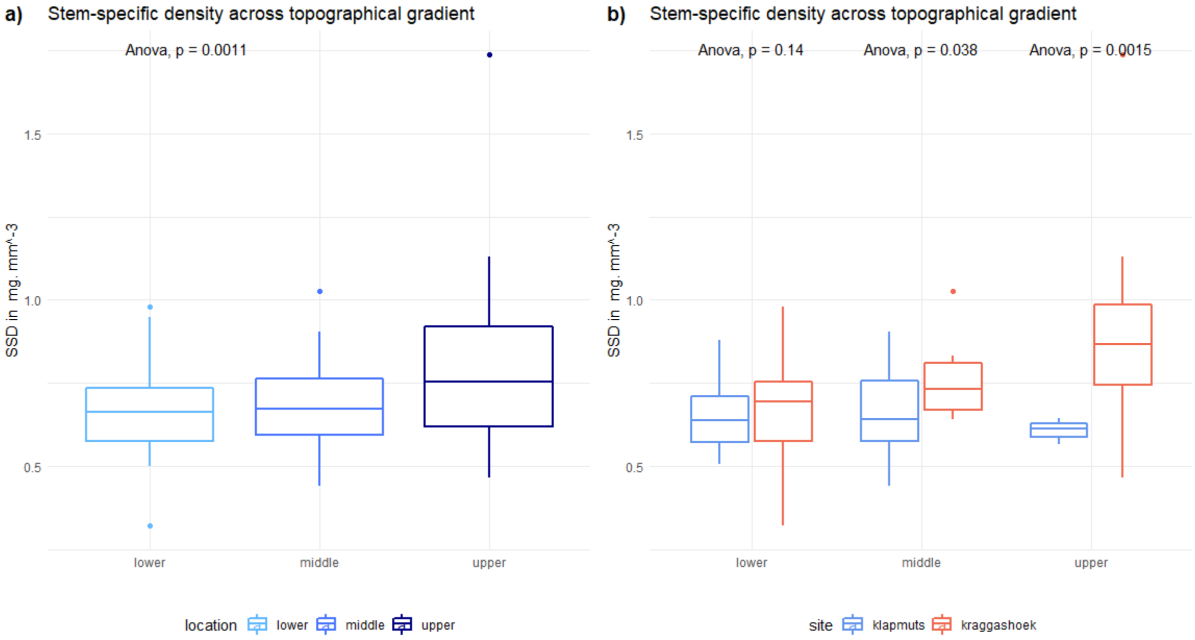


Figure S5.5.4: Stem specific density (SSD) along a topographical gradient for a) across sites, b) wetter and drier sites separated. For a) significant differences between upper-lower ($p<0.01$) and upper-lower ($p<0.01$). Significant differences were tested using Anovas (see Table S5.4 for details on location analysis).

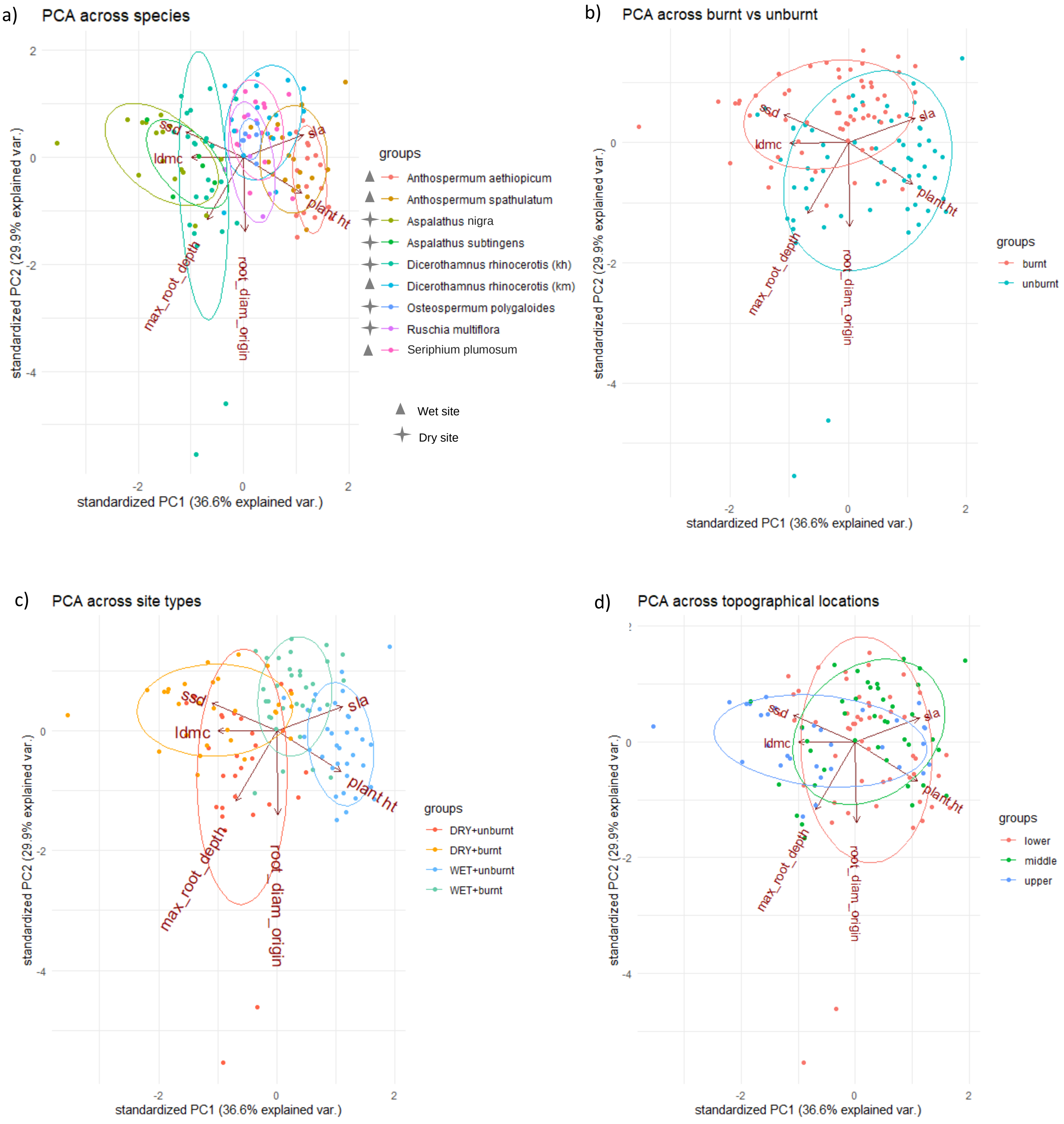


Figure S5.6: PCA of selected traits across species where PC 1 represents resource economics and PC 2 represents belowground investment. Ellipses are groupings at a 68% confidence interval.

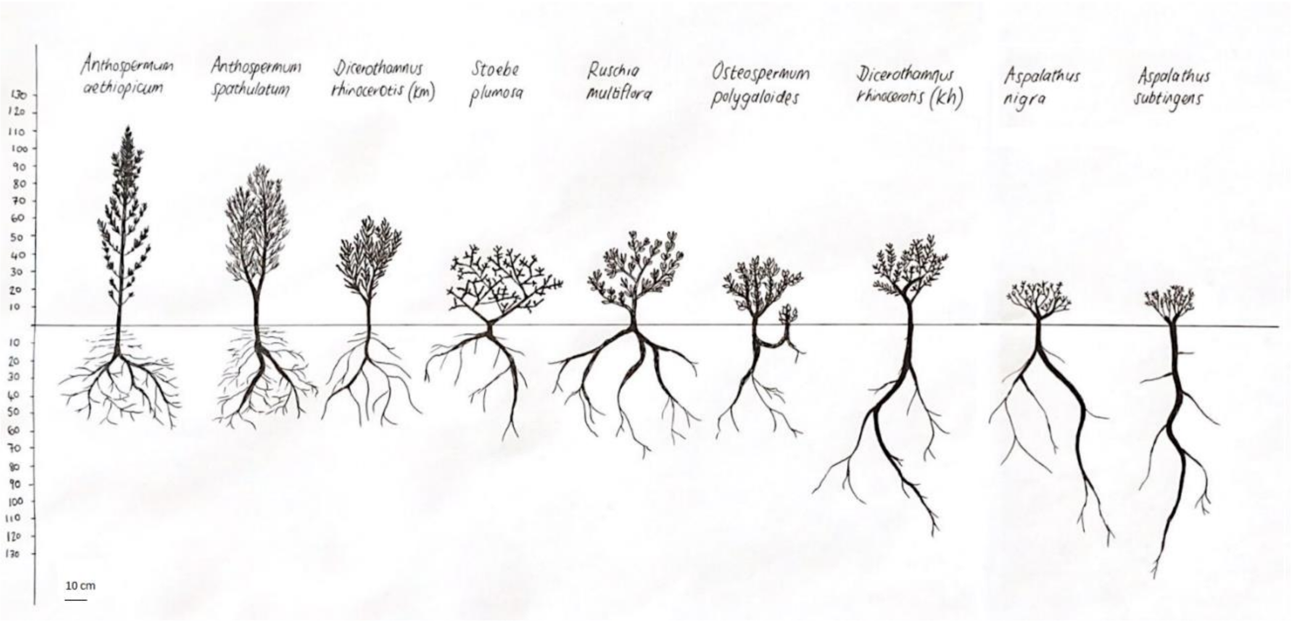


Figure S5.7: Plant profiles of typical aboveground and belowground sizes and structures based on mean values of root depth, lateral extent, plant height and canopy width. Dicerothamnus rhinocerotis (km) is from the wetter site and (kh) from the drier site. Source: drawn by Nicola Kühn.

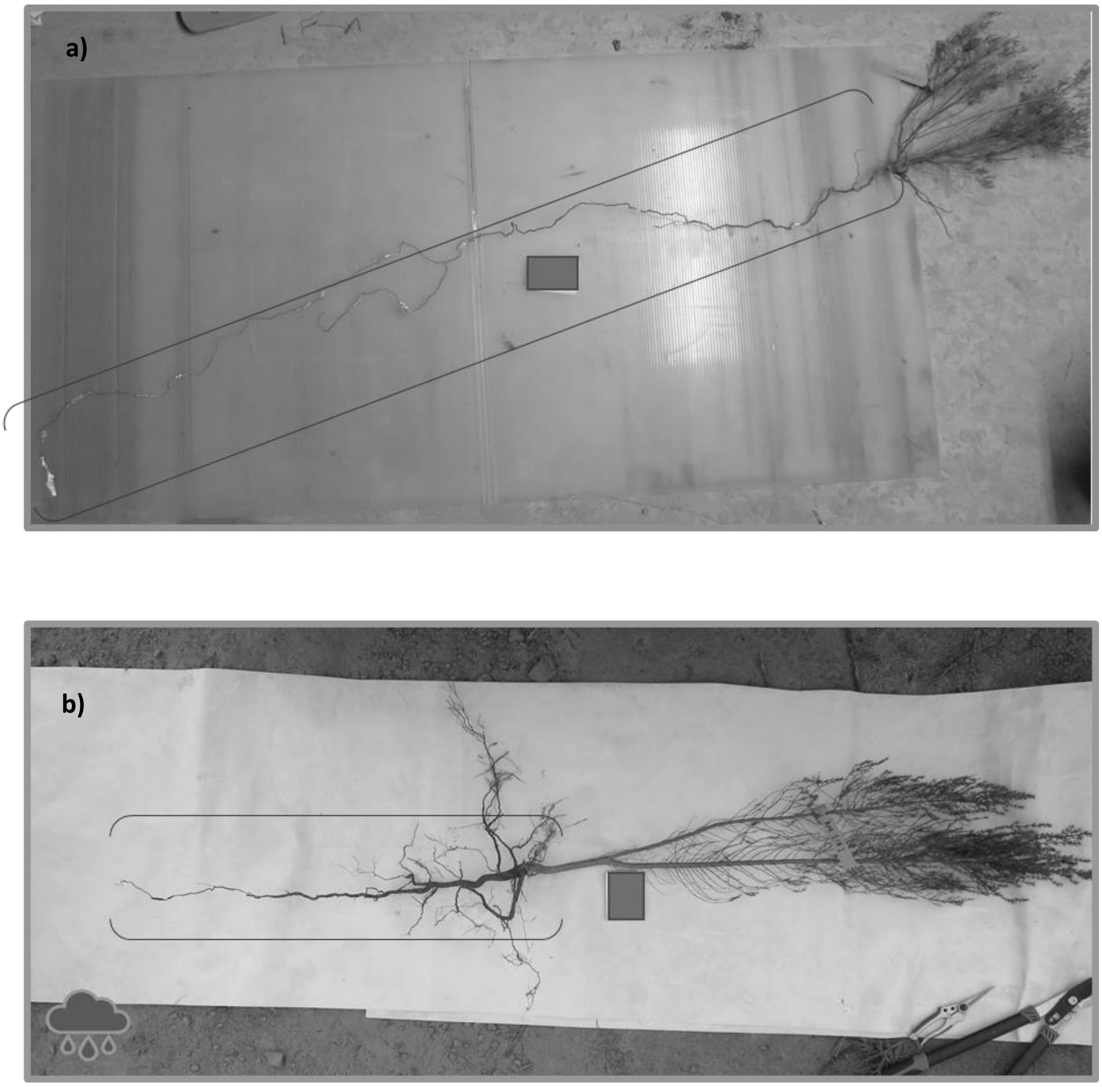


Figure S5.8: Scaled photographs of a typical dry site plant (a) and a typical wet site plant (b). This shows the more than double root:shoot ratio of plants at the drier site. Rectangle scale marker = 10cm x 8cm.

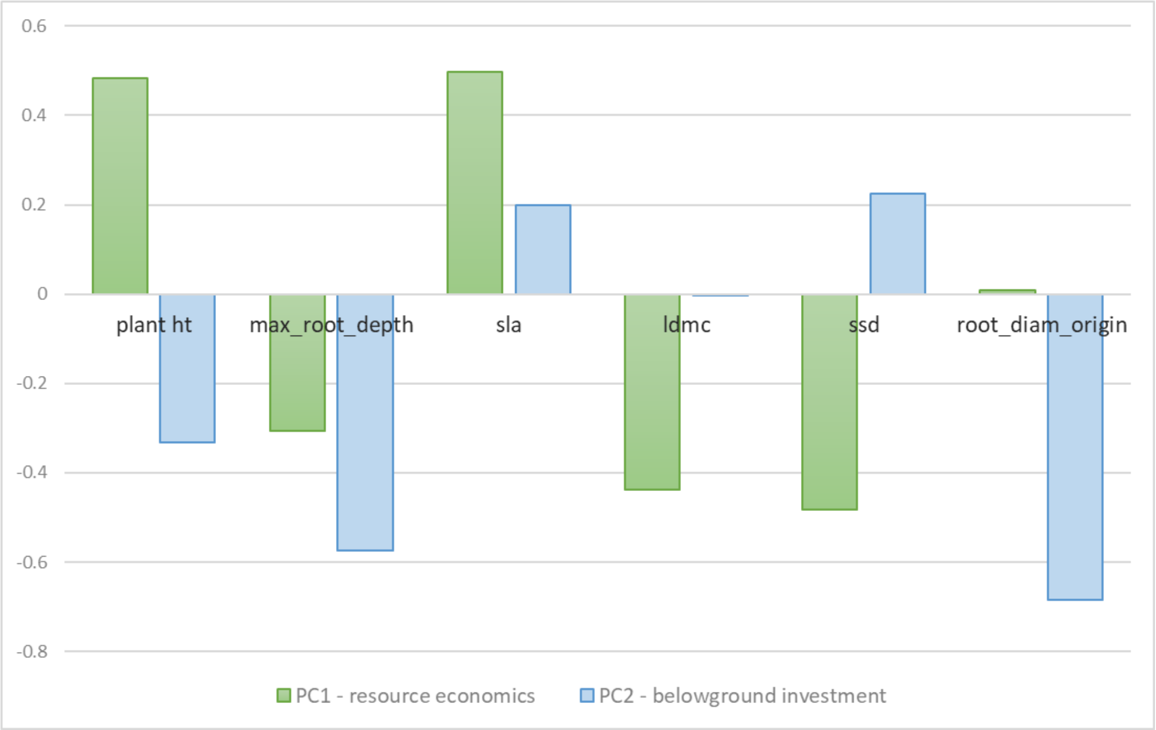


Figure S5.9: PCA loadings for PCA presented in Fig. 8. Principal component 1 (explaining 36.6% variation) representing the resource economics axis shows primary loading by plant height, SLA, LDMC and SSD. Principal component 2 (explaining 29.9% of the variation) representing the belowground investment shows primary loading on maximum rooting depth and root diameter.

