Vegetation in an age of global change: encroachment, succession, and phenology

By

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DECLARATION

I, Samantha-Leigh Jamison-Daniels (the undersigned) declare that the thesis/dissertation, which I hereby submit for the degree PhD (Plant Science) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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DATE: November 2022

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“*It was the kind of favourite puzzle that keeps forcing its way back because its very intractability makes it perversely pleasant*”.

Edward O. Wilson, *The Diversity of Life* (1992).

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THESIS ABSTRACT

To successfully predict how ecosystems and associated species will respond to global change drivers, an understanding of the underlying drivers of the assembly, diversity and functional responses of biological communities is needed. The objective of this thesis was to provide insights into the ecology of vegetation through means of exploring phenological and successional patterns and drivers in an age of global change. First, using herbarium records, the timing and climatic drivers of fruiting phenology of 58 widespread South African fleshy- and dry-fruited tree species, which possess different physiological requirements, were tested. Second, the patterns of succession through bush clump formation (a form of woody encroachment) in a South African savanna were explored, and the microclimatic determinants of succession determined. Third, a systematic review to assess whether consistent trends exist in plant functional traits across successional gradients, and to assess whether a bias exists in trait-based successional studies (e.g., between geographic distribution, growth forms, and vegetation types) was conducted. Significant differences in fruiting phenology of fleshy- and dry-fruited species were found: fleshy-fruited species fruited earlier than dry-fruited species, and the effects of climatic predictors on fruiting phenology across species depended on fruiting type: only fleshy-fruited species were limited by winter temperatures, while high temperature seasonality typically resulted in later fruiting for both fleshy- and dry-fruited species. Bush clump formation was initiated by the establishment of a founder individual which resulted in microclimatic changes, facilitating the establishment of other species, and resulting in a deterministic successional change (as bush clump size increased) from an open habitat (characterised by savanna species) to a closed habitat (characterised by forest species). Out of 398 recorded traits reported in successional studies, only six were frequently reported across trait-based successional studies; however, all traits showed consistent trends across successional gradients. Clear biases in trait-based successional studies were observed: woody communities have been studied more often than herbaceous communities, with forest communities being disproportionally studied; and most studies have been conducted in Europe. By linking patterns of phenology and succession to environmental drivers, the impacts that global change drivers may have

on community assembly patterns could be inferred. The dependence of phenology on climatic factors suggests that climate change will result in shifts in phenology with implications for seed dispersal and food availability of frugivorous animals. Changes in the microclimate conditions brought about by the associated succession of bush clump formation suggests that microclimate plays a role in the replacement of ancient savannas by forest species; such replacement will compromise the diversity and ecosystem services of savannas. This suggests that management interventions should include processes that naturally keep the system open, such as fire. Finally, our ability to generalise how traits change with succession, over broad vegetation types and geographic regions, is mostly limited to forest systems, and consistent trends observed may not hold in other biomes. Therefore, in a changing, disturbance-driven world in which succession may become increasingly important in community assembly, it is pertinent to predict how communities other than forests, and non-woody taxa, assemble post-disturbance.

CHAPTER 1: GENERAL INTRODUCTION

The study of global change biology, which collectively refers to the biotic consequences of anthropogenic influences, is currently a hot topic in the field of ecology. Global changes have resulted and continue to result in the creation of novel environmental conditions, the impacts of which are apparent and will continue in the near and distant future. Anthropogenic influences have a profound effect on the global environment and its associated ecosystems (Kerr, Kharouba & Currie, 2007). By influencing and changing climate patterns, altering, and increasing land use practices, polluting, overharvesting resources, and aiding in the spread of invasive species (Gibert, Debat & Ghalambor, 2019), human activities have ultimately resulted in negative impacts for global ecosystems, species, as well as human health (Kerr, Kharouba & Currie, 2007, Gibert, Debat & Ghalambor, 2019). Indeed, the impacts of global change have become increasingly apparent; over the last few decades much research illustrating these impacts has become readily available. Phenomena that have been reported include climate-related species distributional shifts pole-wards and towards higher elevations, increased incidences of woody encroachment within grassy ecosystems, changes in community composition and structure, and changing phenological patterns and relationships amongst others (Walther et al., 2002). To successfully understand the impacts of global change on global ecosystems and associated species responses thereof, the findings of a multitude of scientific disciplines need to be used to infer on suitable policy responses.

Global Change Drivers

Global change drivers are responsible for the creation of new environmental conditions and selective pressures which ultimately impact on species and communities in a variety of ways (Walther et al., 2002, Matesanz & Gianoli, 2014).

Several major drivers of global change that impact the Earth's biodiversity have been identified (Table 1.1). Although the immediate impacts of global change drivers are not always harmful, they have the potential for cascading, harmful consequences for biodiversity (Sage, 2020). For example, although increased carbon dioxide (CO_2) levels are likely to promote plant growth, the differential responses of different species and ecosystems to such conditions can impact on ecological interactions such as competition and predation (Polley, Jin & Fay, 2012). As species respond positively to increased levels of atmospheric CO_2, they can subsequently impact species connected to it in ecosystems; benefiting species may subsequently suppress those that simultaneously suffer leading to a reduction in ecosystem integrity and diversity (Thompson et al., 2018). Reductions in species diversity consequently impact on interacting species, thus resulting in cascading impacts along the lines of connected species. For example, in savannas, increased CO_2 levels result in the apparent increase of C_3 trees at the expense of C_4 grasses. The loss of C_4 grasses typically results in the loss of other species (including vegetation, specifically C_3 trees, faunal species, as well as microbiota species) (O'Connor, Puttick & Hoffman, 2014, Archer et al., 2017a).

TABLE 1.1 Examples of major global change drivers with selected examples of the impacts they pose to ecosystems. Selected references have also been provided. CO_2 = carbon dioxide.

EXAMPLES OF IMPACTS RESULTING FROM GLOBAL CHANGE DRIVERS
Increased CO_2 levels
• Ocean acidification (e.g., Wittmann and Pörtner (2013)) • Woody encroachment (e.g., Bond and Van Wilgen (2012)) • Increased fuel loads yield intensifying fire regimes (e.g., Bond and Midgley (2000)) • Climate change (e.g., Sala et al. (2000))
Climate change
• Changed fire occurrence in grassy biomes (e.g., Bond and Midgley (2000)) • Intensification of aridity in desert biomes (e.g., Foden et al. (2007)) • Coral reef bleaching (e.g., Altieri et al. (2017)) • Altered phenology patterns (e.g., Chambers et al., 2013) • Geographic range shifts (e.g., Foden et al., 2007) • Sea level increases and salinization of wetland systems (e.g., Lindsey (2018))
Land use changes
• Conversion of biomes to agricultural land (e.g., Zhang, Liu & Henebry (2019)) • Habitat fragmentation and loss (e.g., Leimu et al. (2010)) • Loss of species within ecosystems (e.g., Giam (2017)) • Altered phenological patterns (e.g., Lieberman (1982))
Eutrophication
• Increased incidence of toxic algal blooms (e.g., Seitzinger et al. (2002)) • Species diversity declines because of competitive exclusion by eutrophilic species (e.g., Rabalais et al. (2009)) • Changes in trophic cascades (e.g., David and Storkey (2018))
Over-exploitation
• Overfishing and hunting (e.g., de Souza & Prevedello, 2019)) • Overgrazing in grassy biomes (e.g., Hempson, Archibald and Bond (2017)) • Overharvesting of forest ecosystems (e.g., Estes et al. (2011))
Alien Invasions
• Competitive displacement of native species by exotic species (e.g., Richardson et al. (2020)) • Alterations in food webs which subsequently impacts native species (e.g., Walsh, Carpenter and Vander Zanden (2016)) • Altered fire regimes (e.g., Hui (2016))

In the subsequent sections, I *briefly* discuss the implications of a subset of global change drivers on terrestrial ecosystems; because of their influence on terrestrial ecosystems and the associated impacts they pose on community assembly patterns, discussions are focussed on the following global change factors: increased atmospheric CO_2 levels, climate change, and land use alterations.

Increased atmospheric CO_2 levels

Each year, anthropogenic activities, such as the burning of fossil fuels and deforestation, release more CO_2 into the atmosphere than natural processes can remove. Indeed, atmospheric CO_2 levels have increased by approximately 48% from 1750 to 2019 (increasing from 280 ppm to 415 ppm), and they are expected to reach 500 ppm by 2050 (Zhongming & Wei, 2022). Although CO_2 levels have historically varied between glacial and interglacial cycles, natural CO_2 levels typically averaged 250 ppm. Increased levels of atmospheric CO_2 directly impact the physiological mechanisms (e.g., photosynthesis, metabolism, respiration, and carbon allocation patterns) of plants; the most noticeable impact of increased CO_2 levels are through alterations to the photosynthetic pathway, e.g., increased leaf photosynthetic pathways (Dusenge et al., 2018). Increased CO_2 levels can also impact other physiological factors such as the formation and release of volatile organic compounds; however, these topics are beyond the scope of this thesis.

Although increased CO_2 levels can directly impact plants, they can also indirectly impact ecosystems through subsequent cascading impacts (Sage, 2020). For example, altered climatic conditions (e.g., higher temperatures) brought about by higher CO_2, alter the thermal environments of plants, which impact plant performance through effects on, e.g., water stress management (Dusenge et al., 2018), or through changes to biotic interactions. For example, plant-herbivore interactions can be influenced by elevated CO_2 levels; in particular, elevated CO_2 levels result in changes to the chemical composition of plant tissues, e.g., altered carbohydrate and protein compositions (Taub, 2010). As available nitrogen content and protein levels are related, changes in protein concentrations can affect herbivores. For example, at higher atmospheric CO_2 levels, a “nitrogen dilution effect” occurs in plant tissues, as an increase in carbon availability increases the carbon:nitrogen ratios within plant tissues (Stiling & Cornelissen, 2007). Lowered leaf nitrogen, and thus lower protein content, results in a decrease in the nutritive value of the plant to herbivores. Herbivores must compensate for the decreased food quality by increasing their plant consumption rates (Stiling & Cornelissen, 2007, Taub, 2010). Reduced nutritional value of plants impacts herbivores through slowing their growth rates, and prolonging development periods, which increases potential mortality rates of larval and nymph stages (particularly in invertebrates) to predation because of increased periods of vulnerability (Goverde & Erhardt, 2003). This can ultimately impact on herbivore abundance and richness within ecosystems (Kopper & Lindroth, 2003).

Climate change

Of the six global change drivers, climate change arguably receives the largest amount of attention in politics, the media and science (Matesanz & Gianoli, 2014). Climate change scenarios forecast increases in global surface temperatures. Other climatic factors are subsequently anticipated to change in relation to increasing surface temperatures, e.g., increases in the frequency and intensity of extreme weather conditions such heat waves, frost events, precipitation, and droughts, and reductions in snow cover and permafrost (Allan et al., 2021). Furthermore, with increasing temperatures, the global water cycle will be impacted, with predicted changes in variability and intensity of precipitation events. At a local scale, model simulations predict that southern Africa will experience an increase in temperatures, including an increase in annual heatwaves and the frequency of very hot days, with a decrease in the number of cold days and cold extremes (Allan et al., 2021, Rotter et al., 2021). Associated with the increasing temperatures, southern Africa is likely to experience lower precipitation levels and decreased soil moisture (Erasmus et al., 2002; Allan et al., 2021). These postulated scenarios have raised questions about how changing climate will impact the structure and dynamics of population and community assembly patterns (Thibault & Brown, 2008). This notion is also relevant under the impacts of other global change factors (e.g., altered land use practices).

Climate change has drastically affected the variability and seasonality of temperature and precipitation and the rate and intensity of extreme climatic and weather events globally (e.g., drought events, heavy precipitation events) (Warburton, Schulze & Maharaj, 2005, Blois et al., 2013, Zhongming & Wei, 2022). As climate is an important factor influencing plants, a change in variability and intensity of climatic factors has consequences for plants. Due to their sessile nature, the ability of plants to respond to unsuitable climate conditions is restricted (Leimu et al., 2010). Climate change results in changes in phenology, the timing of seasonal life history events such as flowering or migration of plant and animal species respectively (Visser & Both, 2005, Neil & Wu, 2006, Tang et al., 2016) and physiological processes, species distribution/range shifts, impacts on community composition (e.g., through introduction of invasive species) and the subsequent changes in species interactions which impacts ecosystem structure and dynamics (Leimu et al., 2010).

Plastic responses of sessile organisms to rapid climate change are constrained (as they may reach a physiological limit in which they can no longer persist in novel climatic conditions related to their shifted distributions); thus species extinctions or population extirpations are possible, especially for species that experience extensive range contractions, are unable to successfully track suitable climate space, or are unable to survive in their current locations where novel climate conditions have developed as a result of changing climate patterns (Davis & Shaw, 2001).

Land use changes

Land use changes result from the alteration of natural ecosystems through means of anthropogenic activities such as agricultural practices, urbanisation, forestry, and industrial expansion, e.g., conversion of natural ecosystems for human use (Smith et al., 2016). Land use changes cause habitat fragmentation and habitat loss and are linked to biodiversity loss, soil degradation and nutrient enrichment, changes in surface hydrology, changes in the provision of ecosystem services (e.g., carbon sequestration, food provision), and desertification, as well as changes in ecological processes (e.g., changes in fire and herbivory regimes), amongst others (Matesanz & Gianoli, 2014, Marques et al., 2019). The impacts of land use changes have accelerated in recent decades as human populations and living standards have increased (Smith et al., 2016). Because of the scale at which land use changes occur, and the subsequent ecological degradation associated with these changes, land use changes are currently considered the greatest threat to biodiversity (Sala et al., 2000, Vermaat et al., 2017).

Deforestation is a land use type that has received the most research attention. Deforestation is typically associated with forests and although these systems have been significantly impacted by land use changes, they are not the most impacted vegetation type; indeed, global grassy ecosystems (including grasslands and savannas) have also been significantly impacted (Giam, 2017, Stanton Jr et al., 2018), especially by conversion for agricultural purposes. This is of particular importance as grassy biomes, which cover an estimated 25% of the Earth's land surface, are important for human livelihood and wellbeing, e.g., grassy biomes contribute important ecosystem services, including provisioning, supporting, regulating and cultural services (Wieczorkowski & Lehmann, 2022). Despite this, many grassy ecosystems, particularly savannas, are mistook as degraded forests (Kumar et al., 2020). Such misinterpretations have consequences for the management and conservation of the different systems, especially as the underlying drivers of savannas vs forests are different (Ratnam et al., 2011). Attempts to develop a suite of morphological, physiological, and life-history traits that differ between tropical mesic savanna and forest species have been proposed are likely ways of ensuring savannas are awarded the protection they deserve under the title, rather than the lack of protection they would receive under the notion of being a (misidentified) degraded forest (e.g., see Ratnam et al., 2011).