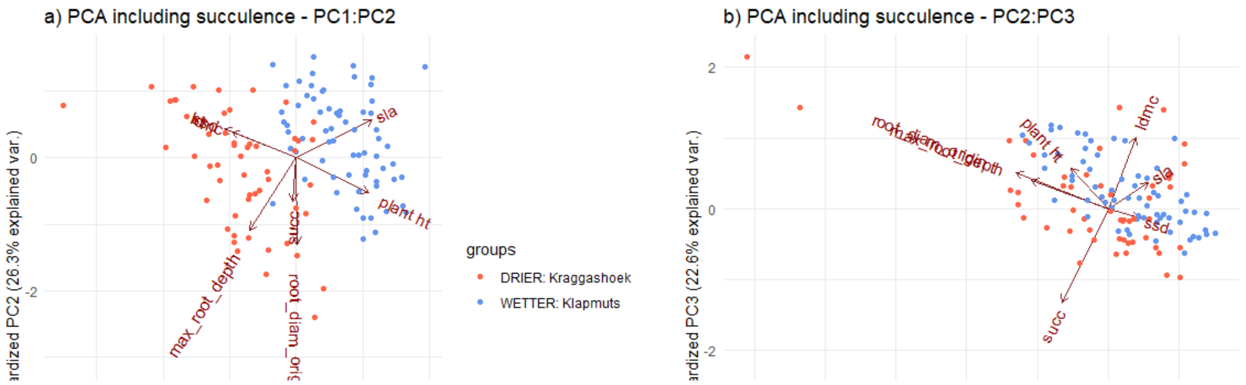


Figure S5.10: PCA including succulence plotting a) PC1: PC2 and b) PC2: PC3. The overall trait variation explained by including succulence drops by more than 10% (PCA excluding succulence (Fig. 5.7) explains 66.5% vs this PCA explains 57.3%). However, this analysis suggests that succulence could represent an additional axis of variation (PC3) not sufficiently explained by the resource economics (PC1), or root size (PC2) axis. Note: Truly succulent leaves were only found in one species, Ruschia multiflora in one location at the drier site.

CHAPTER 6: DEEPER ROOTS REDUCE VEGETATION SENSITIVITY TO CLIMATE VARIABILITY IN DRY BIOMES

By Nicola Kühn, Marcus Spiegel, Carolina Tovar, Kathy Willis, and Marc Macias-Fauria

Photo: Nicola Kühn

Linking statement:

The research approach of the final research paper of this thesis (**Chapter 6 (Research Paper 3)**) was inspired by the variation in root traits observed along water availability gradients within the Fynbos biome as presented in **Chapter 5 (Research Paper 2)**. These findings hinted at the potential importance of root traits in determining access to deeper water resources in times of water stress and thus reducing vegetation sensitivity to climate change. The following chapter therefore presents results of an analysis comparing root depth observations to remote-sensing derived vegetation sensitivity to climate variability metrics across dry biomes in Southern Africa.

Author contribution statement:

NK and MM-F conceptualised the research and designed the approach with comments from all authors. NK and MS collected, processed, and analysed the data with assistance from MM-F and CT. NK wrote the first draft of the manuscript with significant contributions from all authors (MM-F, MS, CT and KJW).

ABSTRACT

Globally drylands are set to get warmer and drier, increasing water stress for the vegetation in these regions. Plant sensitivity to drier periods and drought events will largely depend on trait strategies to access and store water, often linked to the root system. We analysed the relationship between root depth and Vegetation Sensitivity (VSI) (after Seddon et al. (2016)), which empirically assesses time series of vegetation responses to changes in three climatic variables (air temperature, water availability and cloud cover). Results show that a significant relationship between root depth and vegetation sensitivity (as defined by VSI) exists in Southern Africa, as well as a significant positive relationship between root depth and temporal autocorrelation in vegetation productivity, an intermediate product of the VSI calculations interpreted as the importance of memory effects. These relationships were significantly influenced by both biome and growth form, but generally imply that deeper roots reduce vegetation responses to climate variability. Our results provide empirical evidence that accessing deeper water resources during times of lower water availability through deeper roots is a potential mechanism determining vegetation sensitivity to climate variability and thus a key trait for dryland vegetation resilience under future climate change. We also show that belowground traits in drylands leave a fingerprint on aboveground plant-climate interactions, an important finding to aid in scaling up data-scarce belowground research.

Word count: ~4928

6.1 INTRODUCTION

Plant traits play a fundamental role in mediating responses to climate change and have thus come under focus recently with the hopes of enhancing our understanding of response mechanisms. Recent work (Kühn *et al.* (2021)) has demonstrated that belowground traits (e.g. rooting depth, resprouting ability, belowground storage) might be as important as above ground traits in promoting plant fitness and performance during intervals of climate change. In particular, these understudied traits might allow plants in dryland biomes to cope with climate and associated environmental changes.

The relationship between below-ground plant traits and climatic/environmental factors is thus important in determining mechanisms of plant resilience to future change. However, the difficulty in studying roots (Laliberté 2017) has historically meant slower progress in our understanding of belowground trait-environment relationships. Early root research based on a limited global dataset (n=475), found that deeper roots were more prevalent in arid and semi-arid systems than in humid ones, and more prevalent in certain growth forms (trees from savanna/thorn scrub, or seasonally dry forests) (Schenk and Jackson 2002, Schenk and Jackson 2005). Recent collation of existing data in online trait databases (GRooT, FRED, TRY, BIEN) (Guerrero-Ramírez et al. 2021, Iversen et al. 2017, Kattge et al. 2011, Kattge et al. 2019, Enquist et al. 2009) and the advancement of remote root measuring techniques (i.e., isotope analysis and remote sensing techniques) has enabled some testing of these relationships over larger spatial scales. For example, using remotely-sensed data of ground water depth and existing root depth data from the GRooT database, Fan et al. (2017) showed that ground water plays a key role in driving root depth patterns at both the landscape and global scale. Deep roots have also been found to strongly correlate with the ability to access deep soil water in studies using water balance models in combination with root trait data (Fort et al. 2017) and satellite-derived predictions of root trait data (Liu et al. 2021). Advances in isotope analysis techniques have also enabled the determination of where in the soil profile plants access water. A recent study in sub-tropical coniferous shrubs, for example, showed that during dry seasons the majority of water uptake occurred in deep soil layers (Jiang et al. 2020). Water availability can therefore be a key driver of root trait variation generally (de la Riva et al. 2018) and root depth specifically (Weigelt et al. 2021) from local landscape (Kühn et al. *In Prep* **(Chapter 5: Research Paper 2)**) to global scales (Laughlin et al. 2021).

Deeper roots, and thus access to deep soil water in times of water stress, have been hypothesised to play a role in reducing sensitivity to changes in the hydro-climate, particularly in the drylands of the world with current and predicted further future aridification (Huang et al. 2017). However, this hypothesis has not yet been widely demonstrated and remains poorly understood globally, and crucially, in global drylands. Furthermore, there is little understanding of whether this relationship is consistent across functionally different biomes within drylands. Analysing the relationship between root characteristics and patterns of vegetation sensitivity to observed climate variability may shed light on resilience-enhancing vegetation strategies to cope with future climate change.

The Vegetation Sensitivity Index (VSI), developed by Seddon et al. (2016) present the opportunity to analyse whether root depth has affected vegetation sensitivity patterns and is thus likely to play a role in future responses to climate change. The VSI is based on the relationship between monthly vegetation productivity (using the Enhanced Vegetation Index, EVI (Didan 2015) and monthly climate data (air temperature, cloud cover, and water availability – measured as the ratio of actual to potential evapotranspiration) together with the EVI of the previous month, which encapsulates past vegetation productivity. In the calculation of the VSI, the coefficient associated with the previous month's EVI (Coefficient *t-1*) is the one-month-lagged temporal autocorrelation in productivity and represents the potential influence of memory (lagged) effects. Greater magnitude in *t-1* indicates that vegetation productivity is more strongly determined by its previous state than by the current climate. Seddon *et al.* (2016) generated a coarse (5km), spatially-continuous global map of vegetation sensitivity considering the period 2000-2013. Within this global analysis, southern Africa was shown to contain large areas showing either high sensitivity to water availability or high temporal autocorrelation, making it a suitable case study to observe VSI patterns in a global dryland. Our study recomputes the VSI at finer spatial resolution (1km) to analyse the relationship between root depth and sensitivity to climate variability between 2000-2019 in the biodiverse dryland biomes of Southern Africa and test the following hypotheses:

i) Deeper roots are found in areas with lower VSI and greater temporal autocorrelation in productivity (Coefficient *t-1*), suggesting a lower synchrony of productivity with month-to-month climate variability mediated by belowground traits.

ii) The relationship in i) is modulated by overall growth form and vegetation characteristics captured by biome type.

If deeper roots do confer more resilience to climate variability, we would expect to see a lack of association between vegetation productivity and precipitation in drylands, and this would be associated with deeper roots. We therefore also hypothesize that:

iii) The statistical association between remotely sensed vegetation productivity (EVI) and monthly precipitation is weaker (stronger) in areas of greater (smaller) rooting depth.

We tested these hypotheses using spatially continuous, remotely-sensed vegetation indices and climate data together with empirical field root depth data.

6.2 METHODS

6.2.1 STUDY SITE AND CLIMATE

We conducted our analysis in Southern Africa including the entirety of South Africa, Lesotho and Eswatini and major southern portions of Namibia, Botswana, Zimbabwe and Mozambique. The study extent included all land area between 20°S and 40°S and 10.59°E and 39.20°E. This area encompasses 11 biomes, with varying vegetation types and growth forms (**Fig. 6.1** and see supplementary **Table S6.1**).

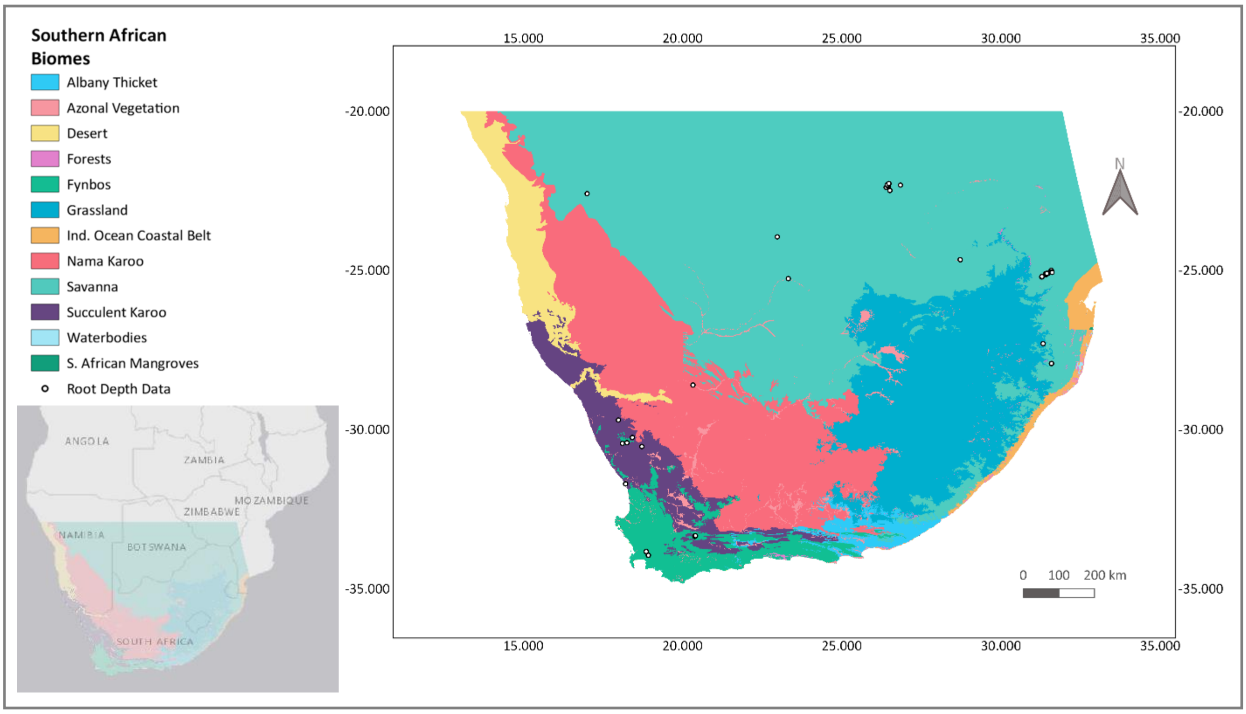


Figure 6.1: Map of study region in Southern Africa, which encompasses South Africa, Lesotho, Eswatini and portions of Namibia, Botswana, Zimbabwe, and Mozambique. shown are the biomes from the best available data for the region (see below for data sources). Also represented by the yellow points are the locations of the root depth data used in this study collated from prior fieldwork (Kühn et al. *In prep)*, existing literature (Zhou et al. 2020) and online trait databases (n=100) (see supplementary Table S6.2 for full dataset sources).

Most of Southern Africa experiences a colder dry season (April-October) and a warmer wet season (November to March). However, in the south-western tip of the region (covering Fynbos and Succulent Karoo biomes), the seasons are reversed with dry summers and wet winters produced by mid-latitude cyclones. Observed past climate change in Southern Africa indicates warming of 0.4˚C per decade (between 1961-2014), making it one of the regions experiencing the greatest warming in Africa (Davis and Vincent 2017). Warming has been accompanied by declining trends in rainfall, resulting in an aridification trend that is predicted to continue and to be accompanied with increased frequency and intensity of droughts implying even greater future water stress across the region (Davis and Vincent 2017, Naik and Abiodun 2019).

6.2.2 TRAIT DATA

Root depth data were collated from field-based collections (Kühn et al. *In Prep* **(Chapter 5: Research Paper 2)**) and existing datasets from published literature and online trait databases (See supplementary **Table S6.2** for a full list of data sources used). Data were included in this analysis if the associated geographic coordinates were available. In total we obtained 100 records of root depth across biomes and growth forms from existing datasets. Six out of the 11 biomes had root depth data, with the most data points in Savanna (n=67) and Fynbos (n= 22) and fewer in Succulent Karoo (5), Nama Karoo (3), Azonal Vegetation (n=2), Grassland (n=1). Four growth forms were considered, with most data being on trees (n=64) and shrubs (n=30) with a few observations for graminoids (n=4) and herbaceous (n=2) plants. Root depth data collected by a prior study (Kühn et al. *In Prep* **(Chapter 5: Research Paper 2)**) (n=124) were treated differently due to their high spatial density (see methods section 6.2.6).

6.2.3 CLIMATE AND VEGETATION DATA

Climate data used in this study included: MODIS 8 day composite ratio of actual vs potential evapotranspiration (Running et al. 2019) at 0.5km resolution over 2000-2019, MODIS daily cloudiness(Vermote and Wolfe 2020) at 1 km resolution over 2000-2019 which was calculated following Wilson & Jetz (2016), CHELSA monthly timeseries of maximum temperature (period 2000-2019) and total precipitation at 1km resolution over the period 2000-2018 (Karger et al. 2017, Karger 2018). Vegetation productivity data included the MODIS monthly Enhanced Vegetation Index (EVI) (Didan 2015) at 1km resolution over the period 2000-2019.

6.2.4 VEGETATION SENSITIVITY TO CLIMATE VARIABILITY AND COEFFICIENT *T-1*

We calculated the Vegetation Sensitivity Index (VSI) and associated temporal autocorrelation in plant productivity (Coefficient *t-1*) for Southern Africa at a spatial resolution of 1km over the time period 2000-2019 using the methodology developed by Seddon & Macias-Fauria *et al.* (2016). The details of the algorithm are fully described in Seddon & Macias-Fauria et al. (2016) and summarised in here. This involved modelling the relationship between the EVI, the climate variables (evapotranspiration, cloudiness, temperature) and the *t-1* variable, for each month by running a principal component regression on a pixel-by-pixel basis. Regression coefficients (or "climate weights") were obtained for each of the climate variables, which were then averaged over all months for which a significant relationship was found, multiplied by the relative variance of EVI compared to the climate variance and summed to give the vegetation sensitivity (VSI). The *t-1* coefficient was also an intermediate output of the calculation which was scaled and mapped over the pixels to give the relative variation in the importance of temporal autocorrelation over the region.

6.2.5 COMPARISON OF ALL VSI DATA ACROSS BIOMES

We used best available data for biome designations for Southern Africa: The Vegetation Map (SANBI 2018) for South Africa, Lesotho and Eswatini, Atlas of Namibia Project (Directorate of Environmental Affairs Ministry of Environment and Tourism 2002) for Namibia, and WWF Ecoregions (Olson et al. 2001) biomes data for the remaining extent. Maps from these sources were merged and rasterized using the “raster” package in R (Hijmans 2012). Mean and median VSI and *t-1* values were calculated for each biome to facilitate comparison of their central tendencies. A one-way ANOVA and Tukey HSD test (with a 95% confidence interval) were performed on a 10% random subsample of pixels for each biome to compare whether VSI and *t-1* differed across biomes.

6.2.6 STATISTICALLY EXPLORING THE RELATIONSHIP BETWEEN ROOT DEPTH *VS.* VSI AND *T-1* (HYPOTHESES *I* AND *II*)

We used generalised least squares modelling to test the relationship between VSI (and *t-1*) vs root depth because it accounts for heteroskedasticity and correlation between residuals. VSI and *t-1* values were extracted for each point within each of the 1-km pixels where root depth data were present (n=100 in total). Twelve of these 100 root depth data points were randomly selected as 10% of a dataset (n=124) from a prior study (Kühn et al. *In Prep*). We did this because the dataset represents locally abundant data points in the Fynbos biome, which did not match the resolution of the VSI adequately. For each of the models, we ran 10 iterations selecting different random subsets of Kühn et al.'s data each time (described above) to test the relationship between VSI, *t-1* and root depth, biome and growth form:

$$\text{VSI} = \alpha_{\text{VSI}} + \beta_{\text{log (root depth)-VSI}} \times \log(\text{root depth}) + \beta_{\text{biome-VSI}} \times \text{Biome} + \beta_{\text{growth form-VSI}} \times \text{growth form} + \varepsilon$$

$$t\text{-}1 = \alpha_{\text{t-1}} + \beta_{\text{log (root depth)-t-1}} \times \log(\text{root depth}) + \beta_{\text{biome-t-1}} \times \text{Biome} + \beta_{\text{growth form-t-1}} \times \text{growth form} + \varepsilon$$

Where α is the random intercept and β is the slope with standard error $\varepsilon \sim N(0, \sigma^2)$. Model assumptions were tested to verify that they were met using diagnostic plots (supplementary **Fig. S6.1**).