Land use change can be seen as either the removal of primary vegetation (as in usually the case of deforestation) or the removal of important processes (e.g., fire and herbivory within grassy ecosystems) that drive and maintain the ecological features of the applicable systems. For example, within southern Africa, one consequence of land use change, particularly within in grassy ecosystems, is woody encroachment. Following changes to ecosystem processes (including altered fire and herbivory regimes) within grassy ecosystems, increases in woody species, at the expense of grass species, have become apparent (Archer et al., 2017a). In rural South Africa, unmanaged land use changes within grassy biomes (e.g., for grazing purposes) have resulted in woody encroachment. Changes to the land use (including heavy, unregulated grazing of domestic animals) result in an increase in woody species as grass species fail to compete with woody vegetation for necessary resources (O'Connor et al., 2014). Similarly, in areas where the natural fire regime is impacted, woody vegetation can escape the "fire trap" resulting in an increase in woody abundance (Bond & Midgley, 2000).

Vegetation Dynamics in an Age of Global Change

Plant communities are significantly impacted by global change drivers and the degree and the way in which these global change factors impact communities vary. A key objective of vegetation ecology is the need to better understand not only how vegetation communities are assembled from available pool sources but also the how global change drivers alter the trajectories of community assembly patterns (Spasojevic & Suding, 2012, Münkemüller et al., 2014). Over the last decades, there has been an increasing trend in research aimed at studying these community dynamics (Monuquet et al., 2012). An important component of this field of study has been to disentangle and understand the drivers of assembly patterns (Vellend et al., 2014), including the roles of environmental filtering, dispersal ability, biotic interactions (e.g., competition), and niche evolution (Peres-Neto et al., 2012, Kraft & Ackerly 2014). Although each factor influences community assembly (including composition, diversity, and abundance), they are often intertwined and thus do not operate independently of each other. The factors that are important for community assembly are susceptible to impacts associated with global change; indeed, global change drivers can alter ecological communities by influencing the drivers of community assembly. Without a clear understanding of the drivers of community assembly, our ability to predict how species assemblages respond in the presence of global change is challenged (Prach & Walker, 2011).

The processes responsible for community assembly operate in different ways to shape plant diversity and composition. For example, environmental filtering occurs when the abiotic environment “filters out” species that are not suited to persist within a particular environment (Kraft & Ackerly 2014). For example, seeds may be dispersed into given environments or locations where conditions for germination or long-term survival are unfavourable. In such instances, abiotic filters such a moisture availability, photoperiod, and temperature select for species that are capable of surviving within the present conditions. Such filters are not restricted to operating at specific life stages (e.g., seed), but can operate at any time during a plant’s life cycle (i.e., when conditions are no longer suitable for survival, these filters may result in mortality or prevent efficient reproduction) (Kraft & Ackerly, 2014). Indeed, the consequence of environmental filtering is particularly evident in plant communities and their organisation into vegetation types/biomes (Moncrieff et al., 2016). Plant communities often change in predictable ways along environmental gradients (e.g., changes in water availability, temperature, elevation, and latitude) that manifest in various groupings of species (from a wider species pool) that are capable of surviving within particular environmental conditions (Dolédec, Chessel & Gimaret-Carpentier, 2000). Indeed, this phenomenon is illustrated in this thesis (Chapter 3), where changing microclimate conditions along a bush clump successional gradient are associated with a species compositional change that culminate. In this chapter, I illustrate how succession by woody encroachment into a savanna, that culminates in forest formation, is the likely result of global change drivers (in the form of altered land use practices and ecological processes in the form of the suppression of fire and herbivory).

Environmental filtering further "filters out" species by selecting for species with specific functional traits (Kraft & Ackerly, 2014), i.e., the physiological, morphological, behavioural, or phenological characteristics that are related to the fitness and performance of an organism (Violle et al., 2007). Environmental filtering selects individuals that possess traits that will enhance survival and reproduction (Dolédec, Chessel & Gimaret-Carpentier, 2000). The use of functional traits within ecology has proved useful in improving our understanding of ecological patterns and phenomena (e.g., see Hooper et al., 2005, Vogt, Beisner & Prairie, 2010). Indeed, different abiotic conditions require varying sets of traits to establish and persist in a particular environment (Cornwell & Ackerly, 2010). Therefore, as succession progresses and abiotic (and biotic) conditions change, it is generally believed that species are replaced by others whose traits enable them to be better adapted to the environmental conditions that are experienced across successional gradients (Huston & Smith, 1987, Douma et al., 2012b, Prach & Walker, 2020). In such instances, it should be possible for the functional traits of individual plants to be scaled up to infer on broader community dynamics (Prach & Walker, 2020). In this thesis (Chapter 4), I outline the significance of functional traits and their associated use in understanding community dynamics and organization. Functional traits effectively operate as filters, selecting for specific species at different stages of community assembly. The ability to understand how community assembly changes with the aid of functional traits proves useful in an era under threat from global change. Although environmental filtering processes are important for influencing community assembly patterns, other factors are also important to consider.

Biotic interactions, as with abiotic interactions, serve as filters during community assembly processes (Cornwell & Ackerly, 2010). Interactions, such as competition, facilitation, mutualism, commensalism, parasitism, and predation, can determine how a community is organised (Cornwell & Ackerly, 2010, Kraft & Ackerly, 2014). For example, competition operates to reduce survival and growth of a species at a particular site. In contrast, mutualism impacts assembly processes by, for example, allowing species to persist in an environment that typically would not be suitable in the absence of mutualistic relationships. Another example of how biotic interactions influence community assembly dynamics is through the effects that plants have on other plants (Paddilla et al., 2006); for example, the amelioration of environmental stress by some plants can benefit the establishment of other species (Paddilla et al., 2006). Nurse plants are those plants that can facilitate the growth and establishment of other plants beneath their canopy as they provide ameliorated microhabitats that are more favourable for seed germination and/or seedling recruitment. An example of such amelioration is observed in bush clumps, where changing microclimate brought about by successional changes ameliorates the environment for the establishment of forest type species beneath the clump canopy. Furthermore, interactions between dispersers and the type of fruit produced by a plant will have implications for community assembly processes, especially as, for example, plants dispersed by frugivores are directly dependent on these frugivores to facilitate their spread (Howe & Smallwood, 1982). As such, biotic interactions are aligned to factors that influence a species' survival ability, e.g., phenology (i.e., the timing of seasonal life history events such as flowering or migration of plant and animal species respectively (Visser & Both, 2005, Neil & Wu, 2006, Tang et al., 2016)). If phenology patterns are altered, there are likely to be associated impacts to interacting organisms that are dependent on the plant organs that show phenological cycles. For example, temporal mismatches in the phenology of plants and their seed dispersers so that plant fruiting period and peak disperser abundance no longer overlap, resulting in reduced seed dispersal (Clark & Clark, 1984; Chapman et al., 2018).

As plants are sessile organisms, dispersal is a considered a major driver of community assembly processes (Howe & Smallwood, 1982, Kraft & Ackerly, 2014). Generally, dispersal only occurs during the seed stage of the life cycle (except for a small subset of species that can reproduce vegetatively) (Kraft & Ackerly, 2014). The ability to disperse is a major component of community assembly processes, especially as a plant will need to arrive at a particular location (i.e., disperse) before it can become part of the associated community (Clark & Clark, 1984). Thus, dispersal mechanisms have major consequences for community assembly patterns (including diversity and abundance). For example, it is generally accepted that the morphology of fruit and seed produced by a plant is indicative of its dispersal mode (Howe & Smallwood, 1982). Furthermore, the anatomy of fruits impacts the dispersal of the seed (Van der Pijl, 1982). Understanding dispersal syndromes of plants and is thus important for investigating the underlying drivers of community assembly processes. For example, during the early stages of succession, wind-dispersed species that produce many, small seeds are typically favoured (environmental filtering at play) as the associated likelihood of a few seeds landing in a location of suitable environmental conditions is higher (Kraft & Ackerly, 2014). In contrast, during the later stages of succession, animal-dispersed fruits, in which dispersal is more directed (e.g., seed deposited beneath a perch) is typically favoured, especially as more energy is used to produce few, high quality seeds with a higher germination establishment (provided the seed is within suitable conditions) (Smith & Goodman 1987; Franco-Pizana et al. 1996). As the anatomy, and often the dispersers, between fleshy- and dry fruited species differs, it can be expected that there will be differences in energy investment and the types of strategy employed by fleshy and dry fruited species for effective seed dispersal (Howe & Smallwood, 1982). Such factors have implications for community assembly processes within ecosystems, including the diversity and abundance of species within a community. Understanding phenology patterns is important for interpreting community assembly patterns as fruit maturation is thought to correspond with suitable conditions for effective seed dispersal (Griz & Machado, 2001, Chapman et al., 2005). This is illustrated in this thesis (Chapter 2), where I illustrate how climatic factors influence the fruiting phenology of a subset of fleshy- and dry-fruited tree species from the summer rainfall regions of South Africa.

In this thesis, I use large community datasets that span not only large spatial scales, but also broad temporal scales, together with measures of functional diversity to investigate community assembly patterns, in the face of global change. Although no direct manipulations of global change drivers *per se* were investigated here, the conclusions drawn from this thesis enable inferences to be drawn about how different global change drivers can potentially influence vegetation dynamics. Focus on phenological patterns, woody encroachment patterns and trait-based successional patterns and how global change drivers impact these factors is provided. These three factors were selected as they are important facets of terrestrial vegetation communities. Furthermore, in the context of this thesis, these factors allow for important conclusions to be drawn to inform management efforts within various South African ecosystems (e.g., savannas). Understanding such facets, and how these factors impact each other, is thus of importance. A brief literature review of relevant information pertaining to phenological patterns, woody encroachment patterns and trait-based successional patterns is provided below:

Phenology: an overview

Most aspects of plant phenology are intrinsically related to climate (Wolkovich, Cook & Davies, 2014). Consequently, plant phenology responds quickly to changing environmental conditions to allow individuals in a given population to achieve synchronised sexual reproduction (and growth) to ensure successful gene flow, and to allow individuals to avoid unfavourable climatic conditions, without significantly impacting on the individual's fitness (Visser & Both, 2005). The phenological patterns displayed by plants and animals are thus a consequence of the seasonality these organisms experience within their habitat (Menzel, 2002, Visser & Both, 2005). Within a species' suitable habitat, there is a limited period in which conditions are favourable enough to allow for reproduction and/or growth. Phenology is thus an adaption to local environmental conditions; organisms react to cues that indicate suitable conditions for reproduction and/or growth activities. Generally, a life history event (such as flowering) that occurs outside the period of favourable conditions can negatively impact the species' fitness (Visser, Both & Lambrechts, 2004, Visser & Both, 2005).

One consequence of global change is changes to phenology patterns; indeed, phenological observations have become useful in illustrating the impacts that changing environments can have on interacting species and ecosystems (Menzel, 2002). Such observations have proven useful in understanding and visualising how global change factors, and the subsequent creation of novel environmental conditions, impact ecosystems. Although climate change is considered the leading driver of observed phenological shifts, other global change factors (e.g., land use changes) have also been shown to influence phenology. For example, land use changes, which can result in changes to vegetation type, and thus species composition, have been shown to influence ecosystem-scale phenology patterns (Zhang, Liu & Henebry, 2019); greenup onset trends have shifted from a delayed onset to an advancing onset in systems that were historically forest systems but have subsequently shifted to shrublands because of increased fire patterns (Wang & Zhang 2017). For example, plant pollinator interactions have been negatively impacted by rising atmospheric CO_2 levels (Taub, 2010). Another global change factor that impacts phenology is climate change. Phenological shifts because of mismatching climate patterns and lifecycle events have been reported for a number of organisms, including vertebrates (e.g. Lehikoinen, Sparks & Zalakevicius, 2004, Mills, 2005), invertebrates (e.g. Navarro-Cano et al., 2015, Pureswaran et al., 2015), and plants (Doi & Takahashi, 2008, Gordo & Sanz, 2010).

Therefore, as global change drivers (e.g., climate change, land use changes etc.) continue to worsen, a clear understanding of how these drivers impact phenology is required. However, to successfully estimate the direction and magnitude of change that these drivers (e.g., climate change) could have on the phenological responses of species, we require an understanding of which drivers (e.g., climatic variation) affect phenology (Doi & Takahashi, 2008).

Over the last few decades, there has been an increase in research focussing on phenology (Visser & Both, 2005, Neil & Wu, 2006, Tang et al., 2016). There are three main factors are attributed to this increase in scientific attention, 1) ecological impacts associated with climate change are generally illustrated through phenological shifts, thus increasing focus on climate change has resulted in increased research attention associated with phenological shifts, 2) ecosystem structure and function (e.g., photosynthesis, species composition, carbon cycling etc.,) is impacted by potential phenological shifts, thus increasing the need to understand ecosystem resilience during phenology shifts, and 3) advancement in technological developments, including remote sensing and citizen science projects (Tang et al., 2016), has expanded the scale at which phenological observations are collected and the quality and quantity of data available for the analysis of phenological trends (Tang et al., 2016).

Regional climatic conditions are considered as the main regulator of phenology patterns (Giorgi, 2006, Chambers et al., 2013). As climate differs considerably between latitudes (Giorgi, 2006), it can be assumed that phenological patterns vary across the globe. However, phenological studies are biased towards temperate systems, especially within in the Northern Hemisphere (Chambers et al., 2013). In these regions, temperature and day length are often the main driver of ecological and phenological patterns (Giorgi, 2006). In contrast, the drivers of phenological patterns have been poorly examined in tropical and subtropical regions (but see Van Schaik, Terborgh & Wright, 1993, Boulter, Lambkin & Starick, 2011, Pennec, Gond & Sabatier, 2011), where precipitation is thought to play a significant role in driving phenological patterns (Folland, Karl & Salinger, 2002, Dunn et al., 2009). Another important factor influencing phenology in these regions, especially in temperate regions, is photoperiod, i.e., day length (Way & Montgomery, 2014). This cue is not linked to climate pattens and thus does not change as temperatures change (Way & Montgomery, 2014). However, this could potentially lead to asynchrony in functionally paired cues (Hänninen & Tanino, 2011). For example, organisms that use photoperiodic cues for determining the arrival of seasons (e.g., spring and autumn) may have constrained responses to warming (Way & Montgomery, 2014). Reduced temperature fluctuations at lower latitudes allow more species to reproduce year-round than at higher latitudes where extreme winters impose distinct periods of latency (Morellato, Camargo & Gressler, 2013). Therefore, as the effects of climate are predicted to differ substantially between latitudes (Giorgi, 2006), it can be assumed that phenological patterns will not be consistent across the planet and assumptions drawn from research conducted in lower latitudes (in temperate systems), cannot be suitably applied to regions of lower latitudes (e.g., sub-tropical and tropical systems) respectively. It could thus be expected that phenological patterns in lower latitude areas are not mainly driven by temperature, as they are in the higher latitudes (Chambers et al., 2013). Instead, in these higher latitude regions, where wet and dry seasons are more pronounced, rainfall and photoperiod may be predicted as an important driver of phenological patterns (Morellato, Camargo & Gressler, 2013).