6.2.7 EVI *VS.* MONTHLY PRECIPITATION (HYPOTHESIS *III*)

To identify areas where there is no concurrent vegetation response to precipitation, we statistically explored the relationship between per pixel annual time-series of time-integrated EVI (sum of EVI in all months with EVI above 0.1) and total precipitation for the months considered by the VSI algorithm (hereafter referred to as the EVI-precipitation correlation coefficient). To determine whether areas showing low EVI-precipitation correlation were also those with lower VSI, greater *t-1* and deeper roots, we compared the EVI-precipitation correlation coefficient to these variables for the subset of pixels that we had root depth observations for (n=100). Although the computation of the VSI uses EVI anomalies, the resulting VSI index is uncorrelated with EVI, justifying the exploration of this relationship to further test our theoretical framework ($R^2 = 0.11$ for the whole study area (2406261 pixels), Supplementary **Fig. S6.2**).

6.3 RESULTS

6.3.1 VEGETATION SENSITIVITY VARIES ACROSS BIOMES

Vegetation sensitivity differed across Southern Africa (**Fig. 6.2a**) and significantly among biomes (supplementary **Fig. S6.3i**, **Table S6.3**) (F=14033, Df=11, p<2e-16; Tukey's HSD Test for multiple comparisons): most biomes were significantly different from one another. Notably, the Succulent Karoo biome shows the lowest sensitivity. Temporal autocorrelation in productivity (*t-1*) also differed significantly among biomes (supplementary **Fig. S6.3ii**) (F=105588, Df=10, $p<2e-16$; Tukey's HSD Test for multiple comparisons): most biomes were significantly different from one another and showed even more inter-biome contrast than VSI, with the drier biomes (Succulent Karoo, Desert, Fynbos and Nama Karoo) having greater *t-1* values, showing a higher response of lagged effects on productivity and a lower response to the climate conditions of the current month than wetter biomes (e.g., Indian Ocean Coastal Belt, Forests and Albany Thicket biomes).

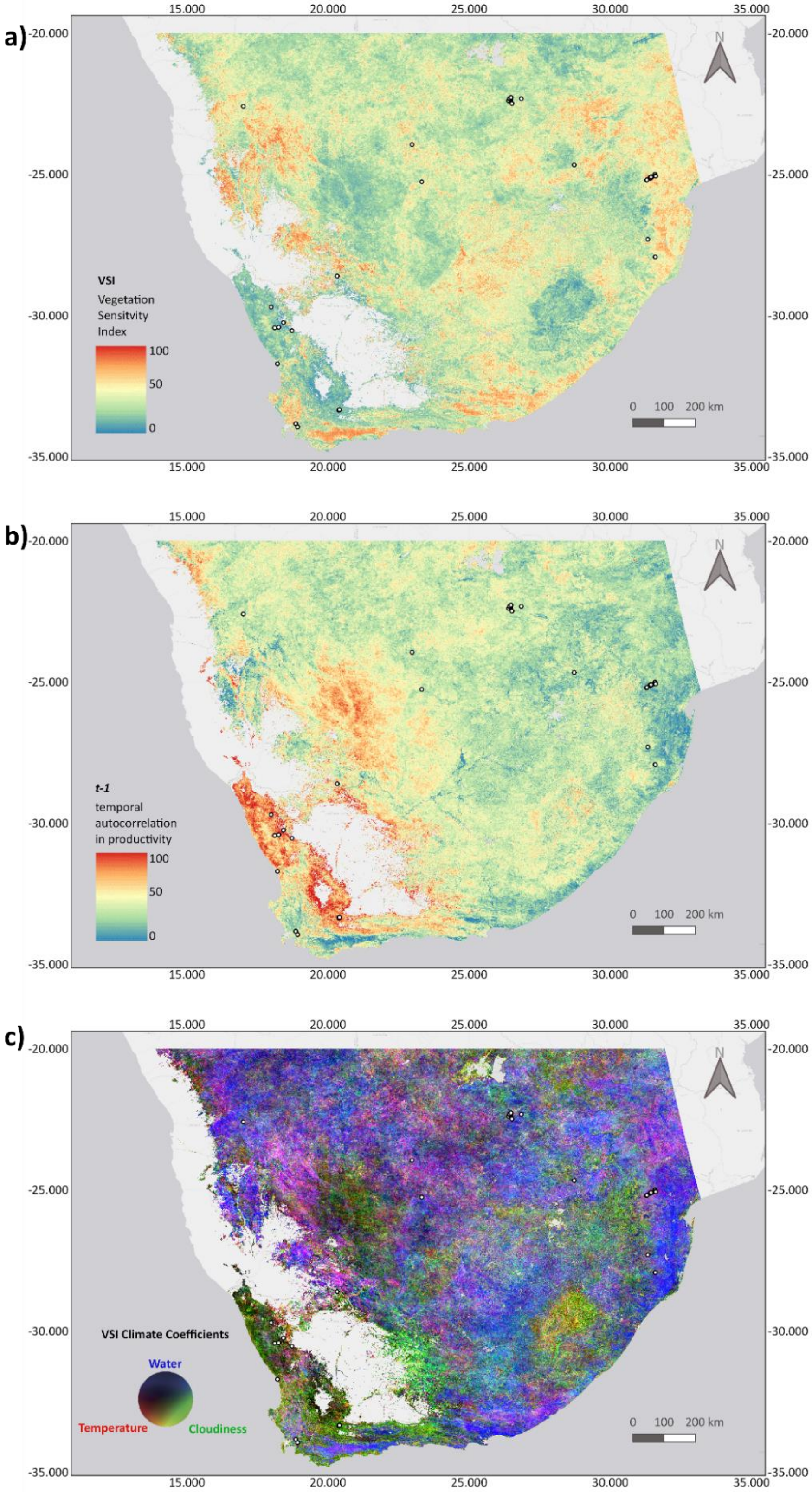
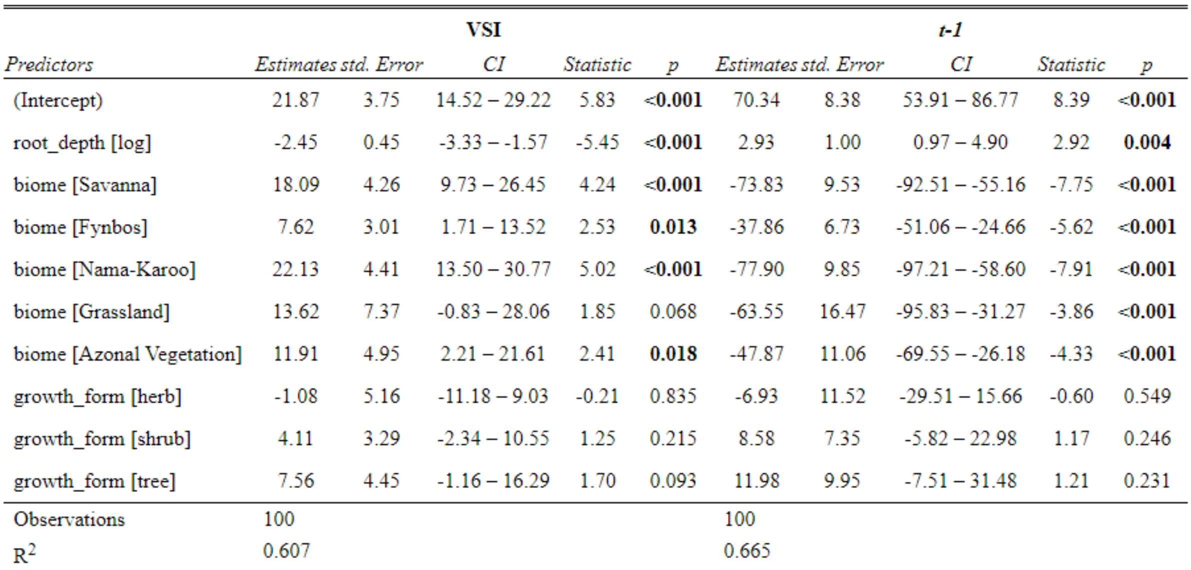


Figure 6.2: a) Vegetation Sensitivity Index (VSI), b) temporal autocorrelation in productivity (t-1) and c) climate weights of VSI across our study extent in Southern Africa. Areas with EVI < 0.1 are devoid of vegetation and show as no-data in light grey. Dark grey denotes sea.

6.3.2 VEGETATION SENSITIVITY VS. ROOT DEPTH

Results from the Generalised Least Squares model indicate that root depth, in combination with biome and growth form, significantly explains vegetation sensitivity across Southern Africa (**Table 6.1**) (R^2=0.607, $p<0.001$) (**Fig. 6.3a** and supplementary **Fig. S6.4a**). The model including root depth, biome, and growth form displayed the lowest AIC of all possible combinations (**Table S6.4** and **Table S6.5**). A negative linear relationship between VSI and root depth exists (i.e., deeper roots are found in areas with lower sensitivity)), and a positive linear relationship between root depth and temporal autocorrelation in productivity (*t-1*) exists (i.e., deeper roots are associated with areas with a higher influence of past productivity and less associated with climate conditions of the current month) (R^2=0.665, $p<0.001$) (**Fig. 6.3b**, and supplementary **Fig. S6.4b**).

Table 6.1: Generalised Least Squares model estimates, standard error, confidence interval, test statistic (t-value), p-value and R^2 for VSI and *t-1* models



	VSI					***t-1***				
Predictors	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*
(Intercept)	21.87	3.75	14.52 – 29.22	5.83	**<0.001**	70.34	8.38	53.91 – 86.77	8.39	**<0.001**
root_depth [log]	-2.45	0.45	-3.33 – -1.57	-5.45	**<0.001**	2.93	1.00	0.97 – 4.90	2.92	**0.004**
biome [Savanna]	18.09	4.26	9.73 – 26.45	4.24	**<0.001**	-73.83	9.53	-92.51 – -55.16	-7.75	**<0.001**
biome [Fynbos]	7.62	3.01	1.71 – 13.52	2.53	**0.013**	-37.86	6.73	-51.06 – -24.66	-5.62	**<0.001**
biome [Nama-Karoo]	22.13	4.41	13.50 – 30.77	5.02	**<0.001**	-77.90	9.85	-97.21 – -58.60	-7.91	**<0.001**
biome [Grassland]	13.62	7.37	-0.83 – 28.06	1.85	0.068	-63.55	16.47	-95.83 – -31.27	-3.86	**<0.001**
biome [Azonal Vegetation]	11.91	4.95	2.21 – 21.61	2.41	**0.018**	-47.87	11.06	-69.55 – -26.18	-4.33	**<0.001**
growth_form [herb]	-1.08	5.16	-11.18 – 9.03	-0.21	0.835	-6.93	11.52	-29.51 – 15.66	-0.60	0.549
growth_form [shrub]	4.11	3.29	-2.34 – 10.55	1.25	0.215	8.58	7.35	-5.82 – 22.98	1.17	0.246
growth_form [tree]	7.56	4.45	-1.16 – 16.29	1.70	0.093	11.98	9.95	-7.51 – 31.48	1.21	0.231
Observations	100					100				
R^2	0.607					0.665				

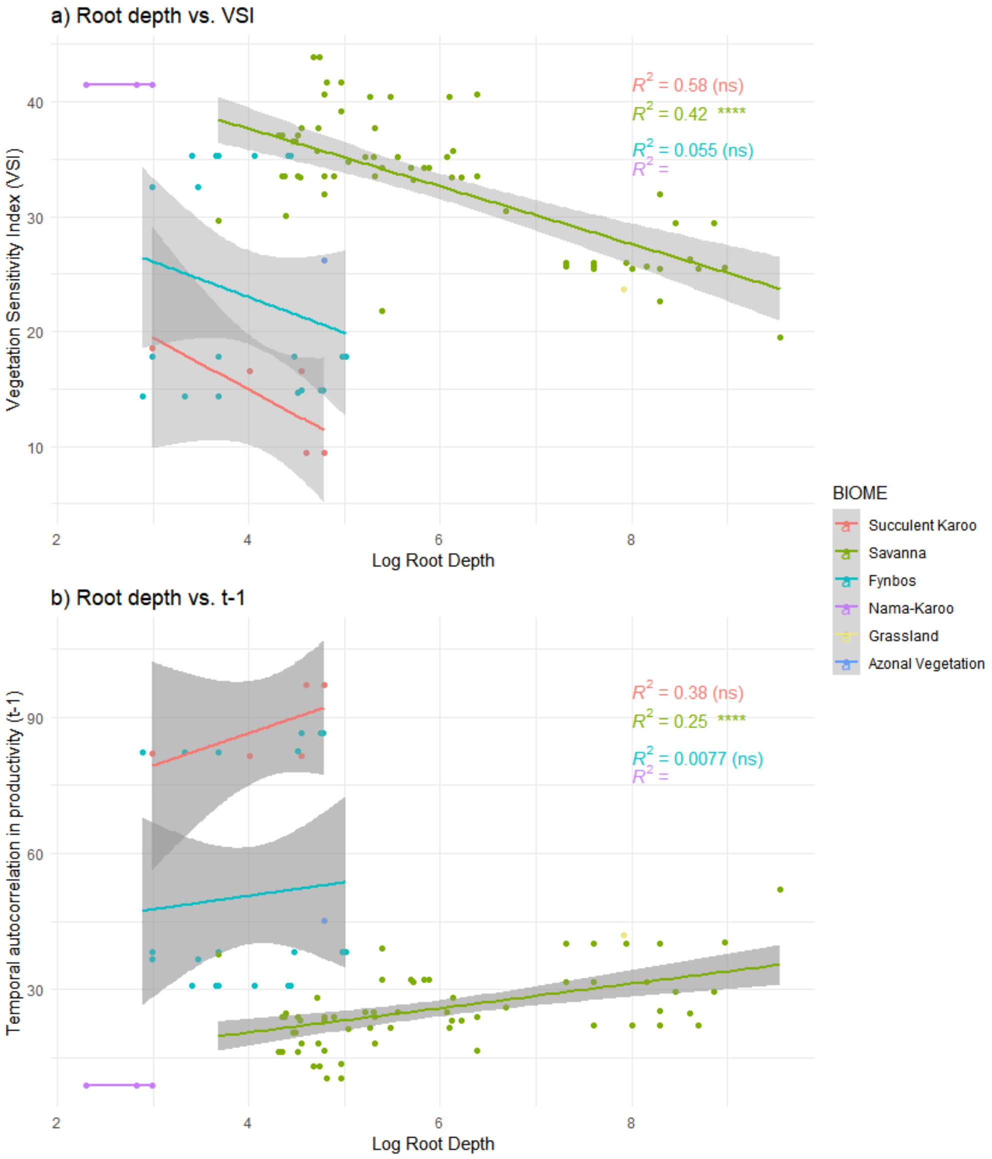


Figure 6.3: Regression of log root depth as a function of a) Vegetation Sensitivity (VSI) and b) Temporal autocorrelation in productivity (t-1), separated by biome. Regression line and associated R^2 value is shown for each biome with sufficient data (Nama-Karoo, Grassland and Azonal Vegetation biomes did not have enough data). Significance levels are denoted as follows: *** p<0.001, **p<0.01, * p<0.05, NS= not significant.

6.3.3 EVI *VS.* PRECIPITATION

The relationship between EVI precipitation correlation coefficient and VSI, *t-1*, Root depth is insignificant however, when considering biome significant relationships emerge (**Fig. 6.4** and Supplementary **Table S6.6**)**.** For the Savanna biome and for the limited data available for the Succulent Karoo biome, the EVI-precipitation correlation coefficient is positively related to VSI, negatively related to *t-1*, and negatively related to Root depth (**Fig. 6.4**). For Fynbos, the relationships are opposite than those for the savanna and Succulent Karoo.

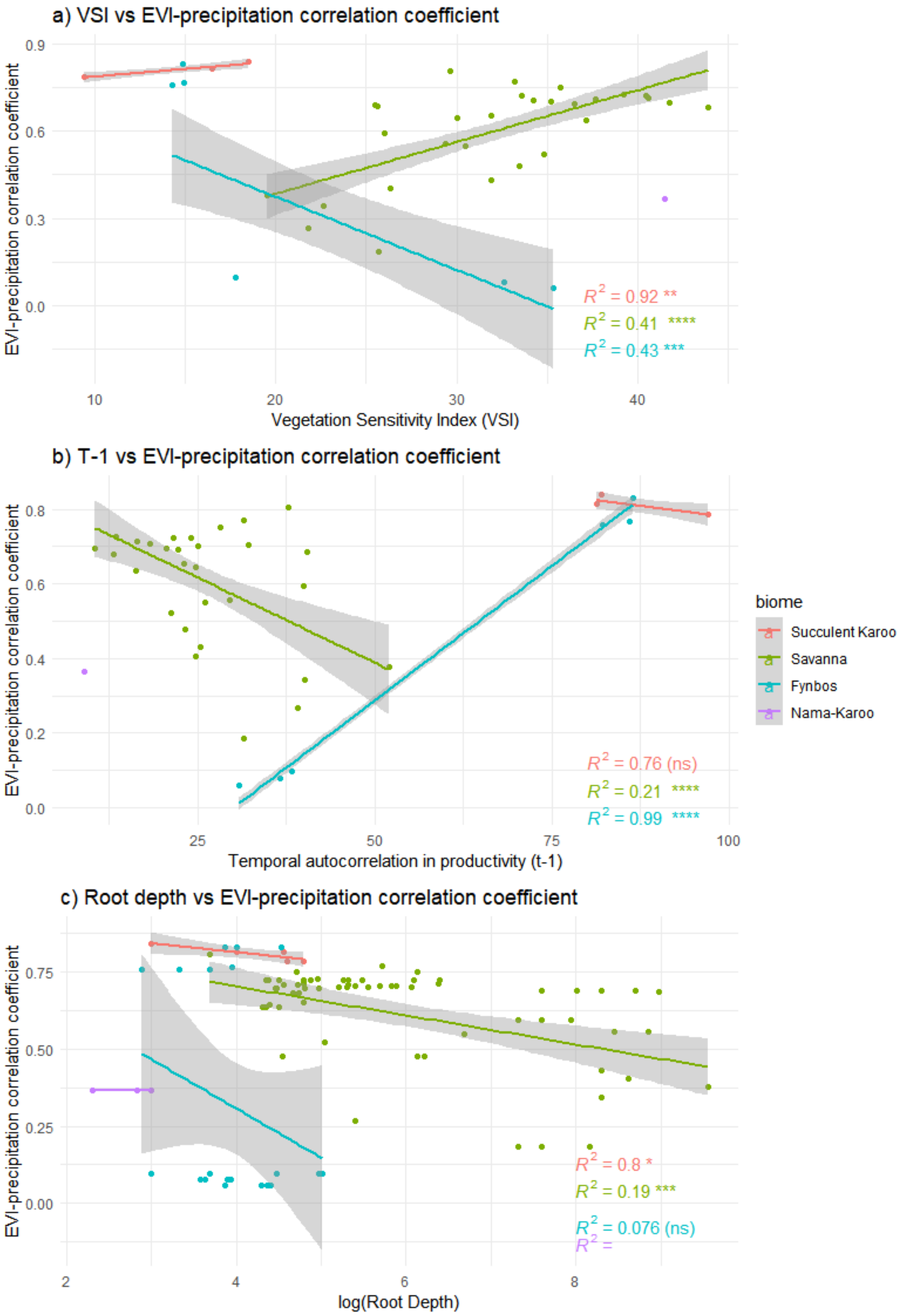


Figure 6.4: Correlation of EVI and Precipitation (R value) potted against Vegetation Sensitivity Index (VSI), Coefficient T-1 (T-1) and Root depth of n=100 records. Regression line and associated R^2 value is shown for each biome with sufficient data (Nama-Karoo). Significance levels are denoted as follows: *** p<0.001, **p<0.01, * p<0.05, NS= not significant.

6.3.4 ROOT DEPTH IN SAVANNA

In the Savanna biome of Southern Africa, VSI (and *t-1*) can be significantly explained by root depth alone (R^2=0.418, p<0.001; **Table 6.2**). Using this relationship, we compare predictions vs observed values of root depth for the Savanna biome of Southern Africa (**Fig. 6.5**).

Table 6.2: Generalised Linear Model estimates, standard error, confidence interval, test statistic (t-value), p-value and R2 for VSI model for the Savanna biome.

	VSI				
Predictors	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*
(Intercept)	48.43	2.41	43.71 – 53.15	20.11	**<0.001**
root_depth [log]	-2.60	0.39	-3.37 – -1.83	-6.61	**<0.001**
Observations	63				
R^2	0.418				

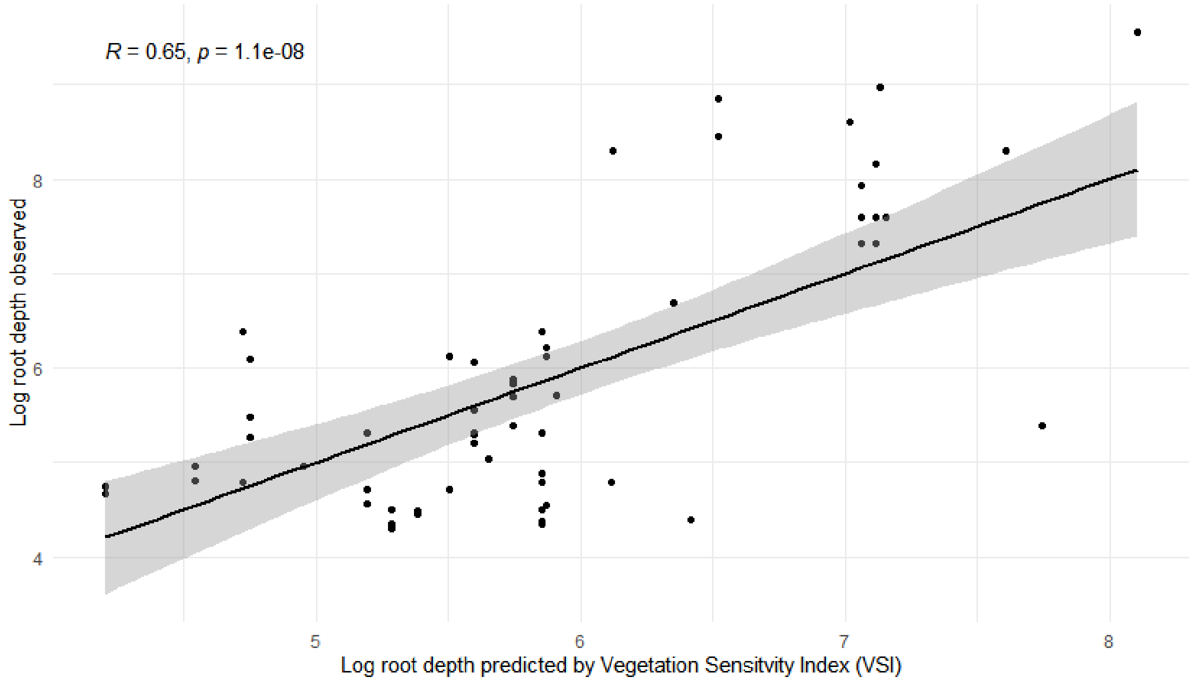


Figure 6.5: Regression of log observed values of root depth *vs.* predicted (by the relationship with VSI) values of root depth. The black line indicates the regression with 95% confidence intervals.

6.4 DISCUSSION

6.4.1 VEGETATION SENSITIVITY AND TEMPORAL AUTOCORRELATION IN PRODUCTIVITY VARIES ACROSS BIOMES

Biomes in the study region show significantly different vegetation sensitivity to climate variability (VSI) and temporal autocorrelation in productivity (*t-1*) from one another, reflecting the varying ability of species, plant functional types and ecosystems to respond to climate variability in drylands: the Succulent Karoo biome stands out with considerably lower VSI values than the rest. In the four driest biomes in the study region – Desert, Succulent Karoo, Nama Karoo and Fynbos (10-80, 20-290, 100-520 and 200-800 mm annual precipitation respectively), we observe the highest lagged effects, whereas in the wetter, more forested biomes, we observe the lowest influence in current productivity from productivity in previous month. Thus, in the driest biomes considered, vegetation productivity shows a weaker relation to current climate conditions and is more linked to the vegetation state of the previous month. The best explanation for the lack of association between vegetation productivity and current climate conditions is that vegetation in these dry biomes tends to have traits that allow for buffering short-term (monthly) climate variability (e.g., drought and high evaporative demands) through facilitating access to groundwater reserves.

6.4.2 VEGETATION SENSITIVITY CAN BE EXPLAINED BY ROOT DEPTH

Our model results provide evidence in favour of the hypothesis that the observed variation in sensitivity to climate can, to a significant extent, be explained by root depth (*hypothesis I*), especially in water-limited environments, is consistent across the studied biomes and growth forms of Southern Africa. Landscape dominant individuals (in terms of land cover, and thus in terms of the dominant reflectance signal at the remote-sensing grain of our analysis – 1km) with deeper roots are able to tap into deeper water resources, reducing sensitivity to month-to-month climate variability. This is also supported by the association between higher temporal autocorrelation in productivity (*t-1*) and deeper roots. Evidence for this relationship in other studies is very limited. However, in the Kgalagadi Transfrontier Park in Botswana it has been observed that *Vachellia erioloba* and *Vachellia* *haematoxylon*, (previously *Acacia)* known to root very deeply have not seen significant canopy dieback in times of drought even though they are facultatively deciduous species (Shadwell and February 2017), suggesting that they can support photosynthesis by tapping deeper water resources.. Remarkably, the regions known for these deep-rooted *Vachellia species* coincide with the areas in our study with lower vegetation sensitivity and the deepest roots in our dataset (e.g. *Vachellia erioloba* and *Senegalia flecki* in the Botswanan Kalahari (Obakeng 2007). This link is worth exploring, especially considering research demonstrated by Stevens et al. (2016) in semi-arid South African Savannas, where deciduousness has water cues as opposed to the globally more common temperature and light cues.

Relationships between vegetation sensitivity and root depth display the same trends across the biomes with sufficient data (i.e., Savanna, Fynbos and Succulent Karoo, **Fig 6.3a, b**), but the range of sensitivity values vary. This suggests that while similar plant rooting strategies exist, biome-and growth form play an important role on the way this is then manifested in terms of response, in agreement with our *hypothesis II*. It should be noted, however, that herbaceous and graminoid growth forms require further study as our results for these growth forms were inconclusive due to limited data.

The environmental correlates associated with the VSI data (**Fig. 6.2c**) predictably indicate that across most of Southern Africa the primary driver of climate sensitivity is water availability. Moreover, areas with low VSI – and hence low sensitivity to current climate conditions and high temporal autocorrelation in productivity (*t-1*) – also tend to show a lack of association between EVI and current precipitation (low EVI-precipitation correlation coefficient), in agreement with our *hypothesis III* (e.g., in Savanna biomes, **Fig. 6.4**). Likewise, areas with lower sensitivity (which correspond to the driest biomes e.g. Desert, Succulent Karoo, Fynbos and Nama Karoo) do not indicate sensitivity to current water availability as defined in the VSI (Seddon, Alistair W.R. Macias-Fauria et al. 2016).

Our results for Savanna and for Succulent Karoo provide evidence that areas with deeper roots tend to not only have lower sensitivity to current climate anomalies (VSI), and greater dependence on previous month productivity (*t-1*), but they are also the areas where vegetation productivity (EVI) is less associated with current precipitation (low EVI-precipitation correlation coefficient). This further suggests that deeper roots play a key role in the aboveground patterns detected through remote sensing. However, this overall pattern is not observed for Fynbos. One possible explanation might be linked to this biome's diverse functional responses to water limitation (Skelton et al. 2015, Skelton 2014), both between and within growth forms (e.g., coexisting shallow-rooted, isohydric restioids and deep-rooted, isohydric proteoid shrubs were mostly unaffected by drought, but anisohydric ericoid shrubs were negatively affected (West et al. 2012)). However, a greater spatial spread across the Fynbos biome of data for diverse growth forms is required to further unpick these patterns.

6.4.3 ROOT DEPTH IN THE SAVANNA BIOME OF SOUTHERN AFRICA

The strong relationship between root depth and response to both current climate variability and previous productivity (VSI and *t-1*) in trees of the Savanna biome indicates that root depth is likely to play a key role in buffering sensitivity to future climate change. It is therefore important to understand which regions have deep roots that offer this enhanced resilience, and which ones may be more vulnerable to short-term climate anomalies. The ability to predict root depth as we have shown in the Savanna biome of Southern Africa represents a step forward in this direction and could inform future natural resource management strategies of ground water reserve management and conservation strategies under changing climates.

6.4.4 IMPLICATIONS

The results of our study hold important implications for the understanding of vegetation resilience to current and future climate change. Applications of this knowledge may prove key for dryland biodiversity conservation under future climate change by answering questions about which biomes, growth forms, belowground trait strategies and indeed species may be more vulnerable in a drier future, as determined by the ability to access groundwater resources with deeper roots. This knowledge can further inform conservation management strategies under climate change, where for example, restoration of dry regions may select for species that have traits such as the ability to root deeply, to improve the future resilience of these systems.

These applications can be extended to agricultural systems in Africa, where along with aridification, irrigation of crops is very limited. Our findings support calls for a shifted focus in drylands, to crops with resilient traits such as enhanced root investment which preliminary findings suggest could be favoured under future climates (Manners et al. 2021). Additional benefits of this approach could exist for crops where yield is gained from belowground plant parts, which would be less affected by short-term drought than aboveground plant parts.

The relationship we demonstrate in the Savanna biome of deeper roots found in areas of lower sensitivity to climate variability may hold key potentially negative implications for the tree-grass dynamics of the Savanna biome of Southern Africa. It has been widely observed that woody encroachment in Savannas is accelerating, including in Africa where woody cover increased on average by 0.25% per year across multiple land uses (i.e. conservation with and without elephants, on large scale and subsistence grazing lands) (Stevens et al. 2017). One of the key drivers of woody encroachment is elevated atmospheric CO2 (Stevens et al. 2017, Donohue et al. 2013), which drives a CO2 fertilisation effect of C3 tree species (Bond and Midgley 2012, Kgope et al. 2010). We therefore hypothesize that, the ability of savanna trees to root deeply, and thus be less sensitive to climate variability under water stress may be exacerbating woody encroachment patterns and continue to do so in a more arid future.

Another implication of these results would be to consider the limits of the advantage that deeper roots can offer plants in times of drought. In those biomes already using deeper roots to deal with water stress, inevitable decline in ground water resources, due to climate change and human extraction (Mamuye and Kebebewu 2018, Chiloane et al. 2021, Liu 2011), will present a major challenge to these plants' survival. In those biomes that are considered wetter and thus do not have species that have evolved deeper roots as an adaptation or do not have the ability to plastically alter root depth (or other traits), plants may not be able to tolerate future drier climatic conditions. This could result in mass plant mortality during drier times or drought periods, and/or gradual shifts in species compositions where some species can tolerate drier conditions and will replace those that cannot. Related to this, deeper-rooted species play a key role in maintaining ground water resources themselves (Le Maitre et al. 1999). If these species are no longer able to survive in drier times due to groundwater decline, and are subsequently lost to these systems, ground water reserves will significantly be impacted and consequently affect ecosystem functioning and services. This feedback is an unwelcome revelation for drylands such as Southern Africa, where severe water shortages are predicted for the future (Davis and Vincent 2017).

Our work thus calls for the maintenance and protection of ground water resources, particularly across the worlds' drylands. The recent droughts witnessed in the Western Cape of South Africa (2015-2018 – (Naik and Abiodun 2019) saw increased extraction of ground water through existing and newly sunk household level boreholes (Ziervogel et al. 2019). More frequent and severe droughts, such as this, could fundamentally change ground water reserves which are already declining due to invasive plant species in this region (Le Maitre et al. 2019).

6.4.5 FUTURE DIRECTIONS

Although great progress has been made in the field of root ecology with the collation of existing root data and the ability to use remotely-derived data to predict root depth, as we have shown for the Savanna biome, and is shown in other work (Fan et al. 2017, Jiang et al. 2020, Yang et al. 2016, Stocker et al. 2021), we still require more efforts in field-based root data collection. We still lack comprehensive spatial and taxonomical coverage, including the relative contributions of intraspecific variation and trait plasticity. Field studies are key and existing data cannot be scaled up using species means linked to occurrence data (supplementary **Fig. S6.5**) because it is likely that intraspecific differences modulated by local climate factors cannot be ignored (e.g., topography-related water gradients Kühn et al *In Prep.*, and Fan et al. 2017). Systematically designed trait collection field campaigns (accounting for spatial spread, inclusion along topography, intraspecies variability) are required, and in the case for Southern Africa, with a focus on under-sampled but potentially vulnerable biomes (e.g., Desert, Fynbos). This would allow for the models in our study to be applied more widely.

Although the focus of this study was rooting depth, other traits show patterns of variation across water availability (Kühn et al. *In Prep* **(Chapter 5; Research Paper 2)**) and thus play a role in enhancing resilience to drier climates. Within below-ground traits, and beyond root depth, root investment in general (e.g., maximum length, root dry matter content, root diameter and root-to-shoot ratio) appears to be key across water gradients within a biome (Kühn et al. *In Prep* **(Chapter 5; Research Paper 2)**). These investment patterns need to be quantified to understand which plants show strategies that enable them to respond to drier periods. Within above-ground traits, alternative strategies to cope with drought and drying can also manifest in trait patterns across water gradients. For example, succulence may be an important factor determining low sensitivity in the Succulent Karoo biome. It is therefore key for the holistic view of vegetation sensitivity across the region to consider alternative trait strategies.