In Chapter 2, I use herbarium records to investigate which climatic factors influence the fruiting phenology of 58 (summer rainfall) South African fleshy- and dry-fruited tree species. Understanding the climatic drivers of such broad scale phenological patterns has implications for understanding how plants will respond to future global changes, particularly climate change (which threatens the integrity of environmental cues that have evolved with interacting species, and thus results in knock-on effects throughout ecosystems (Cleland et al., 2007)).

Woody encroachment: an overview

Woody encroachment is the result of several global change drivers, including increased atmospheric CO_2 levels, associated climate change, and land use changes. Woody encroachment threatens the biological diversity and natural processes of grassland and savanna ecosystems as it can result in shifts from open grassy systems to closed savannas/woodland which bring about changes in ecological function and productivity (Hoekstra et al., 2005, Ratajczak, Nippert & Collins, 2012). Generally associated with a reduction in the herbaceous cover within grassland and savanna ecosystems, woody encroachment often leads to a point at which return to the original state becomes difficult (Schlesinger et al., 1990). In grassy ecosystems, an increase in woody cover leads to a decrease in grass cover (Bond, 2008). As grass acts as a fuel for fire, a change in the proportion of grass cover/biomass could lead to fewer fires, thus altering both the biological diversity and underlying ecological processes of ecosystems. For example, through changes to the structure, composition, and function of an ecosystem, bush encroachment effectively influences the ability of an ecosystem to deliver different ecosystem services (Eldridge et al., 2011, Mace, Norris & Fitter, 2012, Stafford et al., 2017).

From an economic perspective, bush encroachment can reduce the land available for crop and livestock production (Asner et al., 2004). By reducing the herbaceous layer and increasing the number of unpalatable woody species, bush encroachment forms a serious threat to the economic outputs of cattle production (Reed et al., 2015). Furthermore, this has implications for ecosystem services derived for cultural reasons. Much of southern Africa’s rural population farms cattle, which are often associated with aspects of wealth (Reed et al., 2015). Bush encroachment has also been found to decrease species richness (Reed, Dougill & Baker, 2008, Ratajczak, Nippert & Collins, 2012); encroachment has been linked to changes in the abundance and distribution of bird and invertebrate species (O'Connor, Puttick & Hoffman, 2014). As an estimated 25% of the Earths land surface is comprised of savanna and grassy biomes, woody encroachment is of global significance (Wigley, Bond & Hoffman, 2010, Chapin, Sala & Huber-Sannwald, 2013).

An increase in the abundance of woody vegetation within savanna and grassy biomes has been recorded worldwide (e.g., Stevens et al., 2017, Stevens et al., 2022). This increase in woody vegetation is considered a serious threat to global grassland and savanna ecosystems (Wigley, Bond & Hoffman, 2009, Wigley, Bond & Hoffman, 2010). Encroachment has been described globally (e.g., see Bond, Woodward & Midgley, 2005, Stevens et al., 2017) as well as locally (e.g. O'Connor & Crow, 1999, Wigley, Bond & Hoffman, 2009, Wigley, Bond & Hoffman, 2010, O'Connor & Chamane, 2012); however, encroachment is thought to be the result of a combination of both local and global factors (Wigley, Bond & Hoffman, 2009, Wigley, Bond & Hoffman, 2010, O'Connor & Chamane, 2012, Skowno et al., 2017). Often altered land use practices and management efforts, such as altered fire regimes and herbivory rates, are regarded as important local drivers of woody encroachment (Brown & Archer, 1989b, O'Connor & Chamane, 2012, Russell & Ward, 2014), whereas the impact of climate change and the alteration of atmospheric CO_2 levels have been proposed as global drivers of woody encroachment (Brown & Archer, 1989b, O'Connor & Chamane, 2012). As no agreement on any one individual driver has been made, woody encroachment is likely a consequence of several interacting factors (O'Connor & Chamane, 2012, O'Connor, Puttick & Hoffman, 2014, Archer et al., 2017a), including altered fire and herbivory regimes, alterations in soil characteristics, climate change, and altered atmospheric CO_2 levels amongst others (each discussed in more detail below).

Fire is an important natural component within savanna and grassland ecosystems (Joubert, Smit & Hoffman, 2012). As it is considered a global factor that controls some of the world's plant distributions (e.g., within grassy biomes), fire ensures a reduction in plant biomass (especially woody plant biomass) and can prevent trees from establishing in certain ecosystems (Bond, Woodward & Midgley, 2005). In particular, by favouring grassy components over woody components, fire prevents a transition from grassy or savanna ecosystems to closed woodland or forest type vegetation by inhibiting tree establishment (Bond, Woodward & Midgley, 2005, Joubert, Smit & Hoffman, 2012). Fire is thought to negatively impact the establishment of woody vegetation by influencing factors such as seedling regeneration, growth and survival (Bond, Midgley & Woodward, 2003, O'Connor, Puttick & Hoffman, 2014). Thus, in the absence of fire, woody vegetation can proliferate (Bond, Midgley & Woodward, 2003, Russell & Ward, 2014, Skowno et al., 2017). This increase in woody vegetation further affects the community as grassland and savanna fires are fuelled by grasses (Mucina & Rutherford, 2006, Russell & Ward, 2014). In the event of woody encroachment, the proportion of grasses within the encroached habitat decreases, leading to a decrease in potential fuel for fires, consequently, less severe and fewer fires result (Russell & Ward, 2014). Several studies have found support that the suppression of fire is a driver of woody encroachment (Bond, Woodward & Midgley, 2005, Briggs et al., 2005, Archibald et al., 2010, Joubert, Smit & Hoffman, 2012, O'Connor, Puttick & Hoffman, 2014).

Altered herbivory regimes are also considered important factors influencing woody encroachment within grassy ecosystems. A frequently reported cause of woody encroachment is high grazing pressure (e.g. Asner et al., 2004, Kraaij & Ward, 2006, Tessema et al., 2012, Tedder et al., 2014). Intense grazing can result in woody encroachment by altering tree-grass competition for nutrients and soil moisture (O'Connor, Puttick & Hoffman, 2014). Both fire and grazing have a similar effect on the ecosystem where both create ‘gaps’ that make above- and below-ground resources, such as water and nutrients, available for the establishment of woody seedlings (Belayneh & Tessema, 2017). The removal of browsers from grassy ecosystems also results in woody encroachment. Browsers selectively reduce woody biomass, and in their absence, woody plants proliferate (O'Connor, Puttick & Hoffman, 2014).

Soil factors have been proposed as important in determining the patterns of woody plants in grassland and savanna ecosystems (Sankaran, Ratnam & Hanan, 2008). The apparent covariance that has been reported between soil structure and soil nutrients plays an important role in determining tree: grass ratios across grassland and savanna ecosystems (Britz & Ward, 2007, Sankaran, Ratnam & Hanan, 2008). Nitrogen is an important nutrient that limits the growth of fast-growing grasses (Belayneh & Tessema, 2017). In high quantities, nitrogen is thought to favour the establishment of herbaceous plant species, which would generally outcompete their slow-growing tree competitors (Belayneh & Tessema, 2017, Chen et al., 2021). However, tree species (e.g., species with nitrogen-fixing abilities such as legumes (Britz & Ward, 2007)) will benefit in environments where soil nitrogen is limiting as they have a competitive advantage over their neighbouring grass species (Sankaran et al., 2005, Sankaran, Ratnam & Hanan, 2008, Belayneh & Tessema, 2017). Consequently, nutrient-poor environments are suspected to be more susceptible to woody encroachment, especially encroaching species that have nitrogen-fixing abilities, than nutrient-rich environments (Sankaran et al., 2005, Belayneh & Tessema, 2017).

Climate change has drastically affected the variability of temperature and precipitation globally (Warburton, Schulze & Maharaj, 2005, Blois et al., 2013). As temperature and precipitation are both important factors influencing plants, a change in variability of these factors has consequences for plants. Increases in temperature in some locations has resulted in a lowered number of frost events (Warburton, Schulze & Maharaj, 2005). Frost generally has a negative effect on the survival of savanna and grassland trees; in the absence of frost, trees that would have previously been excluded from the area may now survive (O'Connor, Puttick & Hoffman, 2014). Changes in precipitation variability have also been identified as a driver promoting woody encroachment (O'Connor, Puttick & Hoffman, 2014, Belayneh & Tessema, 2017, Skowno et al., 2017), where an increase in rainfall variability may result in extended wet periods which promotes the growth of woody vegetation (Sankaran et al., 2005). Increased precipitation may further result in increased soil moisture which promotes the prolonged survival and establishment of woody seedlings, allowing them to develop into coppices (Belayneh & Tessema, 2017).

Altered levels of global CO_2 concentrations have also been proposed as a global driver of woody encroachment (Wigley, Bond & Hoffman, 2010, O'Connor, Puttick & Hoffman, 2014, Belayneh & Tessema, 2017). Increased levels of CO_2 can positively influence the growth of C_3 woody plants at the expense of C_4 grasses (Eldridge et al., 2011, Belayneh & Tessema, 2017). Within grassy ecosystems, woody plants have a C_3 photosynthetic pathway whereas many grasses have a C_4 photosynthetic pathway (Polley, Johnson & Mayeux, 1994, Eldridge et al., 2011). At higher levels of atmospheric CO_2, the rate of C_3 photosynthesis is higher than that of C_4 photosynthesis. The differences between the C_3 and C_4 modes of photosynthesis thus produce contrasting responses to varying CO_2 atmospheric levels. Consequently, the ratio of C_3:C_4 plants within grassy ecosystems responds accordingly to climate change and altering atmospheric CO_2 levels (Lattanzi, 2010).

However, the effects of CO_2 on grassy ecosystems cannot be studied in isolation; important disturbances, such as fire and grazing, need to be considered in conjunction with the impacts from altered atmospheric CO_2 patterns (Bond & Midgley, 2012). Fire is an important natural disturbance that works to maintain grassy ecosystems in areas where climate is suitable for the persistence of forest vegetation (Bond & Midgley, 2012). Saplings within grassy ecosystems need to escape the “fire trap” and quickly attain a size in which they suffer little from frequent fires in order to grow to trees and shade out grasses. Saplings within grassy ecosystems are vulnerable to fire and the associated top kill of above ground biomass (Schutz et al., 2009). However, CO_2 influences the recruitment of saplings. Thus, under increased levels of CO_2, increased recruitment of saplings within savanna systems may result in the conversion of these systems to closed woodlands or forests (Bond & Midgley, 2012). However, large scale changes in the tree-grass equilibrium of grassy ecosystems needs to be better understood.

It has been suggested that both the local and global drivers of encroachment interact together and with other factors, such as the attributes of encroaching species, in complex ways (O'Connor & Chamane, 2012). Encroachment efficiency can be influenced by traits, such as dispersal mechanisms, establishment success, and growth rates, of the encroaching species (O'Connor & Chamane, 2012). The introduction of domestic livestock may aid in the dispersal of specific tree species (Brown & Archer, 1989a, O'Connor, Puttick & Hoffman, 2014). In southern Africa, cattle have been linked to an increase in the density of *Grewia flava*, a common encroaching species that has fleshy fruits (Tews et al., 2004b). In these regions, *G. flava* seeds are deposited beneath the canopies of individual trees and the surrounding grass matrix through the dung of cattle that have consumed the seeds resulting in a woody densification of the area (Tews et al., 2004a, Tews et al., 2004b).

Types of Woody Encroachment

Woody encroachment occurs in many forms, but can broadly be differentiated into two main types, namely densification and forest expansion (including nucleation events) (Stevens et al., 2017). Densification often starts with only a few individual trees; a significant increase in the establishment of a subset of woody individuals (i.e., densification) may result in the progression of somewhat open habitats to that of more closed habitats (Dean, Milton & Jeltsch, 1999). For example, in southern Africa *Vachellia* and *Senegalia* tree species (e.g., *Vachellia karroo* and *Senegalia mellifera*) as well as *Dichrostachys cinerea* have often been identified as the species initiating woody encroachment and largely proliferate within overgrazed ecosystems (e.g., Tews et al., 2004b, Randle, Stevens & Midgley, 2018). The second type of encroachment involves forest expansion – this type of encroachment occurs with the suppression of natural disturbances (e.g., fire or frost) that would otherwise prevent the establishment of forest trees (Swaine, 1992, Coetsee & Wigley, 2013). Examples of this type of encroachment have been identified in Ghana and South Africa (Swaine, 1992, Coetsee & Wigley, 2013). Here, woody encroachment often starts with the formation of small dense clumps of woody species, commonly referred to as bush clumps, which subsequently expand in size (Gower et al., 1992, O'Connor & Chamane, 2012). Of the two broad encroachment types, nucleation events have received the least research attention (O'Connor & Chamane, 2012). Furthermore, the ecological value of these clumps in different ecosystems is debated; for example, bush clumps have been identifed as natural occurences within Ghanaian savannas ecosystems (Swaine, 1992). In contrast, the devlopment of bush clumps in semi-arid regions of South Africa, because of altered landuse practices (e.g., altered fire and herbovory regimes) has implications for both the composition of ecological communities and the provision of ecosystem services such as nutrient cycling and grazing capacity. Thus enchroachment, through the formation of bush clump expansion forms the focus of the discussion below as well as Chapter 3.

The effects of bush clumps can be seen in a South African grassy ecosystem where bush clumps are the result of altered fire and herbivory regimes (O'Connor & Chamane, 2012). Their establishment is thought to be an example of autogenic succession that has resulted from facilitation (Connell & Slatyer, 1977). This process of succession involves the presence of a founder individual that facilitates the establishment of other species through a process of nucleation which is ultimately driven by animal dispersal (Yarranton & Morrison, 1974, O'Connor & Chamane, 2012). The succession of these clumps is unusual in that they do not develop following a disturbance as postulated by the definition of succession, i.e., the sequential change in species composition following a disturbance that results in the abrupt losses of biomass or ecological structure (Wardle, Walker & Bardgett, 2004, Prach & Walker, 2011). However, these clumps do occur where natural disturbance factors (i.e. fire suppression and decreased herbivory) have been reduced. In this example, successional procceses thus occur following the removal of natural (vegetation-driving) disturbance, which in itself is a form of disturbance.