6.5 CONCLUSIONS

Our results show that root depth is a key trait determining vegetation sensitivity to climate variability in Southern Africa, with the proposed mechanisms being that deeper roots enhance access to deeper water resources that remain available in periods of drought or reduced surface water availability. We therefore suggest deeper roots play (and will do so increasingly) an important role in the resilience of vegetation in Southern Africa and potentially across drylands globally, which are set to become warmer and drier. Nevertheless, even the deepest roots will not buffer against long-term, multi-month/multiannual droughts, and may lose their advantage when groundwater resources are diminished due to climate change and human extraction. Further, our work demonstrates the utility of explicitly linking strategically collected field trait data with spatially continuous and readily available remote sensing data, to observe and predict environmental patterns and responses to climatic changes.

AUTHOR CONTRIBUTION STATEMENT

NK and MM-F conceptualised the research and designed the approach with comments from all authors. NK and MS collected, processed, and analysed the data with assistance from MM-F and CT. NK wrote the first draft of the manuscript with significant contributions from all authors (MM-F, MS, CT and KJW).

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Supplementary material

Table S6.3: Biomes of Southern Africa included in this analysis with typical annual precipitation range and dominant vegetation types as described by PlantZAfrica, South African National Biodiversity Institute (http://pza.sanbi.org/vegetation)

Biome	Description of typical annual precipitation range	Dominant Vegetation type
Albany Thicket	250-300mm	Dense shrubland and low forest dominated by evergreen, sclerophyllous or succulent trees, shrubs and vines.
Azonal Vegetation	? Range 600-800	Dominated by vegetation that crosses climatic and geographic boundaries.
Desert	10-80mm	Annual plants (often grasses)
Forests	525 – winter rainfall region 725 summer rainfall region	Evergreen trees
Fynbos	200-800 (lower end renosterveld)	Encompasses two vegetation groups: Fynbos (dominated by ericoid and proteoid shrubs and restios) and Renosterveld (dominated by shrubs, grasses, geophytes)
Grassland	(?) Range up to 600-1000	Grasses
Indian Ocean Coastal Belt	(?) Range 800-1200	Mixture of trees and grasses
Nama-Karoo	100-520mm	Grasses and dwarf shrubs
Savanna	235-1000mm	Mixture of shrub-trees and grasses. The grass component is dominated by C4 grasses (with some C3 grasses in regions experiencing more winter rain).
Southern African Mangroves	(?)	Mangrove trees
Succulent Karoo	20-290 mm	Dwarf succulent shrubs (predominantly from the Mesembryanthemaceae and Crassulaceae families)

Table S6.4: List of data sources, species, growth form, biome, coordinates, root depth and growth form. Note data sources do not reflect the new naming of *Acacia* species therefore: *Acacia Fleckii = Senegalia fleckii*, *Acacia Erioloba = Vachellia erioloba*, *Acacia grandicornuta= Vachellia grandicornuta Acacia nigrescens = Senegalia nigrescens*.

#	dataset source	original reference	dataset ID	species	growth form	Biome	longitude	latitude	root depth (cm)
1	fred	Bornman TG, Adams JB, Bate GC. 2004. The influence of floodplain geohydrology on the distribution of Sarcocornia pillansii in the Olifants Estuary on the West Coast, South Africa. Journal of Arid Environments 56(4):603â€“625.	33221	Sarcocornia pillansii	shrub	Azonal Vegetation	18.2064	-31.706	120
2	fred	Bornman TG, Adams JB, Bate GC. 2004. The influence of floodplain geohydrology on the distribution of Sarcocornia pillansii in the Olifants Estuary on the West Coast, South Africa. Journal of Arid Environments 56(4):603â€“625.	33222	Sarcocornia pillansii	shrub	Azonal Vegetation	18.206	-31.705	120
3	fred	Carrick PJ. 2003. Competitive and facilitative relationships among three shrub species , and the role of browsing intensity and rooting depth in the Succulent Karoo, South Africa. Journal of Vegetation Science 14(5):761-772.	33273	Leipoldtia schultzei	shrub	Fynbos	18.2497	-30.4128	18
4	fred	Carrick PJ. 2003. Competitive and facilitative relationships among three shrub species , and the role of browsing intensity and rooting depth in the Succulent Karoo, South Africa. Journal of Vegetation Science 14(5):761-772.	33274	Ruschia robusta	shrub	Fynbos	18.2497	-30.4128	28
5	fred	Carrick PJ. 2003. Competitive and facilitative relationships among three shrub species , and the role of browsing intensity and rooting depth in the Succulent Karoo, South Africa. Journal of Vegetation Science 14(5):761-772.	33275	Hirpicium alienatum	shrub	Fynbos	18.2497	-30.4128	40
6	fred	Esler KJ, Rundel PW. 1999. Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: the Succulent Karoo and Mojave Desert ecosystems. Plant Ecology 142(1-2): 97-104.	33544	Enarganthe actonaria	shrub	Nama-Karoo	20.3227	-28.6024	10
7	fred	Esler KJ, Rundel PW. 1999. Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: the Succulent Karoo and Mojave Desert ecosystems. Plant Ecology 142(1-2): 97-104.	33545	Zygophyllum prismatocarpum	shrub	Nama-Karoo	20.3227	-28.6024	17
8	fred	Esler KJ, Rundel PW. 1999. Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: the Succulent Karoo and Mojave Desert ecosystems. Plant Ecology 142(1-2): 97-104.	33548	Euphorbia wallichii	shrub	Nama-Karoo	20.3227	-28.6024	20
9	fred	February EC, Allsopp N, Shabane T, Hattas D. 2011. Coexistence of a C4 grass and a leaf succulent shrub in an arid ecosystem. The relationship between rooting depth, water and nitrogen. Plant and Soil 349(1-2): 253-260.	33565	Ruschia robusta	shrub	Succulent Karoo	18.71667	-30.5333	100
10	fred	February EC, Allsopp N, Shabane T, Hattas D. 2011. Coexistence of a C4 grass and a leaf succulent shrub in an arid ecosystem. The relationship between rooting depth, water and nitrogen. Plant and Soil 349(1-2): 253-260.	33566	Stipagrostis brevifolia	graminoid	Succulent Karoo	18.71667	-30.5333	120
11	fred	Haigh H. 1966. Root development in the sandy soils of Zulu land. Forestry in South Africa 7: 31-36.	33692	Pinus caribaea	tree	Savanna	31.5841	-27.9255	500
12	fred	Haigh H. 1966. Root development in the sandy soils of Zulu land. Forestry in South Africa 7: 31-36.	33693	Pinus elliottii	tree	Savanna	31.5826	-27.9265	457.2
13	fred	Haigh H. 1966. Root development in the sandy soils of Zulu land. Forestry in South Africa 7: 31-36.	33694	Corymbia citriodora	tree	Savanna	31.584	-27.9266	94
14	fred	Haigh H. 1966. Root development in the sandy soils of Zulu land. Forestry in South Africa 7: 31-36.	33695	Corymbia citriodora	tree	Savanna	31.5849	-27.9262	155
15	fred	Higgins KB. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley Southwestern Cape Province South Africa. South African journal of botany 53:249â€“258.	33731	Cliffortia ruscifolia	shrub	Fynbos	18.9218	-33.9479	150
16	fred	Higgins KB. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley Southwestern Cape Province South Africa. South African journal of botany 53:249â€“258.	33732	Otholobium fruticans	shrub	Fynbos	18.9218	-33.9479	150
17	fred	Higgins KB. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley Southwestern Cape Province South Africa. South African journal of botany 53:249â€“258.	33730	Erica plukenetii	shrub	Fynbos	18.9218	-33.9479	40
18	fred	Higgins KB. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley	33733	Aristea capitata	herb	Fynbos	18.9218	-33.9479	145

		Southwestern Cape Province South Africa. South African journal of botany 53:249â€“258.							
19	fred	Higgins KB. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley Southwestern Cape Province South Africa. South African journal of botany 53:249â€“258.	33734	Watsonia borbonica	herb	Fynbos	18.9218	-33.9479	40
20	fred	Higgins KB. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley Southwestern Cape Province South Africa. South African journal of botany 53:249â€“258.	33735	Restio gaudichaudianus	graminoid	Fynbos	18.9218	-33.9479	20
21	fred	Higgins KB. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley Southwestern Cape Province South Africa. South African journal of botany 53:249â€“258.	33736	Tetraria bromoides	graminoid	Fynbos	18.9218	-33.9479	88
22	fred	Jennings CMH. 1974. The Hydrogeology of Botswana. Dissertation. PhD thesis. University of Natal, Natal, South Africa.	33825	Boscia albitrunca	tree	Savanna	22.9712	-23.95	14100
23	fred	Jennings CMH. 1974. The Hydrogeology of Botswana. Dissertation. PhD thesis. University of Natal, Natal, South Africa.	33826	Boscia albitrunca	tree	Savanna	23.3172	-25.2608	7860
24	fred	Kuschera-Mitter L. 1996. Growth strategies of plant roots in different climatic regions. Acta Phytogeographica Suecica 81:12-16.	34016	Aloe littoralis	shrub	Savanna	16.9966	-22.5925	40
25	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34220	Ziziphus mucronata	tree	Savanna	26.8402	-22.3243	800
26	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34221	Acacia fleckii	tree	Savanna	26.5081	-22.4924	2800
27	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34222	Dichrostachys cinerea	tree	Savanna	26.5081	-22.4924	2000
28	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34223	Terminalia sericea	tree	Savanna	26.5081	-22.4924	1500
29	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34224	Boscia albitrunca	tree	Savanna	26.3892	-22.3942	2000
30	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34225	Acacia fleckii	tree	Savanna	26.3892	-22.3942	1500
31	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34226	Acacia fleckii	tree	Savanna	26.3892	-22.3942	1500
32	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34228	Boscia albitrunca	tree	Savanna	26.3892	-22.3942	3500
33	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34229	Acacia erioloba	tree	Savanna	26.4662	-22.3626	5500
34	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34230	Acacia erioloba	tree	Savanna	26.455	-22.3506	4000
35	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting	34231	Boscia albitrunca	tree	Savanna	26.4321	-22.3402	4000

		vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i							
36	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34232	Acacia erioloba	tree	Savanna	26.4283	-22.3134	7000
37	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34233	Boscia albitrunca	tree	Savanna	26.4283	-22.3134	7000
38	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34234	Acacia erioloba	tree	Savanna	26.4283	-22.3134	4700
39	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34235	Securidaca longipedunculata	shrub	Savanna	26.4759	-22.277	6000
40	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34236	Securidaca longipedunculata	shrub	Savanna	26.4759	-22.277	4000
41	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34237	Securidaca longipedunculata	shrub	Savanna	26.4759	-22.277	3000
42	fred	Obakeng OT, de Vries JJ, Lubczynski MW. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation. Dissertation (Wageningen University, The Netherlands). Available at: http://www.i	34238	Acacia erioloba	tree	Savanna	26.4759	-22.277	2000
43	fred	Rutherford M. 1983. Growth rates, biomass and distribution of selected woody plant roots in Burkea africana-Ochna pulchra savanna. Vegetatio 52(1): 45-63.	34366	Ochna pulchra	tree	Savanna	28.71667	-24.6667	220
44	fred	Rutherford M. 1983. Growth rates, biomass and distribution of selected woody plant roots in Burkea africana-Ochna pulchra savanna. Vegetatio 52(1): 45-63.	34367	Burkea africana	tree	Savanna	28.71667	-24.6667	220
45	fred	Rutherford M. 1983. Growth rates, biomass and distribution of selected woody plant roots in Burkea africana-Ochna pulchra savanna. Vegetatio 52(1): 45-63.	34368	Terminalia sericea	tree	Savanna	28.71667	-24.6667	220
46	fred	Shiponeni N, Allsopp N, Carrick PJ, Hoffman MT. 2011. Competitive interactions between grass and succulent shrubs at the ecotone between an arid grassland and succulent shrubland in the Karoo. Plant Ecology 212(5): 795-808.	34514	Stipagrostis brevifolia	graminoid	Succulent Karoo	18.4183	-30.2492	95
47	fred	Shiponeni N, Allsopp N, Carrick PJ, Hoffman MT. 2011. Competitive interactions between grass and succulent shrubs at the ecotone between an arid grassland and succulent shrubland in the Karoo. Plant Ecology 212(5): 795-808.	34515	Ruschia robusta	shrub	Succulent Karoo	18.4183	-30.2492	55
48	fred	Shiponeni N, Allsopp N, Carrick PJ, Hoffman MT. 2011. Competitive interactions between grass and succulent shrubs at the ecotone between an arid grassland and succulent shrubland in the Karoo. Plant Ecology 212(5): 795-808.	34516	Leipoldtia pauciflora	shrub	Succulent Karoo	17.9806	-29.7008	20
49	fred	van Wyk WL. 1963. Ground-Water Studies in Northern Natal, Zulu Land and Surrounding Areas.	35106	Eucalyptus sideroxylon	tree	Grassland	31.3193	-27.3033	2743
50	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	19	Ruschia multiflora	shrub	Fynbos	20.38013	-33.3555	91
51	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	63	Anthospermum spathulatum	shrub	Fynbos	18.85527	-33.835	82
52	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	96	Stoebe plumosa	shrub	Fynbos	18.85444	-33.8314	40
53	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	36	Anthospermum spathulatum	shrub	Fynbos	18.85885	-33.8298	32
54	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	87	Dicerothamnus rhinocerotis (km)	shrub	Fynbos	18.85473	-33.8314	58

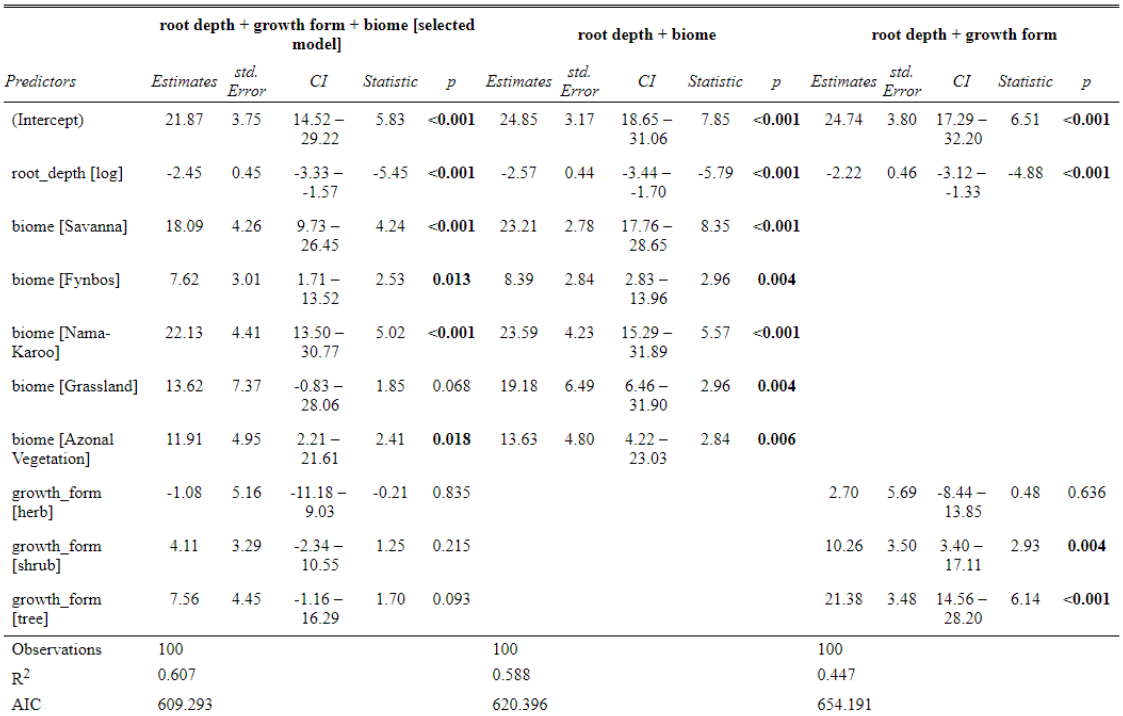
55	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	10	Aspalathus nigra	shrub	Fynbos	20.38593	-33.3366	119
56	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	12	Aspalathus nigra	shrub	Fynbos	20.38608	-33.3367	95
57	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	71	Dicerothamnus rhinocerotis (km)	shrub	Fynbos	18.85313	-33.8335	39
58	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	48	Anthospermum spathulatum	shrub	Fynbos	18.85985	-33.8321	20
59	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	77	Stoebe plumosa	shrub	Fynbos	18.85316	-33.8337	85
60	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	74	Stoebe plumosa	shrub	Fynbos	18.85319	-33.8337	30
61	Kühn_in_prep	Kühn et al. *In Prep*. Deeper roots to survive drier climates? A case study in the Cape Floristic Region	107	Aspalathus nigra	shrub	Fynbos	20.38671	-33.3369	116
62	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	1	Acacia grandicornuta	tree	Savanna	31.57662	-24.9997	199.9
63	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	2	Acacia grandicornuta	tree	Savanna	31.57677	-24.9999	259.2
64	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	3	Acacia grandicornuta	tree	Savanna	31.57672	-25	432.5
65	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	4	Acacia grandicornuta	tree	Savanna	31.57661	-25	201.8
66	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	5	Acacia grandicornuta	tree	Savanna	31.57596	-24.9996	183.1
67	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	7	Acacia nigrescens	tree	Savanna	31.40191	-25.1088	143.6
68	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	8	Acacia nigrescens	tree	Savanna	31.46135	-25.0982	111.5
69	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	9	Acacia nigrescens	tree	Savanna	31.466	-25.096	240.4
70	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	10	Acacia nigrescens	tree	Savanna	31.4662	-25.0958	192.5
71	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	11	Combretum apiculatum	tree	Savanna	31.41327	-25.1067	120
72	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	12	Combretum apiculatum	tree	Savanna	31.39855	-25.109	114.9
73	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	13	Combretum apiculatum	tree	Savanna	31.39942	-25.109	106.7
74	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	14	Combretum apiculatum	tree	Savanna	31.41564	-25.1019	86.4
75	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	15	Combretum apiculatum	tree	Savanna	31.41112	-25.1074	122.9
76	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	16	Combretum hereroense	tree	Savanna	31.41156	-25.1319	112.3
77	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	17	Combretum hereroense	tree	Savanna	31.41272	-25.1324	95.1
78	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	18	Combretum hereroense	tree	Savanna	31.41278	-25.1324	203.1
79	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	19	Combretum hereroense	tree	Savanna	31.408	-25.1303	143.2
80	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	20	Combretum hereroense	tree	Savanna	31.41686	-25.1011	88.4
81	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	21	Dichrostachys cinerea	tree	Savanna	31.28887	-25.1932	90.6

82	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	22	Dichrostachys cinerea	tree	Savanna	31.28687	-25.1931	74.2
83	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	23	Dichrostachys cinerea	tree	Savanna	31.28398	-25.2033	120.4
84	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	24	Dichrostachys cinerea	tree	Savanna	31.27478	-25.2075	80.4
85	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	25	Dichrostachys cinerea	tree	Savanna	31.28677	-25.1948	77.3
86	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	26	Philenoptera violacea	tree	Savanna	31.59126	-25.0488	220.4
87	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	27	Philenoptera violacea	tree	Savanna	31.59271	-25.05	295.7
88	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	28	Philenoptera violacea	tree	Savanna	31.59266	-25.0497	340
89	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	29	Philenoptera violacea	tree	Savanna	31.59266	-25.05	358.1
90	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	30	Philenoptera violacea	tree	Savanna	31.60118	-25.0673	304
91	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	31	Sclerocarya birrea	tree	Savanna	31.43706	-25.0969	203.2
92	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	32	Sclerocarya birrea	tree	Savanna	31.46132	-25.0982	458.9
93	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	33	Sclerocarya birrea	tree	Savanna	31.46285	-25.0976	442.1
94	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	34	Sclerocarya birrea	tree	Savanna	31.43867	-25.0974	595
95	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	35	Sclerocarya birrea	tree	Savanna	31.41358	-25.1065	590.9
96	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	36	Terminalia sericea	tree	Savanna	31.43441	-25.0973	132
97	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	37	Terminalia sericea	tree	Savanna	31.43449	-25.0974	90.7
98	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	38	Terminalia sericea	tree	Savanna	31.43465	-25.0973	77.7
99	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	39	Terminalia sericea	tree	Savanna	31.43468	-25.0973	120.7
100	Zhou_2020	Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. New Phytologist, 227(5), 1350-1361.	40	Terminalia sericea	tree	Savanna	31.4354	-25.0971	79.5

Table S6.3: Mean, median and standard deviation of VSI and t-1 across biomes of Southern Africa.

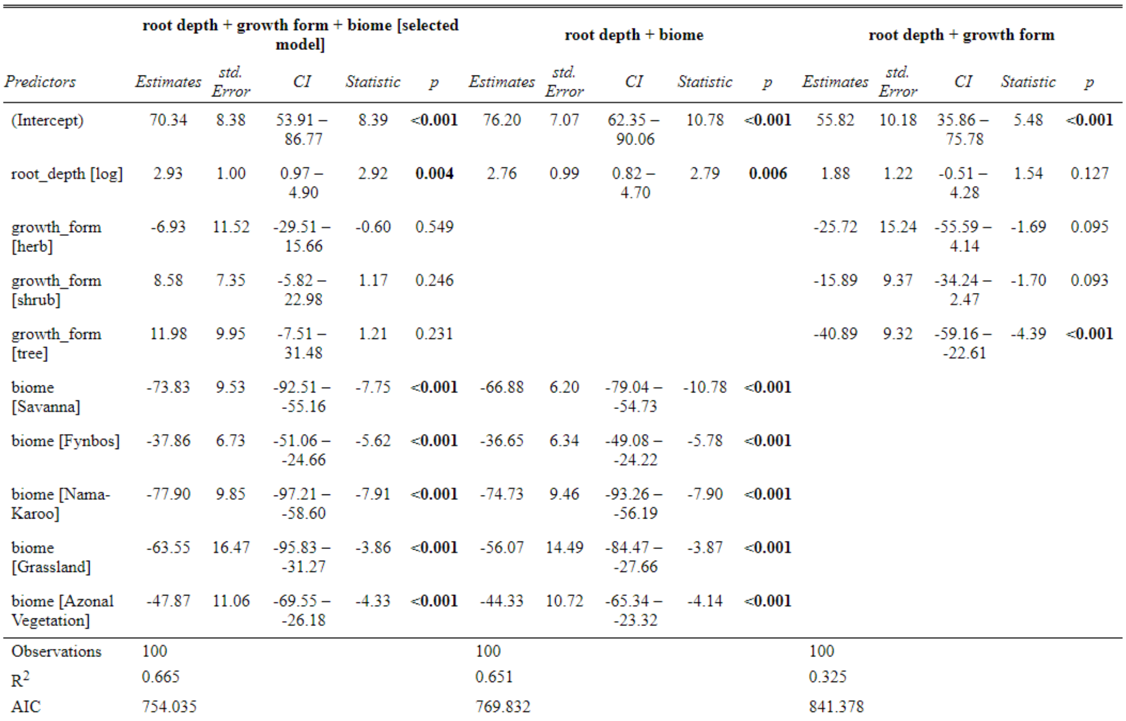
Biome	**Mean VSI**	**SD VSI**	**Median VSI**	**Mean *t-1***	**SD *t-1***	**Median *t-1***
Albany Thicket	34.12	7.307	34.33	29.78	15.815	28.06
Azonal Vegetation	30.56	9.819	31.45	38.65	23.950	33.28
Desert	25.73	13.051	24.60	61.74	25.494	62.42
Forests	25.73	8.842	26.19	25.10	13.420	24.38
Fynbos	26.84	10.804	25.45	46.24	23.682	46.10
Grassland	27.44	7.579	27.73	36.56	12.419	36.34
Indian Ocean Coastal Belt	32.13	7.326	32.92	20.34	13.663	18.71
Nama Karoo	29.90	9.509	29.43	46.65	19.593	45.74
Savanna	28.40	6.875	28.19	37.84	14.723	36.83
Succulent Karoo	19.46	8.500	18.57	73.69	18.112	75.13
Waterbodies	31.69	7.685	32.10	26.65	17.994	23.89
Southern Africa mangroves	29.98	7.934	29.14	20.26	13.470	19.42

Table S6.4: Generalised Least Squares model comparison including different combinations of variables. Model estimates, standard error, confidence interval, test-statistic (t-value), p-value and R^2 for Vegetation Sensitivity Index models.



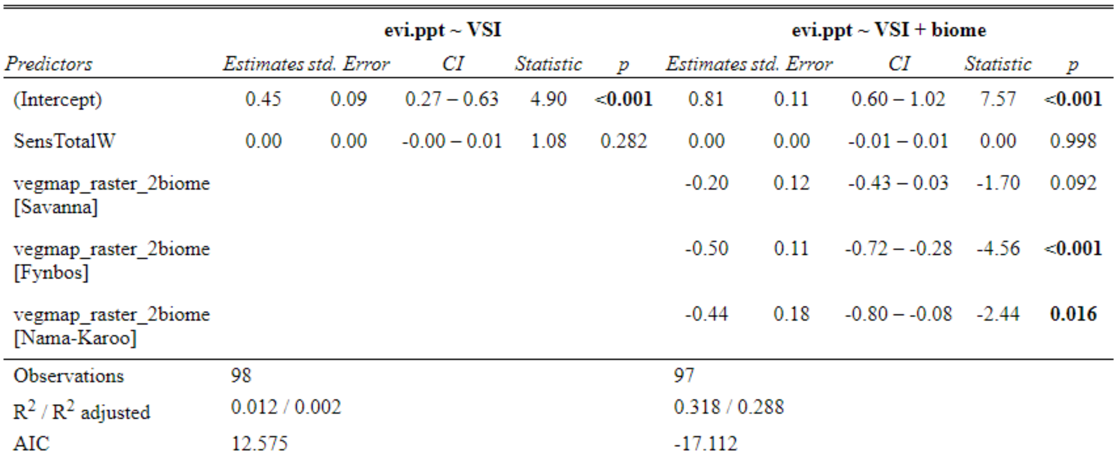
	root depth + growth form + biome [selected model]					**root depth + biome**					**root depth + growth form**				
Predictors	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*
(Intercept)	21.87	3.75	14.52 – 29.22	5.83	**<0.001**	24.85	3.17	18.65 – 31.06	7.85	**<0.001**	24.74	3.80	17.29 – 32.20	6.51	**<0.001**
root_depth [log]	-2.45	0.45	-3.33 – -1.57	-5.45	**<0.001**	-2.57	0.44	-3.44 – -1.70	-5.79	**<0.001**	-2.22	0.46	-3.12 – -1.33	-4.88	**<0.001**
biome [Savanna]	18.09	4.26	9.73 – 26.45	4.24	**<0.001**	23.21	2.78	17.76 – 28.65	8.35	**<0.001**					
biome [Fynbos]	7.62	3.01	1.71 – 13.52	2.53	**0.013**	8.39	2.84	2.83 – 13.96	2.96	**0.004**					
biome [Nama-Karoo]	22.13	4.41	13.50 – 30.77	5.02	**<0.001**	23.59	4.23	15.29 – 31.89	5.57	**<0.001**					
biome [Grassland]	13.62	7.37	-0.83 – 28.06	1.85	0.068	19.18	6.49	6.46 – 31.90	2.96	**0.004**					
biome [Azonal Vegetation]	11.91	4.95	2.21 – 21.61	2.41	**0.018**	13.63	4.80	4.22 – 23.03	2.84	**0.006**					
growth_form [herb]	-1.08	5.16	-11.18 – 9.03	-0.21	0.835						2.70	5.69	-8.44 – 13.85	0.48	0.636
growth_form [shrub]	4.11	3.29	-2.34 – 10.55	1.25	0.215						10.26	3.50	3.40 – 17.11	2.93	**0.004**
growth_form [tree]	7.56	4.45	-1.16 – 16.29	1.70	0.093						21.38	3.48	14.56 – 28.20	6.14	**<0.001**
Observations	100					100					100				
R^2	0.607					0.588					0.447				
AIC	609.293					620.396					654.191				

Table 6.5: Generalised Least Squares model comparison including different combinations of variables. Model estimates, standard error, confidence interval, test-statistic (t-value), p-value and R^2 for temporal autocorrelation in productivity (t-1) models.



	root depth + growth form + biome [selected model]					**root depth + biome**					**root depth + growth form**				
Predictors	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*
(Intercept)	70.34	8.38	53.91 – 86.77	8.39	**<0.001**	76.20	7.07	62.35 – 90.06	10.78	**<0.001**	55.82	10.18	35.86 – 75.78	5.48	**<0.001**
root_depth [log]	2.93	1.00	0.97 – 4.90	2.92	**0.004**	2.76	0.99	0.82 – 4.70	2.79	**0.006**	1.88	1.22	-0.51 – 4.28	1.54	0.127
growth_form [herb]	-6.93	11.52	-29.51 – 15.66	-0.60	0.549						-25.72	15.24	-55.59 – 4.14	-1.69	0.095
growth_form [shrub]	8.58	7.35	-5.82 – 22.98	1.17	0.246						-15.89	9.37	-34.24 – 2.47	-1.70	0.093
growth_form [tree]	11.98	9.95	-7.51 – 31.48	1.21	0.231						-40.89	9.32	-59.16 – -22.61	-4.39	**<0.001**
biome [Savanna]	-73.83	9.53	-92.51 – -55.16	-7.75	**<0.001**	-66.88	6.20	-79.04 – -54.73	-10.78	**<0.001**					
biome [Fynbos]	-37.86	6.73	-51.06 – -24.66	-5.62	**<0.001**	-36.65	6.34	-49.08 – -24.22	-5.78	**<0.001**					
biome [Nama-Karoo]	-77.90	9.85	-97.21 – -58.60	-7.91	**<0.001**	-74.73	9.46	-93.26 – -56.19	-7.90	**<0.001**					
biome [Grassland]	-63.55	16.47	-95.83 – -31.27	-3.86	**<0.001**	-56.07	14.49	-84.47 – -27.66	-3.87	**<0.001**					
biome [Azonal Vegetation]	-47.87	11.06	-69.55 – -26.18	-4.33	**<0.001**	-44.33	10.72	-65.34 – -23.32	-4.14	**<0.001**					
Observations	100					100					100				
R^2	0.665					0.651					0.325				
AIC	754.035					769.832					841.378				

Table 6.6: Generalised Linear model outputs of Enhanced Vegetation Index (EVI)-precipitation correlation coefficient vs. Vegetation Sensitivity Index (VSI), temporal autocorrelation in productivity (t-1) and log root depth alongside models including biome as a variable.



	evi.ppt ~ VSI					**evi.ppt ~ VSI + biome**				
Predictors	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*
(Intercept)	0.45	0.09	0.27 – 0.63	4.90	**<0.001**	0.81	0.11	0.60 – 1.02	7.57	**<0.001**
SensTotalW	0.00	0.00	-0.00 – 0.01	1.08	0.282	0.00	0.00	-0.01 – 0.01	0.00	0.998
vegmap_raster_2biome [Savanna]						-0.20	0.12	-0.43 – 0.03	-1.70	0.092
vegmap_raster_2biome [Fynbos]						-0.50	0.11	-0.72 – -0.28	-4.56	**<0.001**
vegmap_raster_2biome [Nama-Karoo]						-0.44	0.18	-0.80 – -0.08	-2.44	**0.016**
Observations	98					97				
R^2 / R^2 adjusted	0.012 / 0.002					0.318 / 0.288				
AIC	12.575					-17.112				

	evi.ppt ~ t-1					**evi.ppt ~ t-1 + biome**				
Predictors	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*
(Intercept)	0.48	0.05	0.38 – 0.57	9.81	**<0.001**	0.14	0.15	-0.16 – 0.45	0.93	0.354
CoeffPercT1	0.00	0.00	-0.00 – 0.00	1.54	0.126	0.01	0.00	0.00 – 0.01	5.12	**<0.001**
vegmap_raster_2biome [Savanna]						0.27	0.13	0.02 – 0.52	2.12	**0.036**
vegmap_raster_2biome [Fynbos]						-0.23	0.11	-0.44 – -0.01	-2.09	**0.039**
vegmap_raster_2biome [Nama-Karoo]						0.15	0.18	-0.21 – 0.51	0.85	0.398
Observations	98					97				
R^2 / R^2 adjusted	0.024 / 0.014					0.469 / 0.446				
AIC	11.361					-41.449				

	evi.ppt ~ root depth					**evi.ppt ~ root depth + biome**				
Predictors	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*	*Estimates*	*std. Error*	*CI*	*Statistic*	*p*
(Intercept)	0.52	0.09	0.35 – 0.70	5.97	**<0.001**	1.02	0.11	0.80 – 1.25	9.13	**<0.001**
root_depth [log]	0.00	0.02	-0.03 – 0.03	0.20	0.840	-0.05	0.02	-0.08 – -0.02	-3.27	**0.002**
vegmap_raster_2biome [Savanna]						-0.10	0.10	-0.30 – 0.09	-1.06	0.291
vegmap_raster_2biome [Fynbos]						-0.51	0.10	-0.71 – -0.31	-5.09	**<0.001**
vegmap_raster_2biome [Nama-Karoo]						-0.52	0.15	-0.82 – -0.22	-3.47	**0.001**
Observations	98					97				
R^2 / R^2 adjusted	0.000 / -0.010					0.389 / 0.362				
AIC	13.721					-27.774				