However, our knowledge regarding other mechanisms that are important drivers in the development of bush clumps is still unclear. Bush clumps create 'micro-climates' that are speculated to facilitate the establishment of the clump tree species (Dean, Milton & Jeltsch, 1999, O'Connor & Chamane, 2012). It is suspected that the presence of bush clumps can reduce the impact of fire and enable the establishment of trees that result in the suppression of grass species. A study by O'Connor and Chamane (2012) found that the microclimate within bush clumps in the Eastern Cape province of South Africa improved water balance within the soil and thus facilitated the establishment of water-demanding species within the bush clump sub-canopy. Also, changes to the microclimate of the bush clump resulted in increased minimum temperatures, higher relative humidity and increased soil fertility compared to surrounding landscape (O'Connor & Chamane, 2012). Furthermore, maximum air temperature and irradiance become lower while humidity becomes higher as bush clumps increase in size (Jarvel & O'Connor, 1999). These conditions are thought to favour the establishment of trees.

The development of bush clumps within grassy ecosystems has implications for both the composition of ecological communities and the provision of ecosystem services such as nutrient cycling and grazing capacity. In chapter 3, I investigate the successional patterns associated with the development of bush clumps within a South African open savanna. I test whether species composition changes with clump size, how multiple environmental factors in bush clumps relate to changes in species composition, and whether habitat specialisation of species is more dominant in large bush clumps. This chapter provides novel insights into how multiple environmental variables accompany species turnover during succession of South African bush clumps which can inform management of woody encroachment and conservation of savannas and grasslands.

Ecological succession: an overview

The formation of bush clumps within savannas (and the associated directional change in species composition with time) is just one example (and one possible trajectory) of succession (i.e., the sequential change in species composition following a disturbance that results in the abrupt losses of biomass or ecological structure (Wardle, Walker & Bardgett, 2004, Prach & Walker, 2011). Indeed, biodiversity and ecosystems can be significantly impacted by global change impacts (Matesanz &

Gianoli, 2014). One way in which habitats persist following such impacts is through succession. Two types of succession are recognised: primary and secondary succession (Walker & Del Moral, 2003, Walker et al., 2010). Primary succession occurs (1) after a disturbance which destroys the integrity of an ecosystem (Walker & Del Moral, 2003, Walker et al., 2010), or (2) more commonly, on newly formed substrate such as lava flows, retreating glaciers, or new sand dunes. Primary succession involves the sequential change of species composition in an ecosystem that has no remaining animals or plants (Walker et al., 2010). In comparison, secondary succession involves the sequential change in species composition following a disturbance in which the integrity of an ecosystem has not been destroyed and some biological legacy remains (Walker & Del Moral, 2003, Walker et al., 2010, Prach & Walker, 2011). Furthermore, succession is influenced by two underlying processes, namely deterministic and stochastic succession (Dent, DeWalt & Denslow, 2013, Dini-Andreote et al., 2015). In deterministic succession, factors such as site conditions, species sorting mechanisms and disturbance intensity may directionally influence the trajectory of succession (Meiners et al., 2015, Chang & Turner, 2019). In contrast, stochastic succession as an inherent probabilistic biological process, is influenced by less predictable factors such as random chance events, the availability of colonisers in the surrounding landscape, or unique conditions during disturbance events (Chase & Myers, 2011, Zhou et al., 2014).

The outcome of ecological succession is to reach a community whose populations remain stable until disturbed (Walker et al., 2003). This end-point community, termed the climax community, is dependent on several biotic and abiotic factors (which ultimately affect the trajectory of successional processes). Generally, the process of ecological succession is accompanied by changes in biomass, nutrient availability, primary production, species composition and species diversity (Walker et al., 2001, Wardle, Walker & Bardgett, 2004), although there have been instances where decreases in the aforementioned properties have been found (Walker et al., 2001, Wardle, Walker & Bardgett, 2004). As a result, there has been much argument regarding the supposed predictability or unpredictability of community assemblage processes that constitute the process of ecological succession (Prach & Walker, 2011). For example, Gleason (1926) suggested that the environment, and species' movements were important factors regulating assembly processes and that changes along successional gradients are always as predictable as Clements (1936) had originally proposed.

Ecological succession is generally characterised by the presence of different stages of succession. That is, pioneer, early, mid, and late (or climax) stages that indicate the level of sequential change that has occurred within the ecosystem (Walker & Del Moral, 2003, Prach & Walker, 2011). The process of successional change is not always linear and often an unpredictable endpoint is reached (Walker & Del Moral, 2003). Because of this nonlinear directionality, several different trajectory types can be followed during the process of succession (Walker et al., 2010). These trajectories can be cyclic, convergent, parallel, reticulate or divergent in nature (Walker & Del Moral, 2003). However, as ecosystems are dynamic, any form of disturbance can redirect the trajectories of ecological succession, hence, predictable climax systems are not usually met. Furthermore, there is no one mechanism driving the process of ecological succession. Suggested mechanisms responsible for the process of ecological succession include facilitation, tolerance, and inhibition (Connell & Slatyer, 1977). All three mechanisms are based on a replacement sequence which involves the interactions between early and later colonising species (Connell & Slatyer, 1977, Walker & Del Moral, 2003).

Within this thesis, two chapters deal with succession (Chapters 3 & 4). However, the definitions of succession within each chapter are different; this difference is attributed to the underlying drivers of succession. In Chapter 3, the succession of bush clumps does not follow the typical definition of succession, as the clumps develop in the absence of a disturbance. However, given that these clumps are the result of the loss of natural disturbances (e.g., removal of herbivory and/or alteration in fire regimes), the loss of these disturbances (which is considered a disturbance in itself) drive the successional patterns observed within the habitat. Although the succession does not occur following abrupt losses of biomass or ecological structure, it should be noted that the loss of disturbance within grassy ecosystems does impact species composition and structure by influencing life history traits. Although this associated change in composition and structure may not be abrupt, it is still a form of disturbance that allows successional process to proceed. In contrast, the definition used to define succession in Chapter 4, is that of the typical, ideological definition of succession, i.e., i.e., the sequential change in species composition following a disturbance that results in the abrupt losses of biomass or ecological structure.

Functional traits & community assembly dynamics

The ability to understand successional trajectories and community assembly processes is a major objective within plant ecology (Walker & del Moral, 2009, Douma et al., 2012b). Without a clear understanding of the drivers of succession, our ability to predict how species assemblages regenerate after disturbance remains difficult (Prach & Walker, 2011). Successional trajectories cannot be predicted from measures of species diversity and composition alone, as this approach has recently been proposed to have limited predictive ability (Zhou et al., 2014, Norden et al., 2015). How species diversity and composition changes with succession does not necessarily link assembly processes with ecological processes or functions (Piqueray et al., 2015). Plant functional traits, i.e., the physiological, morphological, behavioural, or phenological characteristics that are related to the fitness and performance of an organism (Violle et al., 2007), can reveal the underlying mechanisms that drive species turnover across successional gradients (McGill et al., 2006, Douma et al., 2012b). The advantage of using a trait-based approach over measures of species composition, to predict successional trajectories, is that the driving mechanisms of succession in different ecosystems and vegetation types become comparable and universal trends can be elucidated (Díaz, Noy-Meir & Cabido, 2001, Kahmen & Poschlod, 2004). Thus, traits allow us to predict species turnover and provide insight into the underlying mechanisms that drive community assembly processes over succession (Douma et al., 2012b, Piqueray et al., 2015).

By adopting a trait-based approach, our ecological understanding is guided by focusing on characteristics that describe how organisms interact with their surrounding physical, chemical and biological environments (Hooper et al., 2005, Nock, Vogt & Beisner, 2016). Functional ecology has received more research attention in recent years and a functional trait approach is frequently used within ecology with an aim to (i) characterise the responses of organisms to changes within their environments including how traits change with community assembly patterns (which forms the basis of the topics addressed in Chapter 4), and (ii) to quantify the effect that individual organisms can have on ecosystem function and process (Violle et al., 2007, Díaz et al., 2013). To date, the use of functional traits within ecology has proved useful in improving our understanding of ecological patterns and phenomena (e.g., see Hooper et al., 2005, Vogt, Beisner & Prairie, 2010).

A major goal within the field of functional ecology is to characterise the responses of organisms to changes within their environments and predict how traits change with community assembly patterns (Chang & Turner, 2019, Prach & Walker, 2020). This ability has become particularly important as we enter an age characterised by large and sometimes extreme changes to natural communities and ecosystems because of global change drivers. Functional traits can thus be used to understand fundamental trade-offs within an organism which ultimately determine the organism's ecological role within the ecosystem (Douma et al., 2012a, Piqueray et al., 2015). This understanding comes about as environmental conditions act as filters constraining which individuals within a community (that bear specific traits) can establish and persist within the ecosystem (Keddy, 1992). For example, abiotic factors, together with their interactions with biotic drivers, exert pronounced pressure on the selection of functional traits displayed in plant communities; different abiotic conditions require varying sets of traits to establish and persist in a particular environment (Cornwell & Ackerly, 2010). Therefore, as succession progresses and abiotic (and biotic) conditions change, it is generally believed that species are replaced by others whose traits enable them to be better adapted to the environmental conditions that are experienced across successional gradients (Huston & Smith, 1987, Douma et al., 2012b, Prach & Walker, 2020). In such instances, it should be possible for the functional traits of individual plants to be scaled up to infer on broader community dynamics (Prach & Walker, 2020). If such processes are at work, it should be possible for community assembly processes, which are assumed to be a result of environmental filtering processes, to be predicted from plant functional traits (Violle et al., 2007, Schleicher, Peppler-Lisbach & Kleyer, 2011, Chang & Turner, 2019, Prach & Walker, 2020).

If environmental filtering processes are at play, then it can be expected that functional traits will change consistently as environmental conditions change in accordance with changing successional stages. Indeed, uniform trends are expected between the traits associated with early successional and late successional species (Raevel, Violle & Munoz, 2012). For example, early successional species have typically been reported to have higher leaf nitrogen content (LNC) and specific leaf areas (SLA) and lower leaf life spans (Navas et al., 2003, Chai et al., 2016). These traits can convey an advantage to early successional species through the following: (i) plants with high LNC have fast growth rates, achieved through increased photosynthetic capacity and tolerance to stressful conditions (Wright et al., 2004, Navas et al., 2010, Wilfahrt, Collins & White, 2014), (ii) high SLA results in a high mass-based net photosynthetic rate which is advantageous during the early stages of succession, and (iii) lower leaf spans in early succession typically indicate rapid leaf turnover, which is associated with fast carbon fixation and thus relative growth (Ryser & Urbas, 2000). As succession progresses, and ecosystems become more stable, plant strategies may employ more conservative traits, i.e., investing energy into other strategies such as defensive mechanisms, which trades off against growth rates (Derroire et al., 2016). A competitive advantage is provided later in succession by supporting species that have high leaf dry matter content (LDMC) and leaf carbon content (LCC) (Navas et al., 2010); typically, high LDMC and LCC corresponds to high survival rates and carbon gains (Navas et al., 2010, Chen et al., 2021). The associated life history traits and different resource use strategies employed by different plants at different stages of succession is thus illustrated in trait changes across succession (Violle & Jiang, 2009). However, inconsistent trends across succession have been reported (e.g. see Guariguata & Ostertag, 2001, Schneider et al., 2003, Khurana & Singh, 2004, Purschke et al., 2013), and can be attributed to the systems in which plants are situated; succession may not always follow a directional trajectory (i.e., stochastic succession) and thus directional trends may not always be observed.

To date there exists no comparative analysis on whether a general rule exists for how or if functional traits can be used to consistently predict overall patterns of vegetation change related to succession. Particularly whether consistent trends exist across vegetation types, growth form and disturbances are still unclear (Prach & Walker, 2020). As such, in Chapter 4, I conduct a qualitative systematic review on the available trait-based successional literature. The objective of this chapter is to contribute to the understanding of the possible advantages of using functional traits to infer on community assembly over time (i.e., succession). This will ultimately inform our understanding of community assembly and ecological processes which can thus recommend principles for conservation and restoration.

Global change: summary & relevance to PhD thesis

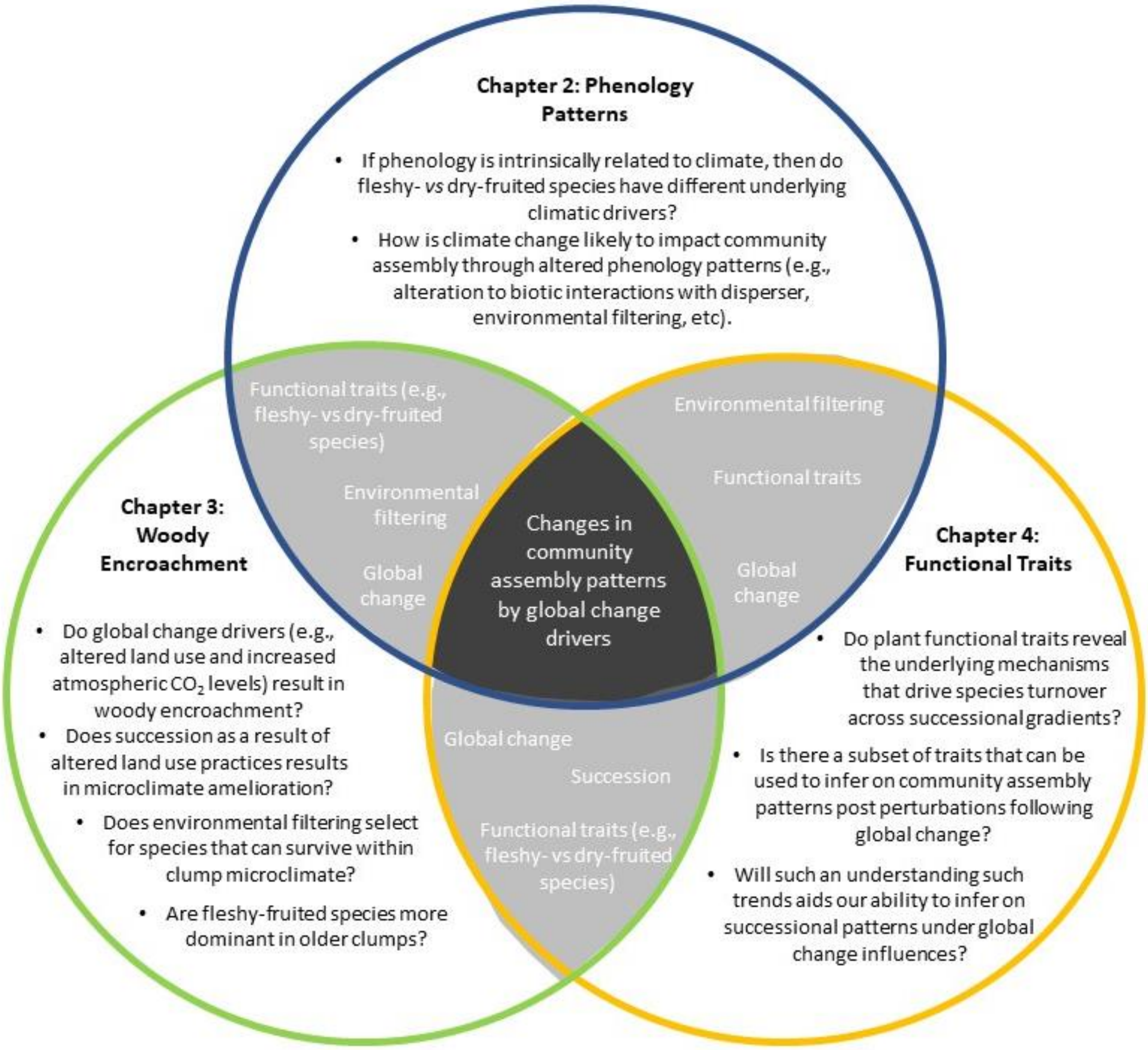
The objective of this thesis was to provide clarity on how inferences of global change drivers can potentially influence vegetation dynamics (which manifest through changes in altered phenology patterns, increased woody encroachment, and altered functional trait patterns assembly patterns). To achieve this, a combination of experimental and observational data was used. This thesis comprises of three research chapters (described briefly below). Each chapter was written as a stand-alone manuscript with a separate study aim. The main aim of each research chapter is provided below (in text). Although the research chapters do not directly examine any global change effects, they do provide an important context and motivation for the thesis and illustrate how ecosystems and their associated community assembly patterns are influenced by global change factors (Figure 1.1).

For example, one major impact that global change drivers have on vegetation communities include associated changes to dispersal ability and biotic interactions (two important factors of community assembly); changes in phenology patterns because of global change factors (e.g., climate change) has ecosystem-wide consequences, including implications for seed dispersal and for animals that rely on fruit as a food source (refer to the "*Phenology: an overview*" section below). In Chapter 2, I tested, using herbarium records, which climatic factors influence the fruiting phenology of 58 South African fleshy- and dry-fruited tree species. This will aid in our understanding of how climate change impacts fruiting phenology and the associated implications for community assembly processes – altered phenology patterns may result in alterations to dispersal ability and biotic interactions (e.g., dispersers),

Another consequence of global change drivers is woody encroachment, which is the result of a combination of both local and global drivers; Wigley, Bond & Hoffman, 2010, Skowno et al., 2017). Encroachment, through nucleation events, is a form autogenic succession that has resulted from facilitation (Connell & Slatyer, 1977). This process of succession involves the presence of a founder individual that facilitates the establishment of other species through a process of nucleation which is ultimately driven by animal dispersal (Yarranton & Morrison, 1974, O'Connor & Chamane, 2012). Ancedotal evidence suggests that these clumps are established by the presence of a founder individual, which is often considered to be a dry-fruited, wind-dispersed species. As this founder tree serves as a perch and/or provides refuge for animals, subsequent tree species that expand the clump are thought to be fleshy-fruited, animal-dispered species. In Buffelskloof Private Nature Reserve, South Africa, the formation of bush clumps has been recorded over the last decades. These clumps tend to culminate in closed vegetation community, anagolous to a forest system. The likely drivers of these clumps within the reserve include the loss of large herbivores within the area (likely local driver) and altered atmospheric CO_2 levels (leikly global driver). In this chapter (Chapter 3), I investigated the successional patterns associated with the development of bush clumps within a South Africa open savanna, and their potential microclimatic drivers. This chapter aids in our understanding of how changes in land use management and altered atmospheric CO_2 levels impact environmental filtering processes following disturbances brought about by global change. Furthermore, understanding how environmental filtering influences biotic interactions (environmental amelioration) and dispersal (fleshy- vs dry-fruited species) will aid in our understanding of how clump succession can progress.

As vegetation communities change with succession, an associated change in functional traits can occur (refer to the "*Ecological succession: an overview*" and "*Functional triats and community assembly dynamics*" sections below). In addition to testing for changes in fruiting and tree size traits with succession in Chapter 2, I investigate whether any patterns exist in functional trait change across bush clumps succession (Chapter 3). Changes to species traits as a reuslt of species compositional changes (brought about by succession) allows species to better utilise and persist in the particular environmental conditions they experience (which changes with succession). Our ability to understand successional trajectories and community assembly processes is a major objective within plant ecology (Walker & del Moral, 2009, Douma et al., 2012b); indeed, without a clear understanding of the drivers of succession, our ability to predict how species assemblages regenerate after disturbance remains difficult (Prach & Walker, 2011). However, to date there exists no comparative analysis on whether a general rule exists for how or if functional traits can be used to consistently predict overall patterns of vegetation change related to succession. In Chapter 4, I aimed to conduct a systematic review to assess if there are consistent trends in plant functional trait responses across successional gradients, and to assess whether existing studies investigating functional trait turnover across successional gradients show biases in geographic distribution, growth form (e.g., woody *vs*. herbaceous species) and vegetation types that are investigated. This will aid in our ability to predict how environmental filtering processes will operate following disturbances brought about by global change.

Although the major research themes and questions of each of the research chapters are variable, each chapter lends to the next to illustrate the broad implications that global change drivers can have on vegetation communities and associated assembly patterns (Figure 1.1).



Chapter 2: Phenology Patterns

- If phenology is intrinsically related to climate, then do fleshy- *vs* dry-fruited species have different underlying climatic drivers?
- How is climate change likely to impact community assembly through altered phenology patterns (e.g., alteration to biotic interactions with disperser, environmental filtering, etc).

Chapter 3: Woody Encroachment

- Do global change drivers (e.g., altered land use and increased atmospheric CO_2 levels) result in woody encroachment?
- Does succession as a result of altered land use practices results in microclimate amelioration?
- Does environmental filtering select for species that can survive within clump microclimate?
- Are fleshy-fruited species more dominant in older clumps?

Chapter 4: Functional Traits

- Do plant functional traits reveal the underlying mechanisms that drive species turnover across successional gradients?
- Is there a subset of traits that can be used to infer on community assembly patterns post perturbations following global change?
- Will such an understanding such trends aids our ability to infer on successional patterns under global change influences?

FIGURE 1.1 Schematic diagram illustrating how the major themes of the thesis are connected. Blue, green, and yellow circles represent the different research chapters (chapters, 2, 3 and 4 respectively). Unshaded areas provide an indication of the main aims of each chapter. The light grey shaded areas of the Venn diagram illustrate the overlapping themes shared across the chapters (e.g., functional traits in various aspects, environmental filtering processes, global change impacts, and succession). The overarching theme, changes in community assembly patterns because of global change drivers (indicated in the dark grey shaded centre), is applicable to all three research chapters.

To successfully predict how ecosystems and associated species will respond to global change drivers, we need to understand the underlying drivers of global change and how these factors work to influence biological communities. To achieve this, research from a multitude of scientific disciplines should be used to infer on the associated consequences that face biological communities. The focus of this thesis was to elucidate on some of the drivers associated with vegetation dynamics. In the following chapters (Chapters 2 - 4), I briefly outline the consequences that vegetation communities experience in the face of global change. The impacts, because of global change drivers (e.g., altered land use changes, altered atmospheric CO_2 concentrations, amongst others) associated with phenology patterns, woody encroachment, and functional trait patterns assembly patterns will be of particular interest as they relate to the research topics dealt with in my research chapters (Chapters 2 – 4).

NOTE: Chapter 3, titled "*The role of deterministic succession during forest development within a southern African savanna*" was published in Biotropica in 2021. Please refer to the link provided (https://onlinelibrary.wiley.com/doi/abs/10.1111/btp.12890), alternatively please see a copy of the paper at the end of this thesis (in the "Published Article" section).

CHAPTER 2

Comparing the drivers of fruiting phenology of fleshy-fruited and dry-fruited trees across South Africa

COMPARING THE DRIVERS OF FRUITING PHENOLOGY OF FLESHY-FRUITED AND DRY-FRUITED TREES ACROSS SOUTH AFRICA

Abstract

Phenology - the timing of seasonal life history events - affects virtually all facets of ecology and evolution. Much of the focus of plant-based phenological studies has been on flowering and leafing phenology, whereas fruiting phenology has received less attention. Understanding fruiting phenology is important because it has ecosystem-wide consequences, e.g., implications for seed dispersal and for animals that rely on fruit as a food source. It was hypothesised that fleshy- and dry-fruited species have different requirements for fruit production because they have different water requirements, sensitivities to frost, and dispersal modes. Using herbarium records, I report on how climatic factors influence the fruiting phenology of widespread South African fleshy- and dry-fruited tree species. Specifically, I test whether fleshy- and dry-fruited species show different seasonal peaks in fruiting periods, if different climatic factors influence the fruiting phenology of fleshy- and dry-fruited species, and if the relative importance of different climatic variables to intraspecific phenological variation differs between fleshy- and dry-fruited species. Fruiting phenology was recorded from 3864 herbarium vouchers for 29 fleshy-fruited and 29 dry-fruited (South African) species. The environmental niche of each species was extracted from climate maps. The mode fruiting day was compared between fleshy- and dry-fruited species. Non-parametric generalised additive models (GAMs) were used to compare the influence of various climatic variables on the mode day of fruiting phenology of fleshy- *vs* dry-fruited species. Random forest regression was used to investigate how the relative importance of different climatic variables influenced the day of fruiting of each tree species, and to test whether the importance of drivers differed between fleshy- and dry-fruited species. The mode fruiting day was significantly earlier for fleshy-fruited (1 December) than dry-fruited (5 March) species. The effects of several climatic predictors on fruiting phenology depended on fruiting type (fleshy- *vs* dry-fruited); fleshy-fruited species typically fruited earlier at low minimum temperatures of the coldest months, during periods of low temperature seasonality, during periods of higher temperature of the warmest quarter, and during periods of high solar radiation. In contrast, dry-fruited species fruited 1) earlier at low minimum temperatures of the coldest months, during periods of low precipitation of the driest quarter, and during periods of high solar radiation. In contrast, only one variable was found to affect the variation of broad-scale phenology patterns within species: the relative importance of minimum temperature of the coldest month to phenology was important for fleshy-fruited species but not for dry-fruited species. From this study, it is evident that climatic variables are important for fruiting phenology, but that fleshy- and dry-fruited species respond to different climatic cues. Understanding which climatic variables influence phenology, particularly phenology patterns within the southern hemisphere, is important as the need to predict the associated impacts on plants because of climate change has become imperative in a world undergoing climate change. As climatic drivers change in accordance with climate change, they bring about associated changes in fruiting phenology patterns which has implications at the level of the ecosystem, including biotic interactions with dispersal agents.

Introduction

Phenology - the timing of seasonal life history events, such as flowering of plants, or migration of animals (Visser & Both, 2005, Neil & Wu, 2006) - affects virtually all facets of ecology and evolution (Forrest & Miller-Rushing, 2010). Climatic factors often shape phenological patterns (Cleland et al., 2007, Wolkovich, Cook & Davies, 2014). The phenology of interacting organisms generally match each other, e.g. the flowering time of a plant matches the timing of emergence of its specialist pollinator (Wolkovich, Cook &

Davies, 2014). However, climate change can modify species interactions through causing phenological mismatches (i.e., unequal shifts in the phenology of interacting species) which can have major consequences for ecosystems (Chambers et al., 2013). Changes in the phenology of one species can therefore result in alterations of both antagonistic and mutualistic species interactions, e.g., predator-prey interactions, plant-pollinator interactions, and plant-disperser interactions (Rafferty, CaraDonna & Bronstein, 2015). In a world undergoing major global changes, including climate change, a clear understanding of the patterns and underlying drivers influencing phenological patterns is thus required. With such knowledge the direction and magnitude of climate change impacts on the phenological responses of species can be predicted.

Much of the focus of plant-based phenological studies has been on flowering and leafing phenology, whereas fruiting phenology has received less attention (Robbirt et al., 2011). Understanding fruiting phenology is important because it has implications for seed dispersal and seed predation, an important factor that ultimately affects seedling establishment and survival (Howe & Smallwood, 1982), as well as implications on animals that rely on fruit as a food source. Effective seed dispersal allows some propagules to reach sites suitable for germination and establishment, generally away from the parent plant where mortality is lower as intraspecific competition is less intense (Clark & Clark, 1984). Indeed, angiosperms vary in several attributes to increase the effectiveness and quality of their seed dispersal, namely seed size and colour, nutritional attributes, presence of accessory structures such as arils, fleshiness, and the timing of fruit ripening (Mazer & Wheelwright, 1993, Griz & Machado, 2001, Bolmgren & Eriksson, 2010). These morphological, physiological and phenological traits are often associated with particular dispersal modes (Van der Pijl, 1982). For example, fleshy fruits (such as drupes and berries), in which seeds are enclosed in a fleshy pulp, act as attractants to seed dispersers (Howe & Smallwood, 1982) and have thus been demonstarted to be predominantly animal-dispersed (Ramos et al. 2006). In contrast, dry fruits (e.g., nuts, capsules, or pods), in which seeds are enclosed in hard, dry material (which can be woody, leathery, or tough), can be dispersed by biotic means (e.g., mammals) or are likely dispersed by wind or other abiotic dispersal modes (Howe & Smallwood, 1982, Wheelwright, 1985). As the anatomy between fleshy and dry fruited species differs, it can be expected that there will be differences in energy investment and the types of strategy employed by fleshy and dry fruited species for effective seed dispersal (Howe & Smallwood, 1982).

Because climate is hypothesised to be an important driver of plant phenology (Cleland et al., 2007, Wolkovich, Cook & Davies, 2014), it is expected that fleshy- and dry-fruited species have different requirements for fruit production, especially as energy investments vary considerably between fruit type (Howe & Smallwood, 1982) and because fruit maturation is thought to correspond with suitable conditions for effective seed dispersal (Griz & Machado, 2001, Chapman et al., 2005).

Furthermore, plant fitness is directly impacted by phenology patterns. . For example, to increase fitness and the probability of being pollinated, plants must flower when pollinators are available and when abiotic conditions are suitable for plant growth and reproduction (Pilson 2000). Similarly, fruit maturation is linked the to the reproductive output of an individual; delayed phenology (e.g., fruiting) may directly result in the reduced fitness of an individual (Lane et al. 2012). As the interval between fruit maturation (with associated seed release) and favourable germination conditions increases, there is an increased risk of seed damage (e.g., seed predation) (Pilson 2000). As the timing of fruiting patterns has implications for plant fitness, the need to predict the associated global change impacts on plants has become imperative in a world undergoing climate change.