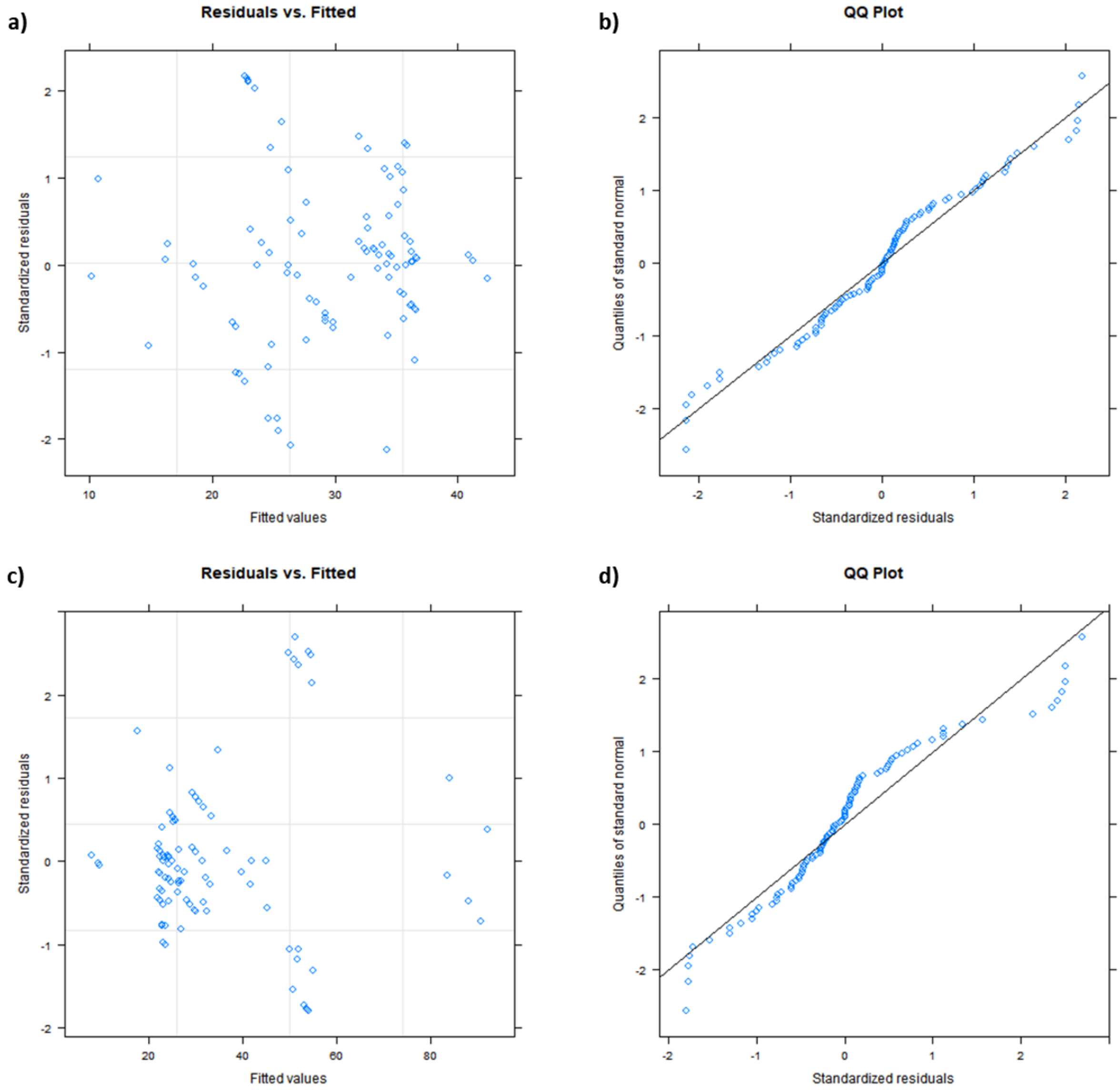


Figure S6.1: Diagnostic plots for generalised least squares models explaining VSI (a, b) and t-1 (c, d). Residuals vs Fitted plots (a, c) show evaluate homogeneity of variances and the Q-Q plots evaluate normality.

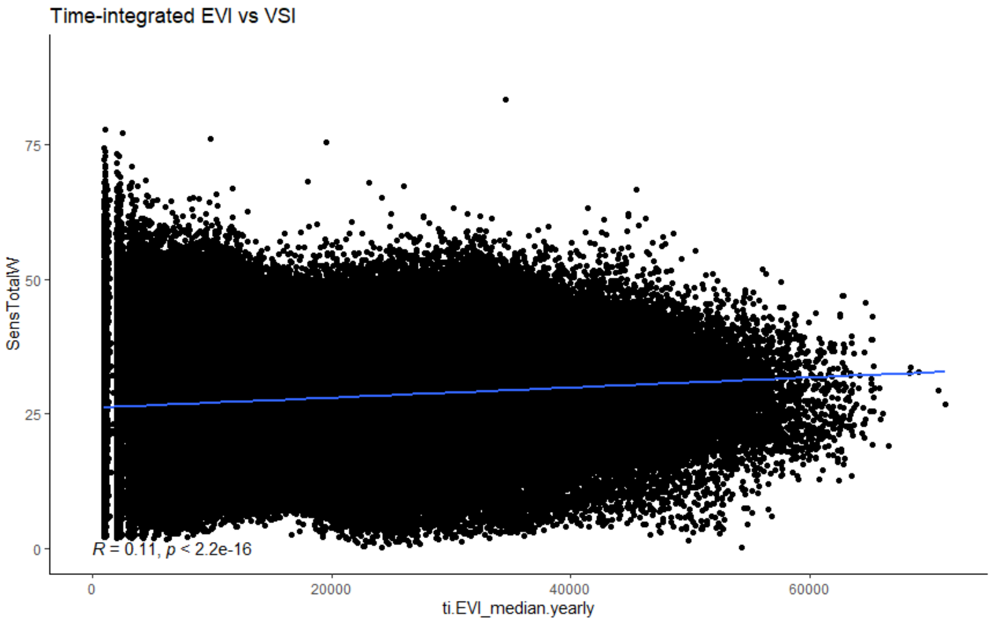


Figure S6.2: Time integrated Enhanced Vegetation Index plotted against Vegetation Sensitivity Index (VSI), indicating that VSI patterns in Southern Africa are not merely reflecting vegetation productivity patterns (EVI).

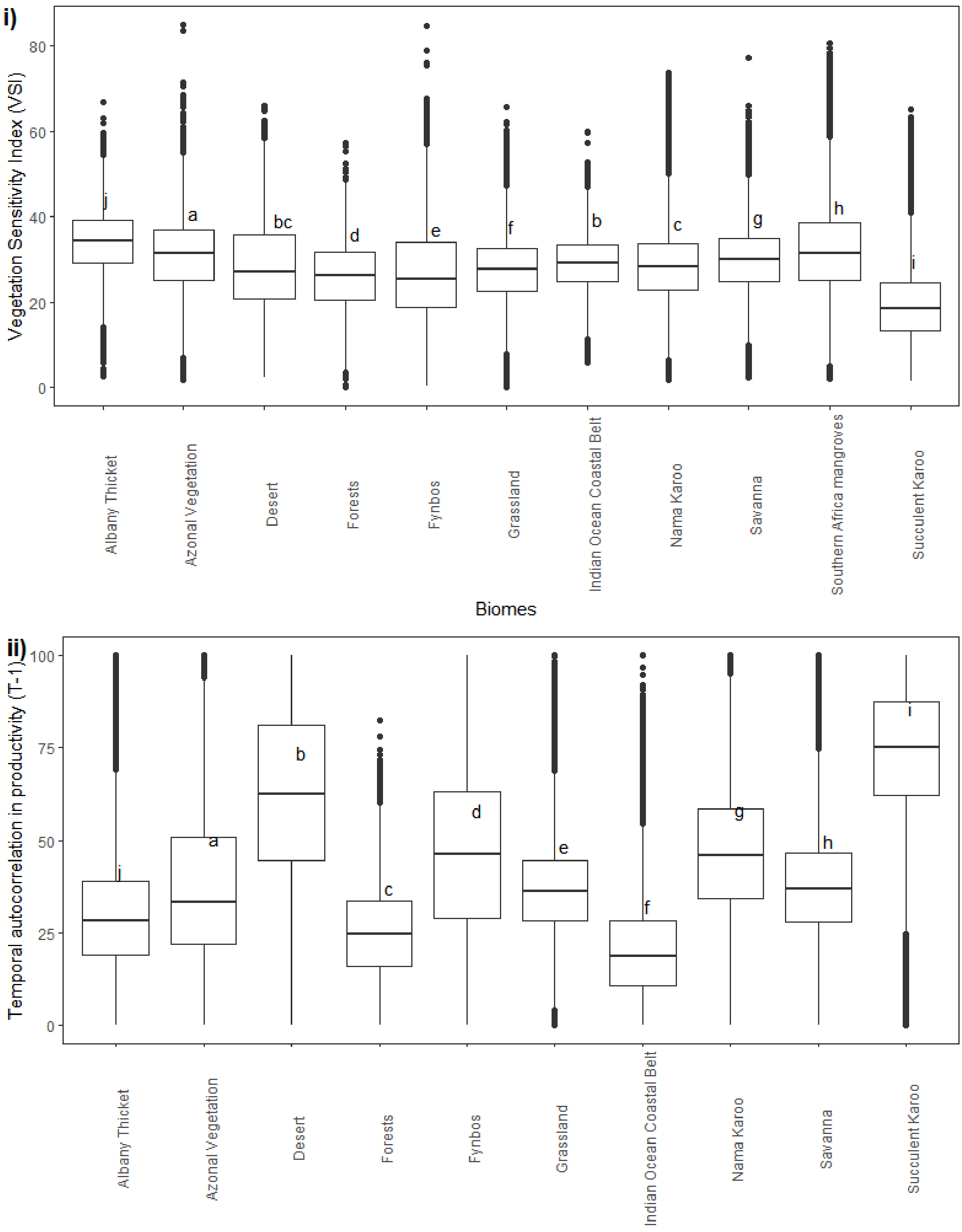


Figure S6.3: Boxplots showing variation in i) vegetation sensitivity index (VSI) and ii) temporal autocorrelation in productivity (t-1), across biomes in southern Africa. Post-hoc Tukey results are presented with letters above boxplots, where different letters (a-j) imply significant differences in the variable among biomes.

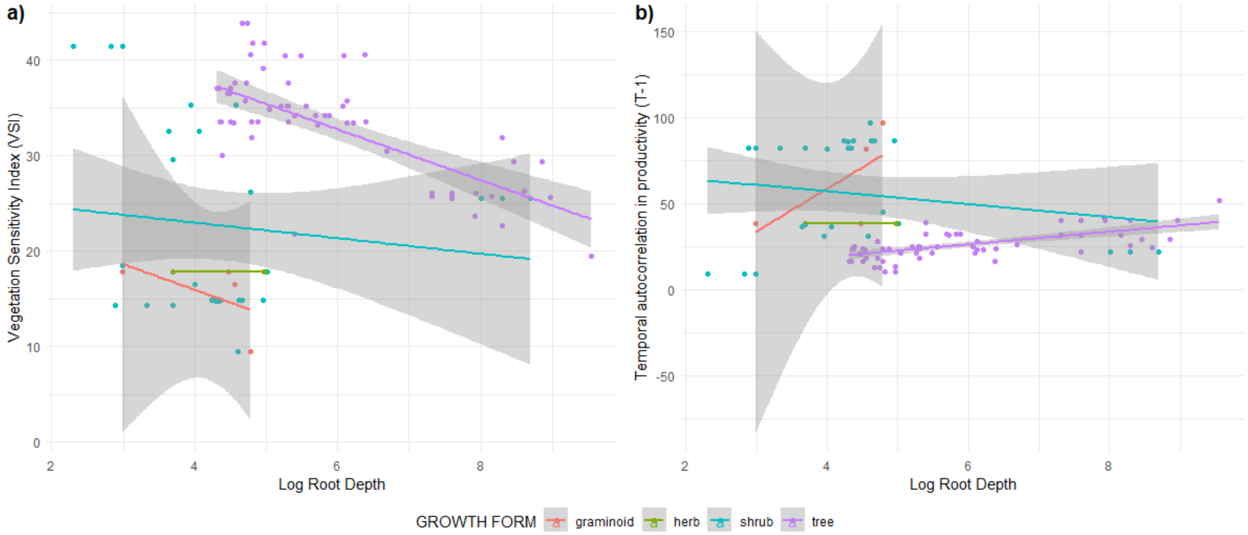


Figure S6.4: Regression of log root depth as a function of a) Vegetation Sensitivity (VSI) and b) Temporal autocorrelation in productivity (T_{-1}), separated by growth form. Regression line is shown for each growth form with sufficient data to note the varying intercepts. Shrub points congregated closer the Savanna trees with deeper roots, were identified as savanna shrubs, suggesting that for these individuals, the combination of biome and growth form is key in determining the expected relationship with VSI and t-1.

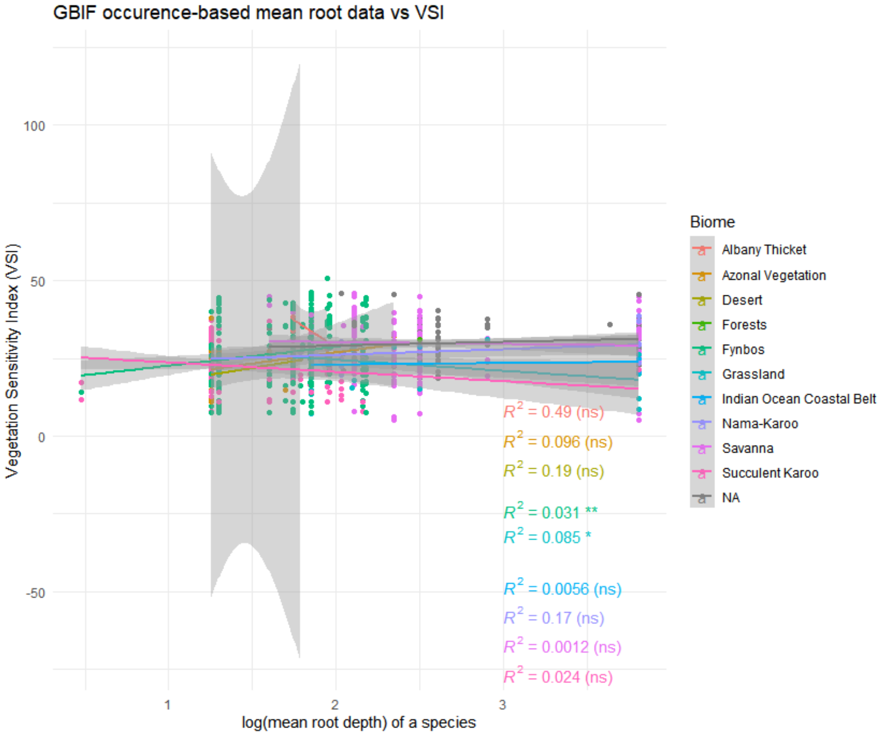


Figure S6.5: Regression of mean values of root depth per species in our dataset for each occurrence point available for those species in GBIF. This indicates the scaling up of root depth data to have more occurrences but sacrificing intraspecific variation in root depth by using species mean root depth data, is not a valid approach for this study region.

CHAPTER 7: THESIS CONCLUSIONS AND SYNTHESIS

By: Nicola Kühn

Photo: Nicola Kühn

> “It is not the strongest of species that survives, nor the most intelligent that survives. It is the one that is most adaptable to change.”
>
> – C. Darwin

7.1 SUMMARY OF KEY FINDINGS & FILLING THE KNOWLEDGE GAPS

This thesis had the overall aim of investigating the role of plant traits in determining vegetation response to climate change with a particular focus on root traits in dry biomes for which there were large gaps in knowledge. Research questions of the thesis (outlined below) centred around which plant traits are important where, by examining trait-environment and trait-climate relationships at global, regional and local scales.

To do this, I first conducted a systematic review to identify key global traits determining positive plant response to climate change. From this, I observed that the most important and understudied traits were root traits, which were the focus of the remainder of the thesis, through a field study of both local and regional trait variation of woody Fynbos shrubs in South Africa, and a regional study linking remote-sensing metrics of vegetation sensitivity to climate and existing root trait data in Southern Africa.

The objectives of this thesis were addressed through three research papers, the conclusions of which are summarised below and in **Fig 7.1**. This rest of this chapter synthesizes the findings of the thesis in the context of the wider implications of this work and discusses future research directions for the field of traits-based, climate change ecology that stem from the results of this thesis.

7.1.1 Conclusions from Objective 1: “Globally Important traits to cope with Climate Change”

Which traits are important in determining a positive response to climate change across biomes and climate/environmental changes globally?

Findings. The data-synthesis work presented in **Chapter 4 (Research Paper 1)** identified a subset of key traits (and associated trait attributes) that linked positive plant responses to climate and associated environmental change. These included greater water-use efficiency (WUE), greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density, and greater rooting depth and higher or lower specific leaf area, higher or lower plant height (the latter two varying across biomes).

Under decreased precipitation, trait attributes were found to be consistent across biomes (e.g., higher wood density, lower SLA, higher WUE, deeper roots). Adaptive traits linked to other climate variables (e.g., increased temperature, increased fire frequency and intensity, increased nitrogen deposition, elevated CO_2) require more data to be conclusive, but existing studies suggest that under increased temperature, both lower and higher SLA may be important (dependent on biome and growth form) and under increased fire frequency or intensity, resprouting ability was a key trait related with positive plant responses.

Impact/significance. Knowledge of which plant traits and attributes are important under different climate and associated environmental changes is key when developing a range of management decisions. For instance, it could help breeding programmes select species or varieties with key traits and trait attributes to cope with predicted future climate change. It could also help conservation and restoration actions to identify species that are resistant vs. vulnerable to climatic changes. Further, our analysis has implications for which ecosystem services will be more resilient to climate change, as many are linked to specific traits (e.g., the size and architecture of root and shoot systems regulate climate, water, and soils of ecosystems, Garnier et al. (2016)). However, I concluded that more effort is needed to overcome the knowledge gaps identified, including an understanding of which traits and climate/environmental changes future studies should focus on, and which biomes these studies should target. Root traits were highlighted as an important knowledge gap especially in understanding dry biome responses to climate change.