Indeed, climatic variables such as mean annual temperature and precipitation can play a major role in driving the geographic distribution of fleshy fruits and dry fruits (Howe & Smallwood, 1982, Wheelwright, 1985). For example, the abundance of fleshy fruits increases with precipitation (Howe & Smallwood, 1982, Chen et al., 2016). It has been proposed that fleshy fruits require substantial amounts of water for fruit production (Matthews & Shackel, 2005). The parenchymatous tissues of fleshy fruits store water and organic compounds during development and are most easily produced when soil water potential is high and the demand for atmospheric water is low (Coombe, 1976, Chen et al., 2016). Thus, fleshy fruits, which are often animal-dispersed, are thought to ripen during the wet season when moisture levels are higher and the demand for water during fruit production can be met (Lieberman, 1982). In contrast, dry fruits are adapted to cold conditions (Vittoz et al., 2009) and require less water during development. Indeed, dry-fruited species are thought to mostly fruit during the dry season. A period of dryness aids seed release i.e., dehiscence, in dry fruit (White, 1994). Additionally, during the dry period leaves are often absent and wind speeds are higher, enhancing dispersal ability of wind-dispersed dry fruit (Lieberman, 1982). Consequently, it can be assumed that plants time the maturation period of their fruits to correspond with suitable climatic conditions for effective seed dispersal.

Furthermore, plant fitness is directly impacted by phenology patterns. There are several ecological factors that affect an individual's fitness under altering phenology patterns (Pilson 2000). For example, to increase fitness and the probability of being pollinated, plants must flower when pollinators are available and when abiotic conditions are suitable for plant growth and reproduction (Pilson 2000). Similarly, fruit maturation is linked the to the reproductive output of an individual; delayed phenology (e.g., fruiting) may directly result in the reduced fitness of an individual (Lane et al. 2012). As the interval between fruit maturation (with associated seed release) and favourable germination conditions increases, there is an increased risk of seed damage (e.g., seed predation). As the timing of fruiting patterns has implications for plant fitness, the need to predict the associated global change impacts on plants has become imperative in a world undergoing climate change.

Most vegetation phenological studies have been conducted in temperate systems of the northern Hemisphere (Chambers et al., 2013, Everingham et al., 2021). In these regions, temperature, and day length (i.e., photoperiod) are often the main drivers of phenological patterns (Giorgi, 2006; Adole et al., 2019). In contrast, the drivers of vegetation phenology patterns have been poorly examined in tropical and subtropical regions (but see Van Schaik, Terborgh & Wright, 1993, Boulter, Lambkin & Starick, 2011, Pennec, Gond & Sabatier, 2011), where precipitation and photoperiod are thought to play a key role in driving phenology (Folland, Karl & Salinger, 2002, Dunn et al., 2009). Much of the focus of plant-based phenological studies in tropical and sub-tropical regions has been on vegetative (e.g., leafing) phenology (e.g., Murali &

Sukumar, 1993, Silveiria et al., 2019, Li et al., 2021, Nagahama et al., 2023), while reproductive phenology has received less attention (though see Pau et al., 2013, Bush et al., 2018, Abernethy et al., 2018).

Within the northern hemisphere, long-term phenological time series are available (Parmesan & Yohe, 2003, Everingham et al., 2021) which are often lacking for the southern Hemisphere (Magurran et al., 2010), particularly in Africa. Hence, other data sources are needed to quantify patterns of plant phenology in the Southern Hemisphere. A valuable resource for investigating the underlying drivers of reproductive phenology over large spatial scales are herbarium records (Gallagher, Hughes & Leishman, 2009, Pearson et al., 2020) which provide long-term datasets often collected during flowering and fruiting periods (Rumpff, Coates & Morgan, 2010, Diskin et al., 2012, Greve et al., 2016). Recent studies suggest that, despite the fact that herbarium data are often haphazardly collected, they are rigorous enough to provide statistically sound datasets (Robbirt et al., 2011, Diskin et al., 2012). Indeed, within the context of phenological patterns, numerous studies, dating back to the early nineteen hundreds (Heyward, 1931), have been conducted with the use of herbarium records (Rawal et al., 2015). For instance, herbarium data have been used to link climate change to temporal changes in phenological plant traits such as flowering period (e.g., Chmielewski & Rötzer, 2001, Rawal et al., 2015, Pearson et al., 2020). Herbarium records have also been used to illustrate mismatches between interacting species, e.g., mismatches between flowering phenology of a plant and the emergence of its associated pollinators (Sparks, Roy & Dennis, 2005, Forrest & Thomson, 2011).

Here, I use herbarium records to test which climatic factors influence the fruiting phenology of 58 fleshy- and dry-fruited tree species from the summer rainfall regions of South Africa. First, I hypothesise that fleshy- and dry-fruited species show different seasonal peaks in fruiting periods, with fleshy-fruited species experiencing fruiting peaks during the warm, wet season and dry-fruited species experiencing fruiting peaks during the colder, dry season as a period of dryness aids seed release i.e., dehiscence, in dry fruit (H1, Table 2.1) (White, 1994, Chen et al., 2016). Second, I hypothesize that different climatic factors would influence the fruiting phenology of fleshy- and dry-fruited tree species; specifically, I hypothesize that fleshy-fruited phenology peaks at higher precipitation than that of dry-fruited species, while temperature variables are important drivers influencing the fruiting phenology of both fleshy-fruited and dry-fruited species (H2, Table 2.1). Lastly, I hypothesise that precipitation contributes more to the fruiting phenology of fleshy-fruited species than dry-fruited species because fleshy-fruited species have higher water requirements. It is expected that minimum temperatures contribute more to the phenology of fleshy-fruited than dry-fruited species (H3, Table 2.1), because the cells of fleshy-fruits are more susceptible to cold injury at low temperatures (Burke et al., 1976, Chen et al., 2016). Although many of the species investigated here are located within sub-tropical areas, their fleshy cells are still at risk of experiencing cold injury as winter temperatures can drop to freezing conditions (Mucina & Rutherford (2006)). Although frost is infrequent within the subtropical coastal regions of South Africa, sporadic cold spells accompanied by frost events have been recorded (Mucina & Rutherford (2006)). Cold injury in fleshy fruits often leads to rapid fruit decay or the failure to ripen, which has implications for reproduction and survival (e.g., seed survival) (Manganaris et al., 2008).

TABLE 2.1 Table summarising the hypotheses investigating how climatic factors influence the fruiting phenology of fleshy- and dry-fruited tree species from the summer rainfall regions of South Africa.

Hypothesis abbreviation	Hypothesis	Relevant references
H1	Fleshy- and dry-fruited species will show different seasonal peaks in fruiting periods, with fleshy-fruited species experiencing fruiting peaks during the warm, wet season and dry-fruited species experiencing fruiting peaks during the colder, dry season.	White, 1994, Chen et al. 2006
H2	Fleshy-fruited species fruit earlier within areas that receive high annual precipitation and temperature compared to areas that experience lower annual precipitation and temperature. In contrast, dry-fruited species fruit later in areas of low annual precipitation, compared to areas that experience higher annual precipitation. Temperature is considered an important driver of both fleshy- and dry-fruited species as fruiting is expected to peak under different climatic conditions (as per H1).	Burke et al. 1976, Chen et al. 2016
H3	The relative importance of different climatic variables to explain intraspecific phenological variation differs between fleshy- and dry-fruited species, with e.g., moisture being potentially more important to explain intraspecific variability of fleshy-fruited species than of dry-fruited species.	Burke et al. 1976, Chen et al. 2016

Methods

Species and area selection

Fifty-eight (58) widespread and common tree species from the summer rainfall regions of South Africa (including Swaziland and Lesotho) were included in this study (Table A1, Appendix A). Common species were selected because they were likely to have sufficient representation of herbarium specimens, and widespread species because their distribution was likely to cover a range of different environmental conditions, which was important for analyses. Only species with more than 20 locality records were selected. The sample size was balanced and represented 29 fleshy-fruited species and 29 dry-fruited species. An attempt was made to cover different plant families for both fleshy- and dry-fruited species, but it was difficult to find good representation of dry-fruited species outside the Fabaceae which met all other criteria. For species whose geographic ranges extend beyond the summer rainfall regions of South Africa, only specimens collected from the summer rainfall regions were considered, thus allowing for a meaningful comparison. The majority of South Africa is characterised by summer rainfall regions; thus, the selection of these areas allows for species that occur over wider geographic regions to be compared. Not all locality records provided within the herbarium vouchers were provided in Geographic Positioning System (GPS) format or Quarter Degree Square (QDS; i.e., 15’ × 15’; approx. 24 km × 28 km) cell format. In some instances, locality records were given by place names. In these cases, the QDS in which the place/town/location was situated was used. To standardise location information, all GPS coordinates were converted to QDS format. The centroids of the QDSs were then used to map the location of the specimen vouchers (Fig. A1, Appendix A).

Data collection

Locality records for the 58 species were collected from several herbaria, including the South African National Herbarium (PRE), the H.G.W.J. Schweickerdt Herbarium (PRU), the C. E. Moss herbarium (MOSS) and the Buffelskloof Herbarium (BNRH). Fruiting phenology was scored from vouchers housed at the aforementioned herbaria. Vouchers from the aforementioned herbaria that had already been electronically databased by the respective herbaria, and that possessed collection dates (date, month, and year) and detailed locality information, were considered in addition to the original herbaria sheets. For each herbarium specimen, fruiting was recorded from specimen sheets. Fruiting phenology was visually scored as present or absent, and, where possible, an indication of whether the fruit was immature or ripe was given. Labels of specimens that had no fruit were also perused to see if fruiting occurrence of the collected plant was mentioned: if it was, fruiting was recorded as present. All specimen records with evidence of fruiting were considered in the study. Duplicates were excluded.

A distinction was made between summer (including year-round) and winter rainfall patterns using biome distinctions (which are correlated to rainfall patterns) as per Mucina and Rutherford (2006). Records of specimens located within summer rainfall areas (including early to late summer rainfall) as well as areas of all year-round rainfall were included in the study (Fig. A2, Appendix A). Areas of summer rainfall included the savanna, grassland, thicket, and Nama karoo biomes (Mucina & Rutherford, 2006). Areas of all-year rainfall included forest patches (embedded within surrounding biomes). Specimen records that were in winter rainfall (Mucina & Rutherford, 2006) were excluded from further analysis (Fig. A2, Appendix A). These areas included the fynbos and succulent karoo biomes (Mucina & Rutherford, 2006).

Climatic variables

Several climatic variables were obtained to assess how phenology varies with climate (Table 2.2). Both temperature and precipitation have been shown to influence leafing, flowering and fruiting phenology (van Schaik *et al*., 1993; Singh & Kushwaha, 2006). Potential evapotranspiration (PET) (1-degree grid cell resolution) was obtained from the Terrestrial Water Budget Data Archive (Willmott & Matsuura, 2001) and resampled, using a bilinear resampling technique, to a 5-degree grid cell resolution. All other climate data were extracted (at 5-minute resolution) from WorldClim v 2.1 (Fick & Hijmans, 2017) which provides interpolated mean monthly climatic data from the period 1950-2000 (including solar radiation and wind speed data). The climate values were extracted for the location of each herbarium record. Data were resampled, using a bilinear resampling technique, to a 5-degree grid cell resolution.

Collinearity of the predictors was assessed by examining a Pearson's correlation matrix of all the predictor variables using the R package 'corr'. If two variables had a correlation coefficient (*r*) higher than

0.75, only one was retained for further analysis (Table 2.2; Table A2, Appendix A); the selection between correlated variables was made by considering which variable would more likely contribute to the phenology of the tree species across South Africa. Potential evapotranspiration (PET) and precipitation seasonality (PSEAS) correlated highly with Temperature of the warmest quarter (TWQ) and Precipitation of the driest quarter (PDQ) respectively. The latter variables were selected as they better reflect extreme temperature and precipitation conditions experienced by season rather than across the period of a year.

TABLE 2.2 Table of the variables used to assess how phenology patterns vary with these climatic factors. The table provides the abbreviation of each climatic variable, the reason for inclusion, and whether the variable was included or excluded from further analysis due to collinearity. PET and PSEAS were excluded from the analyses as they were highly correlated with other variables. Refer to Table A2 for a correlation matrix of the climatic variables.

Climatic variable	Abbreviation	Reason for inclusion/exclusion	Excluded / included from analysis
Minimum temperature of the coldest month	MTCM	This variable reflects extreme cold conditions experienced on a yearly basis and gives an indication of where frost is likely to be experienced.	Included
Temperature of the warmest quarter	TWQ	These variables reflect extreme temperature and precipitation conditions experienced by season. PDQ correlated highly with PSEAS. TWQ correlated highly with PET. As PDQ and TWQ reflect extreme temperature and precipitation conditions it was selected over the use of PSEAS and PET respectively	Included
Precipitation of the wettest quarter	PWQ		Included
Precipitation of the driest quarter	PDQ		Included
Potential evapotranspiration (1-degree grid cell resolution)	PET	PET is a proxy for the water–energy available for reproduction (Ting, Hartley & Burns, 2008) and is an important determinant of plant phenology (Chambers et al., 2013)	Excluded
Temperature seasonality	TSEAS	Seasonality (both temperature and precipitation) have been suggested to be closely linked with phenology patterns (Cleland et al., 2007, Wu et al., 2016). These variables provide an indication of how seasonal an area may be – e.g., experiencing stable climates in areas of low seasonality or experiencing seasonal variation in areas of high seasonality.	Included
Precipitation seasonality	PSEAS		Excluded
Mean monthly solar radiation	Solar	Solar radiation has been suggested in aiding the ripening of fleshy fruits (Wheelwright & Janson, 1985)	Included
Average wind speed	Wind	Wind speed (Wheelwright & Janson, 1985) as wind may be required to help aid in the dispersal of dry-fruited species (White, 1994).	Included

Statistical analyses

Phenology was quantified as the day of the year that a fruiting specimen was collected (i.e., 1 = 1 January; 365 = 31 December). Because day of the year is a circular variable, a histogram of all tree fruiting times was plotted to assess whether there was a time of year that could be considered as the start of the fruiting season. The histogram revealed a gap in fruiting between the end of May and beginning of June. (Fig. A3, Appendix A). Therefore, the fruiting day of each specimen was calculated as the Julian day after 1st June. This date corresponds to early winter in the study area.

Testing for differences in peak fruiting production between fleshy and dry fruited species (H1)

To test whether fleshy- and dry-fruited species show different seasonal peaks in fruiting periods (H1), we calculated for each species the peak fruit production as the mode fruiting day of the year (i.e., the day in which a species experienced the greatest number of fruiting events). Mode fruiting day was used instead of the median day of fruiting as Julian day is a discrete variable. We used Welch two-sample t-tests (Welch, 1947) to assess statistically significant differences in fruiting production peaks between fleshy- and dry-fruited species. We expected the mode day of fruit production for dry-fruited species to occur during the dry season, and for fleshy-fruited species during the wet season.

Investigating whether climatic factors influence fruiting phenology across species (H2)

To test if different climatic factors influence the fruiting phenology of fleshy- and dry-fruited species (H2), I extracted, for each locality record, the relevant information for each of the climatic variables (at that locality). Once information was obtained for each climatic variable (from each locality), I calculated the mean of each climatic variable for each of the 58 species (Fig. A2, Appendix A). A non-parametric generalised additive model (GAM) was used to quantify how climate influences the mode day (calculated as a Julian day with day 1 starting at 1 June) of fruiting phenology of fleshy- and dry-fruited species. GAMs are an extension of generalized linear models (GLMs) which make no assumptions of normal distributions or homogenous variance (Zuur et al., 2009). The fleshy- and dry-fruited categorical term was included as a factor (for each climatic variable) in the model and subsequently used as the '*by*' variable in the model setup. Species was included as a random effect within the model to account for the different influence that species could have on fruiting phenology patterns. The GAM model was specified with the following: (i) a negative binomial distribution as the data was zero-truncated and over-dispersed, (ii) a restricted maximum likelihood (REML) smoothness selection criterion (this criterion was selected as it is less prone to local minima issues and is thus often preferred over other criterion options). GAM models were initially run with all predictors included as smooth terms. The model was then simplified using a backwards/forwards stepwise procedure in which non-significant contributing variables were removed. During the backwards/forwards stepwise procedure, the statistical significance of fitting terms as linear and/or smooth terms was evaluated, and the model built accordingly.

GAM models do not account for phylogenetic relatedness. As all but two of the dry-fruited species are in the Fabaceae family, it is anticipated that observations of these species cannot be considered independent. However, species was included as a random effect within the model to account for the different influence that species could have on fruiting phenology patterns. Although this approach is limited in its approach, it is assumed to be applicable for the purpose of the current analyses.

Investigating what climatic variables are driving the variation in fruiting time within a species (H3)

To test if the relative importance of different climatic variables to intraspecific phenological variation differs between fleshy- and dry-fruited species (H3), I investigated the relative importance of each climatic variable to explaining the day of fruiting of each tree species. First, an indication of phenology deviation was needed; for each specimen of each species, the difference between the day of collection and the mode day of fruiting of that species was calculated (henceforth referred to as phenology deviation, i.e., the deviation of the central tendency). This measure was selected because of the circular nature of a year (Staggemeier et al., 2020).

A random forest regression was used to investigate how climatic variables (see Table 2.2) influence the deviation of timing from the mode for each species, i.e., random forests were used to compute estimates of variable importance for the various climatic variables. Thus 58 random forest models were run, one for each species. These random forest models were trained and configured in the '*randomForest*' package

(Liaw & Wiener, 2015) in R. To configure the model, the number of variable tries (*mtry*) was set to sample randomly as candidates for node splitting during the tree growing process using the R package ‘caret’. A 10-fold cross validation was used during the training process to estimate model performance, avoid overfitting, and improve model accuracy. During model training, random forests can compute estimates of variable importance. These values are obtained by estimating the mean decrease in impurity (MDI) using the Gini Index (Chen & Ishwaran, 2012). The Gini Index calculates the relative importance of a variable as the sum over the number of splits (across all tress) that include the variable, proportionally to the number of samples it splits (Chen & Ishwaran, 2012). The higher the Gini Index, the more important is the variable in the random forest prediction (Chen & Ishwaran, 2012). Thus, from each species’ model, the percentage contribution of each climatic variable to the phenology deviation was quantified. The percentage contribution (= variable importance) of each climatic variable was collated, averaged, and compared between fleshy- and dry-fruited species using a Welch two-sample t-test, to test whether the day of fruiting phenology of the two different fruit types was influenced by different climatic variables (H3).

All analyses were conducted in R, version 3.5.1 using the following packages: ‘*corrplot*’ (Wei et al., 2017), ‘*vegan*’ (Oksanen et al., 2007), ‘*mgcv’* (Wood & Wood, 2015), ‘*caret*’ (Kuhn, 2012), and ‘*randomForest*’ (Liaw & Wiener, 2015).

Results

A total of 3864 specimen vouchers from 58 tree species could be scored for fruiting phenology. Of these, 1840 records were from 29 fleshy-fruited species (mean 63.448 ± 43.169, range: 21 - 202), and 2024 records from 29 dry-fruited species (69.793 ± 61.452, range: 15 - 298; Table A1, Appendix A). The 29 fleshy-fruited species included species from 20 families and 24 genera, whereas the 29 dry-fruited species included species from 3 families and 15 genera (Table A1, Appendix A). Locality records (*n* = 3864) of both fleshy- and dry-fruited species were fairly widespread across South Africa, particularly towards the northern and eastern parts of the country (Fig. A1, Appendix A). This area supports the highest species richness of trees in South Africa (Qian et al., 2009, Jamison et al., 2017).

Differences in peak fruiting production (H1)

The mode day of fruiting was 1 December for fleshy-fruited species and 5 March for dry-fruited species. The difference in the overall mode day of fruiting between fleshy- and dry-fruited species was statistically significant (t = 6.467, p = < 0.001). As expected (H1), the mode day of fruiting for fleshy-fruited species occurred during the summer season (i.e., December) when rainfall is high. However, while the mode day of fruiting for dry-fruited species was expected to be in the dry season (between May and July), it occurred towards the end of the wet season, i.e., already beginning of March.

Investigating whether climatic factors influence fruiting phenology across species (H2)

The effects of several climatic predictors on fruiting phenology depended on fruiting type (fleshy *vs* dry; Table 2.3): (1) fleshy-fruited species typically fruited earlier when minimum temperatures of the coldest months were low, while dry-fruited species' phenology was not predicted by minimum temperatures of the coldest months (Fig. 2.1a-2.b); (2) when temperature seasonality was low, both fleshy- and dry-fruited species typically fruited earlier, while in areas of high temperature seasonality, fruiting typically occurred later (Fig. 2.c-2.d); (3) when precipitation of the driest quarter was low, dry-fruited species typically fruited earlier, while fleshy-fruited phenology was not predicted by precipitation of the driest quarter (Fig. 2.e-2.f); (4) fleshy-fruited species typically fruited earlier in regions with higher temperatures of the warmest quarter, while dry-fruited species' phenology was not predicted by higher temperatures of the warmest quarter (Fig. 2.g-2.h); and, (5) when solar radiation was high, both fleshy- and dry-fruited species fruited earlier (Fig. i-j).

TABLE 2.3 Results of generalised additive models (GAMs) for environmental determinants of mode fruiting day recorded from herbarium specimens of 58 South African tree species (29 fleshy- and 29 dry-fruited species). Covariates are minimum temperature of the coldest month (MTCM), temperature seasonality (TSEAS), precipitation of the driest quarter (PDQ), temperature of the warmest quarter (TWQ); and solar radiation (Solar). Significant p-values are highlighted in bold. The GAM model included *by* terms (i.e., categorical data specified as factors). Fruit Type was included as a random effect within the model to account for the different influence that fruit type could have on fruiting phenology patterns. 'edf' = estimated degrees of freedom (edf); 'Ref. df' = estimated residual degrees of freedom.

Covariates	**Estimates**	**Std. error**	**T-value**	**p-value**
***Smooth* terms**				
Intercept	207.352	21.670	9.596	< **0.001**
Fruit Type	Fleshy < Dry	30.818	-0.973	**< 0.05**
***By* terms (i.e., interaction terms)**				
Covariates	***edf***	**Ref. *df***	**F-value**	**p-value**
MTCM: Dry	2.015	2.555	1.011	> 0.05
MTCM: Fleshy	1.025	1.049	6.231	**< 0.05**
TSEAS: Dry	3.067	3.941	3.420	**< 0.01**
TSEAS: Fleshy	3.048	3.887	6.375	**< 0.01**
PDQ: Dry	1.029	1.056	4.247	**< 0.05**
PDQ: Fleshy	1.003	1.007	1.157	> 0.05
TWQ: Dry	2.134	2.750	0.477	> 0.05
TWQ: Fleshy	5.081	6.239	4.164	**< 0.001**
Solar: Dry	3.936	4.901	4.482	**< 0.001**
Solar: Fleshy	2.424	3.112	7.950	**< 0.001**
Model Performance				
Adjusted R^2	0.112			
p-value	**< 0.001**			

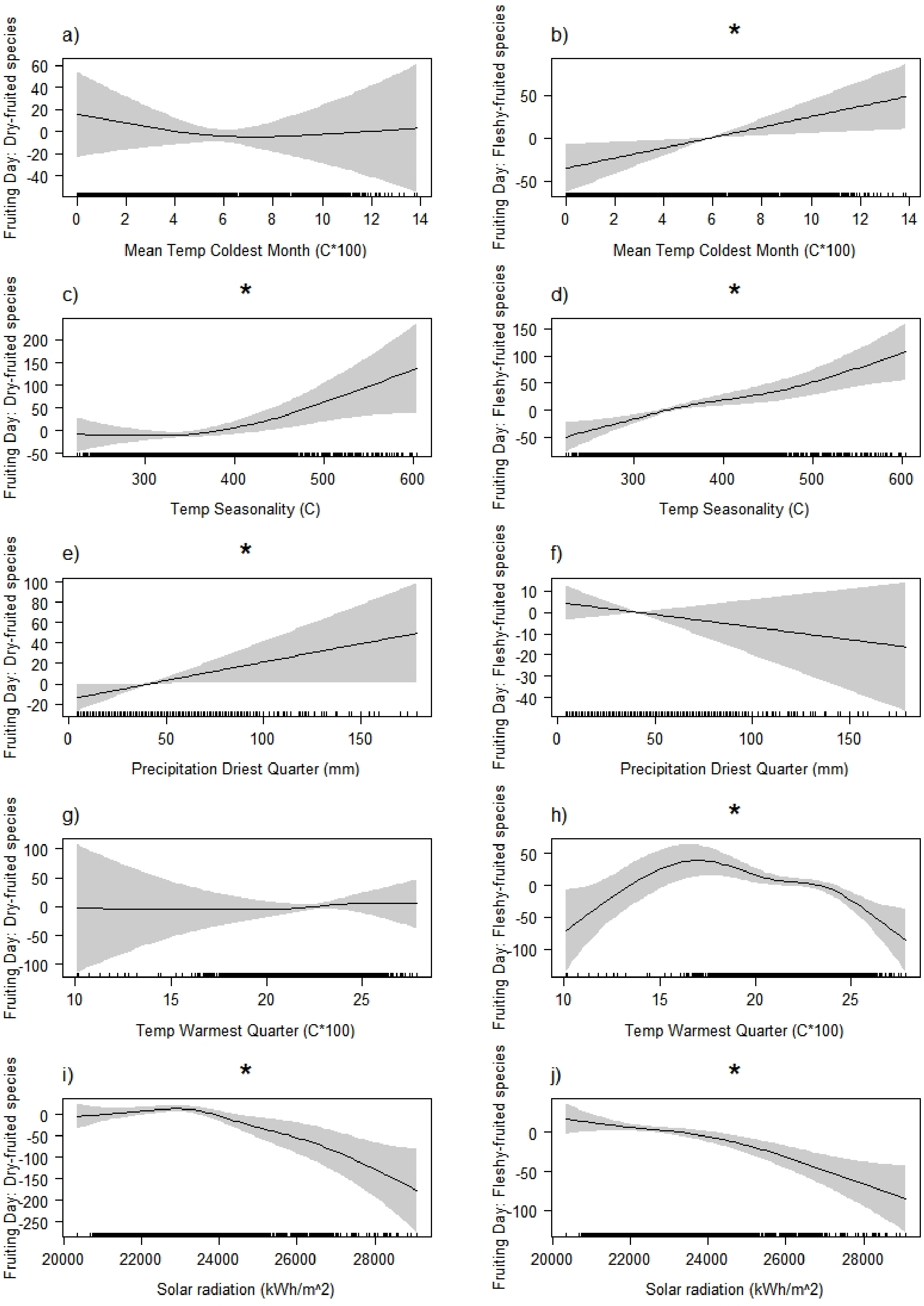

a)
Fruiting Day: Dry-fruited species
60
40
20
0
-20
-40
0
2
4
6
8
10
12
14
Mean Temp Coldest Month (C*100)
b)
*
Fruiting Day: Fleshy-fruited species
50
0
-50
0
2
4
6
8
10
12
14
Mean Temp Coldest Month (C*100)
c)
*
Fruiting Day: Dry-fruited species
200
150
100
50
0
-50
300
400
500
600
Temp Seasonality (C)
d)
*
Fruiting Day: Fleshy-fruited species
150
100
50
0
-50
300
400
500
600
Temp Seasonality (C)
e)
*
Fruiting Day: Dry-fruited species
100
80
60
40
20
0
-20
0
50
100
150
Precipitation Driest Quarter (mm)
f)
Fruiting Day: Fleshy-fruited species
10
0
-10
-20
-30
-40
0
50
100
150
Precipitation Driest Quarter (mm)
g)
Fruiting Day: Dry-fruited species
100
50
0
-50
-100
10
15
20
25
Temp Warmest Quarter (C*100)
h)
*
Fruiting Day: Fleshy-fruited species
50
0
-50
-100
10
15
20
25
Temp Warmest Quarter (C*100)
i)
*
Fruiting Day: Dry-fruited species
0
-50
-100
-150
-200
-250
20000
22000
24000
26000
28000
Solar radiation (kWh/m^2)
j)
*
Fruiting Day: Fleshy-fruited species
0
-50
-100
20000
22000
24000
26000
28000
Solar radiation (kWh/m^2)

FIGURE 2.2 Generalised additive model (GAM) plots investigating the partial effects of predictor variables on the timing of fruiting phenology of dry- (left column) and fleshy-fruited (right column) species. The effect of predictors on fruiting phenology was dependent on fruit type (fleshy vs dry) in all cases. The effects of a-b) minimum temperature of the coldest month, c-d) temperature seasonality, e) precipitation of the driest quarter and dry-fruited species phenology, f) precipitation of the driest quarter and fleshy-fruited species phenology, g) temperature warmest quarter and dry-fruited species phenology, h) temperature warmest quarter and fleshy-fruited species phenology, i) solar radiation and dry-fruited species phenology, and j) solar radiation and fleshy-fruited species phenology. As the GAM models investigated deviation of fruiting phenology from the mode fruiting day, positive values on the y-axis indicate that fruiting patterns occur later than expected (i.e., than the mode day of fruiting), whereas negative values indicate that fruiting patterns occur earlier than expected. The tick marks on the a-axis illustrate the observed data points. The y-axis represents the partial effect of each explanatory variable. The shaded areas indicate the 95% confidence intervals. An asterisk (*) indicates a significant relationship between the phenology of the fruit type (fleshy- or dry-fruited) and the climatic factor.