Novelty. These findings represent the first efforts to compare traits across global biomes and across climate changes, as opposed to previous work focusing on certain biome types (e.g., forested biomes) or certain climate changes (e.g. drought) (O’Brien et al. 2017, Brodribb et al. 2020). Results support the idea that there are generalised trait-climate responses within and between biomes, and plants with these key traits and associated plant phenotypes may cope with or even thrive under current and future climate change.

7.1.2 Conclusions from Objective 2: "Deeper roots to survive drier climates? A case study in the Cape Floristic Region"

What is the contribution of belowground traits to overall variation a) across scales reflecting regional and localised (topographical) changes in water availability, b) between disturbance (fire) conditions?

Findings. This study found that in woody shrubs of the semi-arid Fynbos biome in South Africa, regionally drier sites (precipitation of 200-300 mm annually) had greater root investment as compared with wetter sites (600-700mm annual precipitation). Investment in these root traits included greater maximum rooting depth, length, root dry matter content, and overall root:shoot ratio. Aboveground traits were also found to be consistent with expectations for drier regions, including, but not limited to: lower SLA, shorter plant height and higher stem specific density.

These below and aboveground trait characteristics were found to be consistent at finer scales of water availability along locally drier topographical locations within sites. Furthermore, these patterns were consistent in post-fire sites at an intraspecific level.

Beyond trait differences, this study found that i) roots significantly and independently contributed to whole plant trait variation in drier conditions (e.g., maximum root depth and root diameter), and ii) increased root allocation (at the expense of shoot allocation) deviated from expected global allometric relationships.

Comparing post-fire sub-sites across wetter and drier main sites, showed that the combination of recent fire and drought in the Western Cape, affected the vegetation recovery significantly more in the drier site, with smaller average aboveground plant size (e.g., plant height, leaf area) and lower percentage cover observed.

Impact/significance. This study indicates that trait variation of woody shrubs in the semi-arid Fynbos biome of South Africa, is primarily organised along resource gradients and to a lesser extent aboveground, size-related gradients. This confirms that in this biome, resources (including water and nutrients) are more important drivers of trait variation in drylands than is observed globally (Wright et al. 2004, Díaz et al. 2016, Chave et al. 2009, Reich 2014).

In this study I also observe independent variation of root traits compared to aboveground traits, which represent areas of plant trait variability not explained by (i.e., not correlated with) previous global trait variation (Díaz et al. 2016). These findings, specifically that of maximum rooting depth characterising a unique axis of whole plant trait variation, are thus more in line with recent literature suggesting independent belowground gradients of variation (Weigelt et al. 2021, Bergmann et al. 2020).

The significant separation of traits in drier *vs.* wetter sites (at an inter and intraspecific level) suggests that we cannot assume that at the local scale, the same level of trait variation, nor resulting ecological strategies, will occur and therefore there will be variation in local plant responses to climatic/environmental changes within biomes.

The significance of the drier site showing deviation from expected biomass allocation relationships compared to the wetter sites, and importantly to global predicted and observed relationships, is that it challenges fundamental ecological principles and assumptions about biomass allocation, which may need to be revisited for climatic extremes, such as drylands.

Relatedly, a difference observed in root:shoot ratio along topography in the drier site (an increase in root investment compared to shoot along topography from lower, middle, to upper locations), was not observed in the wetter site. This suggests that in wetter environments, water acquisition at depth (and thus increased investment in roots) is no longer important enough to shape root trait variation. This supports the proposed idea of unidirectional trait expression recently suggested to be common in roots (Laughlin et al. 2021), where plants tend toward one expression of the trait under certain conditions, but not the opposite trait expression under opposite conditions. This again challenges fundamental ecological principles around ecological strategies.

Finding poorer vegetation recovery (in terms of plant height and cover) in post-fire and drought conditions of the drier site alerts to potential lower future resilience of Fynbos vegetation at the drier edges of the biome, a result important to consider for the conservation of this biome, and prompts the question of whether this pattern is reflected globally in drylands at drier edges of biomes.

Novelty. This study is the first (to my knowledge) that has i) considered root and aboveground trait variation along both regional and local topographical gradients and ii) quantified the contribution of root trait variation to overall variation in the Fynbos biome. Further, the full excavation of plant roots allowed for comparison of a greater suite of root traits, including biomass allocation relations than can only be inferred – but not directly measured – from partial excavation or proxy measures (isotope analysis), which are more often the approach to this type of data collection.

7.1.3 Conclusions from Objective 3: “Deeper roots reduce sensitivity to climate in dry biomes”

What is the role root depth plays in reducing vegetation sensitivity to climate variability derived from space-borne remote sensing imagery and, subsequently, do belowground plant traits influence patterns we observe from aboveground plant/climate interactions?

Findings. This study found that in Southern Africa, vegetation sensitivity to current climate variability, as measured by the Vegetation Sensitivity Index (VSI, (Seddon et al. 2016)) varied significantly amongst biomes, with Succulent Karoo showing the lowest sensitivity. Temporal autocorrelation in plant greenness (as measured by the *t-1* coefficient – see **Chapter 6 (Research Paper 3)**) was also found to vary significantly across biomes, with the driest biomes (Succulent Karoo, Desert, Fynbos and Nama Karoo) showing the highest values of *t-1*.

VSI had a significant negative relationship with root depth and *t-1* had a significant positive relationship with root depth across the study region. This relationship is strengthened when biome and growth form are considered. This relationship was further examined in Savanna trees for which most data exist. This work suggests that root depth constitutes a key trait determining vegetation sensitivity to past climatic variability.

Impact/significance. These results indicate that the ability to root to greater depths may be a key strategy in coping with the present – and predicted future warmer and drier – conditions experienced in Southern Africa. It is therefore important to understand which species have these traits and thus the ability to cope with drier times in terms of assessing threats to biodiversity, conservation management and even agricultural/agroecological systems.

Further, understanding plant interactions with deeper ground water resources and thus stability of these water resources for both human and plant use will become increasingly important as these sources face threats from increased human extraction, invasive plants, and reduced replenishment due to drier environmental conditions (Ziervogel et al. 2019, Le Maitre et al. 2019, Davis and Vincent 2017).

Novelty. This research demonstrates the ability to observe aboveground plant-climate interactions reflected by belowground traits. Being able to do this holds great future promise for filling in the missing gaps to understand the belowground dimensions of the plant world.

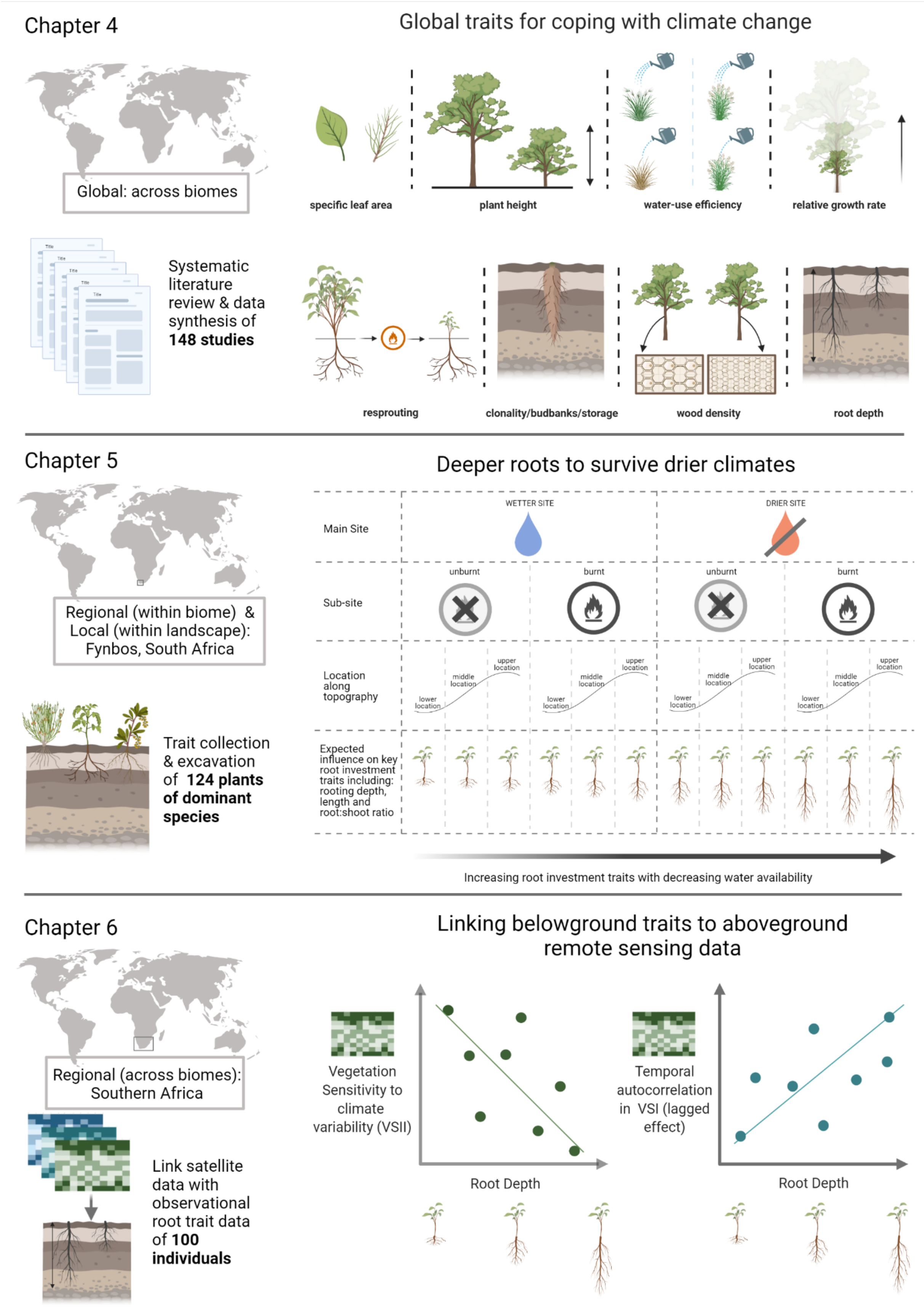


Figure 7.1: Diagram summarising the findings of the thesis. Source: designed in BioRender by Nicola Kühn.

7.2 SYNTHESIS

Through this thesis I have found that plant traits play a key role in determining vegetation response to climate change in dry biomes. This has been evidenced by the objectives of the three research chapters of this thesis, namely: 1) globally synthesizing which traits are important for determining response to climate change, 2) enhancing our understanding of how belowground traits vary along water-availability in dry biomes and 3) investigating the role of root depth in defining vegetation sensitivity to climate variability in dry biomes globally and whether this can be examined using remote sensing.

I conclude that understanding root traits is fundamentally important in the understanding of how plants respond to climate change particularly in environments that are already water-limited. Also, these root traits could mediate plant fitness and performance in the ecosystems most susceptible to climatic and associated environmental change. Consequently, an important takeaway of this thesis is the importance of studying root traits, in water-limited environments.

7.2.1 Roots

The findings from this thesis present a compelling case for researching the neglected belowground component of plants to fully understand plant responses to climate change. My thesis supports that root traits need to be further studied and considered for several key reasons, namely:

1. As demonstrated in **Chapter 4 (Research Paper 1)**, belowground traits (including rooting depth, belowground storage and resprouting ability) are some of the top traits associated with positive responses to climate change despite being the group least studied in this type of research.
2. From **Chapter 6 (Research Paper 3)** it can be concluded that across Southern Africa we don’t yet have enough spatially continuous root data for all biomes. Existing data suggest the key role that rooting depth plays in allowing plants to access deeper water resources and thus

cope with drier periods, which are set to become more frequent and intense in Southern Africa especially.

3. In the context of the wider trends in the field of root ecology, a key finding from my thesis is that root traits can vary independently of aboveground trait variation. Results from **Chapter 5 (Research Paper 2)** of this thesis came to the same conclusions as recent literature (Weigelt et al. 2021) that root trait variation (in this case root size including maximum rooting depth and diameter at root origin) presented an entirely different axis of variation to the two global axes of variation in plant form and function, resource or whole-plant-size related traits (Díaz et al. 2016). Results from **Chapter 6 (Research Paper 3)** then found that one of these traits, maximum rooting depth, and the ability to access deeper water resources may play a key role in determining plant survival in drier conditions.
4. Another indication of the independent nature of roots is shown by biomass allocation relationships in **Chapter 5 (Research Paper 2)**, suggesting that in drier edges of already dry biomes, water resources are scarce enough to select for greater root investment and thus drive shifts in allocation that deviate from established size-scaling relationships between plant parts (Enquist and Niklas 2002).

These findings about root investment traits have far-reaching consequences for plant ecology and climate change research, including how we understand fundamental ecological principles (e.g., global axes of trait variation and isometric scaling relationships). Applying this knowledge can modify how we quantify carbon allocation and storage in plants and whole ecosystems. This means that many assumptions that have been made about root variation in the absence of comprehensive root data should be revisited and potentially challenged (see below for examples of future research avenues).

7.2.2 Drylands

Results from **Chapter 4 (Research Paper 1)** reveal that root traits are key in drylands and may be disproportionately important to understand and thus study due to their mediating survival at climate extremes and through future climate conditions (e.g., increased aridity) and extreme events (e.g., increased intensity and frequency of drought). Results from **Chapter 6 (Research Paper 3)** support this in suggesting that root depth may be a key determinant of plant resilience to climate variability in Southern Africa. This is particularly apparent in more data rich trees of the Savanna biome, where deeper roots are likely allowing plants to access underground water resources and buffer their aboveground productivity against drought conditions. This has important implications for the tree-grass mix in this biome, where rising atmospheric CO_2 concentrations are already favouring tree growth and expansion (Kgope et al. 2010, Wigley et al. 2010, Bond and Midgley 2012, Stevens et al. 2017), resulting in woody encroachment, at the cost of losing grass cover and potentially ancient grass species.

The finding from **Chapter 5 (Research Paper 2)** that there are differences in root traits across multiple scales of environmental variation (primarily water availability) within an already dry biome suggests that closer attention needs to be paid to the potential root variation within biomes, within landscapes, and within species across drylands, because the effects of local topography in ameliorating or exacerbating the effects of water availability are reflected by trait values of both belowground and aboveground traits.

7.2.3 Future research directions: Belowground futures

Despite the historically slow advance in belowground trait collection and collation as compared with other traits, it appears that root ecology has now left the neglected dimensions of plant ecology to find itself front and centre of recent plant literature. In the last year alone, we have seen efforts to standardise (Freschet, Iversen, et al. 2021) and set new priorities (Freschet, Roumet, et al. 2021) for root research, develop new techniques to study belowground traits (Sousa et al. 2021, Stocker et al.

2021, Liu et al. 2021) and redefine plant ecology itself from what we have learnt from roots (Weigelt et al. 2021, Laughlin et al. 2021). This thesis suggests that roots deserve this spotlight due to their unique contribution to plant form and functioning **(Chapter 5 (Research Paper 2))**, due to their buffering vegetation sensitivity to climate variability **(Chapter 6 (Research Paper 3))**, and in their role in determining positive response to climate change **(Chapter 4 (Research Paper 1))**.

The following list presents the potential new research avenues that have been uncovered through this thesis:

1. Future studies on response to climate change should focus on a) understudied countries in Africa and the Middle-East, b) in drier biomes (e.g. Deserts) and those set to see the worst climatic changes (e.g. Tundra), and c) on other climate change variables not studied as much e.g., CO_2, Nitrogen deposition, fire and changes in seasonality **(Chapter 4 (Research Paper 1))**.
2. Future studies need to focus on root and stem traits more than leaf traits because these appear to more often be linked to positive plant fitness responses to the climate/environmental variables analysed **(Chapter 4 (Research Paper 1))**.
3. Strategic field sampling of roots needs to be developed urgently because key information about the structure and size of roots requires at least partial excavation. This is particularly important to do in drylands where roots will play important roles in plant-climate responses.
4. Where root excavation is not possible, predictive and proxy methods should be pursued to advance knowledge on belowground components of plant-environment interactions (e.g. isotopic analysis to estimate water use at depth/infer root depth or remote sensing derived predictions of root depth based on existing data).
5. Although intraspecific variation is found to be significant in shaping trait variation in **Chapter 5 (Research Paper 2)**, this study does not test for phenotypic plasticity at the

individual level. This remains a key gap – as plasticity may be the key to dealing with seasonal differences.

6. There is a need to incorporate potential unidirectionality of root traits (where directional selection for traits consistently occurs in dry and cold extremes but not warm/wet conditions (Laughlin et al. 2021)) into ecological theory to advance understanding of the implications of trait variation on species responses to environmental change.
7. Vegetation models (e.g. Dynamic Global Vegetation Models) that use biomass allocation need to be revisited due to our findings of variation within a biome **(Chapter 5: Research Paper 2)**. This calls for more effort in defining the environmental correlates of root biomass allocation to improve outputs from vegetation models under current and future climate conditions (Ma et al. 2021).
8. Future studies need to include mycorrhizal associations due their contribution to overall root trait variation (Bergmann et al. 2020). This can be aided and upscaled by new techniques that have made it possible to observe mycorrhizal association with remote sensing from signals in canopy chemistry (Sousa et al. 2021).

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