Investigating whether climatic factors influence the intraspecific drivers of fruiting phenology (H3)

The only climatic variable whose importance differed significantly between fleshy- and dry-fruited species was minimum temperature of the coldest month (Table 2.4, Fig. 2.3, Fig. A3, Appendix A). Minimum temperature of the coldest month was found to contribute significantly less to the phenology of dry- than fleshy-fruited species. The remaining variables consistently contributed to the intraspecific variation of fleshy- *vs* dry-fruited species.

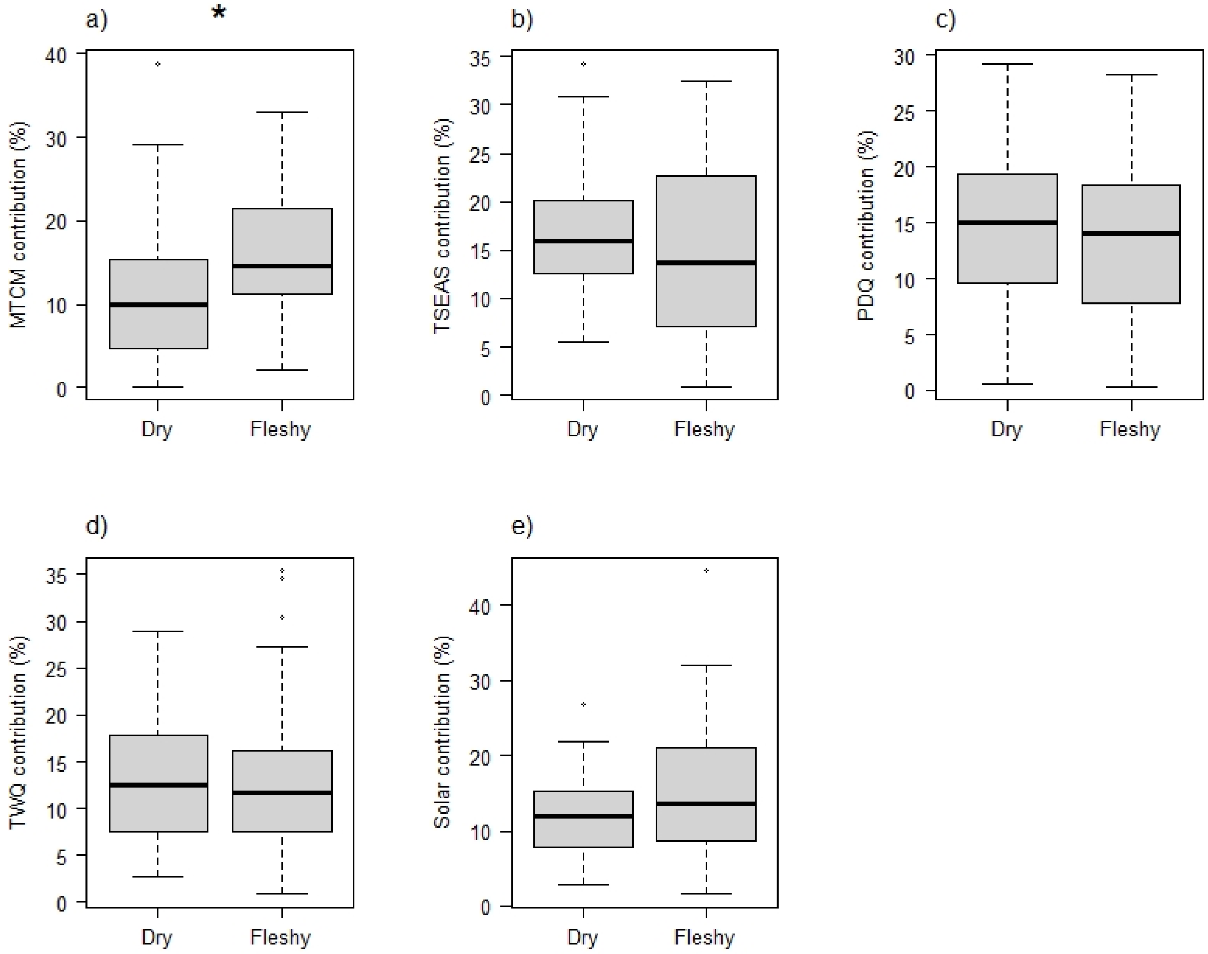


FIGURE 2.3 Boxplot illustrating the relative variable importance of different environmental variables to the phenology of fleshy- and dry-fruited tree species. One environmental variable, namely minimum temperature of the coldest month, contributed significantly less to the phenology of dry- than fleshy-fruited species. Percentage variable contribution is shown for a) mean temperature of the coldest month (MTCM), b) temperature seasonality (TSEAS), c) precipitation of the driest quarter (PDQ), d) temperature of the warmest quarter (TWQ), and e) solar radiation (solar). The boxplot illustrates the median and lower and upper quartiles. Data falling outside of the Q1-Q3 range are plotted as outliers. An asterisk (*) indicates significance. Refer to Table A3 average variable contribution of different environmental variables for fleshy-fruited *vs* dry-fruited tree species and to Table A4 for the relative variable importance of different environmental variables to the timing of fruiting of each of the species investigated.

Discussion

Our results indicate that across 58 South African fleshy- and dry-fruited species the mode fruiting day was earlier for fleshy-fruited (1 December) than dry-fruited (5 March) species. Although the mode day of fruiting for fleshy-fruited species occurred during the summer season (i.e., December) when rainfall is high (as expected), the mode day of fruiting for dry-fruited species (which was expected to be in the dry season (e.g., between May and July)), occurred towards the end of the wet season, i.e., already beginning of March. Furthermore, the effects of several climatic predictors on fruiting phenology across species depended on fruiting type (fleshy- *vs* dry-fruited; H2); for example, fleshy-fruited species typically fruited earlier when minimum temperatures of the coldest months were low, while dry-fruited species' phenology was not predicted by minimum temperatures of the coldest months, and when temperature seasonality was low, both dry- and fleshy-fruited species typically fruited earlier, while in areas of high temperature seasonality, fruiting typically occurred later. Within species, only the relative variable importance of minimum temperature of the coldest month to the phenology of individual species that occur over large geographic areas showed a statistically significant difference between fleshy- and dry-fruited species (H3).

Fleshy-fruited species typically fruited earlier when minimum temperatures of the coldest months were low, while dry-fruited species' phenology was not predicted by minimum temperature of the coldest month (Fig 2.2b). Fleshy-fruited species may fruit earlier to avoid freeze damage to their fleshy fruits. Frost is likely of a concern for many of the investigated species across the distribution of South Africa; however, along the coastal belt, the influence of frost on fruit development may potentially be less as frost is less common in these areas. During cold conditions, the fleshy cells within fleshy fruit can develop ice crystals that lead to extensive cell damage (Burke et al., 1976). If plants fruit during conditions of low temperature (resulting in cold injury), then rapid fruit decay and/or the failure to ripen may result (Manganaris et al., 2008). Furthermore, conditions for germination may not be favourable during such periods; by fruiting earlier seeds will be set during warmer periods that will favour germination and thus fitness. In contrast, dry fruits can withstand cold conditions as the sclerenchymatous tissues of this fruit type are not as susceptible to the formation of ice crystals (Vittoz et al., 2009); thus, the fruiting phenology of dry-fruited species is not driven by potential freeze damage. Indeed, regions that experience low temperature minimums have been found to support lower proportions of fleshy-fruited species (Chen et al., 2016). This phenomenon is also apparent across southern Africa, where the proportion of fleshy-fruited species is lower in the western parts of the region where cold (freezing) temperatures are frequent (Jamison et al., 2017).

Furthermore, as plants synchronise their peak fruit production with peak disperser availability (Aizen, 2003), which is typically associated with summer periods in South Africa (e.g., Bleher et al., 2002), there is an increased potential for dispersal ability which translates into increased fitness. We found that when temperature seasonality was low, both fleshy- and dry-fruited species typically fruited earlier, while in areas of high temperature seasonality, fruiting of both fleshy- and dry-fruited species typically occurred later (Fig 2.2 c-d). This may be related to the seeds of the species investigated, i.e., whether the species possess recalcitrant seeds (i.e., desiccation-sensitive seeds). Within seasonal environments, species time their fruiting to maximise growth under favourable environmental conditions (Tweddle et al. 2003). In areas of high seasonality areas, that are typically associated with lower humidity levels, species may display a higher desiccation tolerance and thus fruit later to maximize seedling growth prior to the onset of winter conditions (Twiddle et al., 2003). In contrast, in areas experiencing low temperature seasonality and thus lower levels of humidity, and fewer temperature extremes, species may possess recalcitrant seeds that are able to take advantage of the low seasonality and thus decreased chance of drying out, providing a higher probability of germination in the same season as seed set. Indeed, it has been shown that the proportion of species with recalcitrant seeds declines as seasonality increases (Twiddle et al., 2003). In the face of climate change, such traits (e.g., seed desiccation) can be considered an important functional trait that affects vegetation dynamics. However, the importance of such traits is often overlooked in during climate change modelling. Given the implications climate change can have on recalcitrant species, these traits warrant further investigation (Joët et al., 2013).

When precipitation of the driest quarter was low, dry-fruited species typically fruited earlier (Fig. 2.1e). Although the production of dry fruit is not as water demanding as the production of fleshy fruit, the production of dry fruit still requires water (Wheelwright, 1985). The parenchymatous tissues of fruits store water and organic compounds during development and are most easily produced when soil water potential is high and the demand for atmospheric water is low (Coombe, 1976, Chen et al., 2016). Dry-fruited species may advance their fruiting periods (i.e., earlier fruiting) to better exploit moisture from late rains of the wet season, as opposed to fleshy-fruited species which were found to fruit during the wet season when the demand for water for fruit production is more easily met, and seeds may fall early enough in the season for seedlings to germinate in the same year as seed set. Furthermore, precipitation of the driest quarter was inversely correlated with precipitation seasonality (r = 0.80, Table A2, Appendix A). This relationship is expected as precipitation seasonality is estimated as the coefficient of variation of monthly precipitation over a year (Fick & Hijmans, 2017); thus, areas in which precipitation of the driest quarter is low are characterised by high precipitation seasonality. Within these more seasonal environments, dry-fruited species may advance their fruiting periods (i.e., earlier fruiting) to better exploit moisture from late rains of the wet season, before the beginning of drier winter periods. In this way, the species enhance their ability to disperse seed during conditions that are more favourable for germination prior to the onset of winter. By maximising conditions favourable to fruit development, bigger, better-quality fruits (and thus seed) can be produced. These fruits will be more attractive to dispersal agents (Howe & Smallwood, 1982, Wheelwright, 1985), thus enhancing the fitness of individuals.

Fleshy-fruited species typically fruited earlier in regions with higher temperatures of the warmest quarter (Fig. 2.2h). Temperature of the warmest quarter was highly correlated with potential evapotranspiration (Table A2, Appendix A). Thus, the fruiting phenology of fleshy-fruited species may be limited by evaporative loss at higher temperatures (this may be an adaptation to avoid the hottest parts of the year when heat stress is a possibility). Furthermore, at low temperatures, it may take plants longer to develop to the fruit stage as the plants are limited by temperature. This phenomenon is in accordance with the thermal kinetic window which defines optimum temperature ranges in which biochemical and metabolic activities can operate (Burke, Mahan & Hatfield, 1988). Plants that experience temperatures above or below the thermal kinetic window experience subsequent stress that limits growth and fruit yield. However, I also found that when temperature of the warmest quarter was low, fleshy-fruited species also fruited earlier. Although the underlying reason for this is unclear, it could perhaps, be related to the process of plant reproduction. Plant reproduction follows a chronological sequence, i.e., flower development, pollination, then fruit development, with each stage taking time to occur (i.e., not occurring concurrently) (Ting, Hartley

& Burns, 2008). The advanced timing of fruiting for fleshy-fruited species when temperature of the warmest quarter is low may be because of the influence that environmental conditions have on subsequent plant reproduction phases (Ting, Hartley & Burns, 2008), for example, if fruting was synchronysed with periods of higher disperser presence. Alternatively, fleshy-fruited species may develop fruit earlier because they require heat for fruit development (i.e., cell functioning) (Reader, 1983, Burke, Mahan & Hatfield, 1988). By developing earlier, they also lessen the risk of exposing their cold-sensitive fleshy fruits to cold temperatures. Furthermore, this avoids seeds from being dispersed during colder periods that would not be favourable for seed germination and persistence.

When solar radiation was high, both fleshy- and dry-fruited species fruited earlier (Fig 2.2i-j). Solar radiation reflects the amount of energy available to produce fruit; high levels of solar radiation illustrate high levels of available energy that can be used during fruit production and fruit ripening (Chapman et al., 2018). There is a link between peak fruiting production and higher levels of solar radiation (Graham et al., 2003, Wright & Calderón, 2006). When solar irradiance is high and fruits are still present on the tree, fruit ripening may be accelerated (Smart et al. 1988), thus decreasing the amount of time seeds are susceptible to predators prior to dispersal processes (Chapman et al., 2018).Solar radiation further impacts seed germination ability; solar radiation drives many plant functions, including the formation and development of plant organs, seeds, and fruits (Yang et al., 2019). The peak fruiting production and higher levels of solar radiation identified in this work is likely related to plant fitness. By fruiting during periods of high radiation (thus decreasing the amount of time seeds are susceptible to predators prior to dispersal processes), a plant also increases its chance of germination success as many seeds require light to germinate. This is however, likely associated with a trade-off – at higher levels of radiation, there is an increased risk that a plant may be exposed to excessive radiation which has implications for seedling establishment (e.g., failure to establish) an/or photosynthesis (e.g., photosynthesis inhibition) (Yang et al., 2019).

Only one variable was found to affect the variation of broad-scale phenology patterns within species: the relative importance of minimum temperature of the coldest month to phenology differed significantly between fleshy- and dry-fruited species. Minimum temperature of the coldest month was a more important predictor of fruiting phenology for fleshy- than for dry-fruited species. Cold temperatures often result in rapid fruit decay or the failure to ripen, which has implications for reproduction and survival (e.g., seed survival) (Manganaris et al., 2008). The parenchymatous tissues of fleshy fruits are cold-sensitive, whereas the sclerenchymatous tissues of dry-fruited species are not as cold-sensitive (Manganaris et al., 2008; Vittoz et al., 2009). Furthermore, this is very apparent in areas where frost is likely to occur. It is likely that the development of fleshy fruit is more constrained by temperature and water availability than that of dry fruit, whose development may be the result of a wider range of conditions.

From this study, it is evident that some temperature variables (e.g., minimum temperature of the coldest month, temperature seasonality, and temperature of the warmest quarter), precipitation variables (e.g., precipitation of the driest quarter), and solar radiation can be considered important drivers influencing the fruiting phenology of tree species across South Africa. Understanding which climatic variables influence phenology, particularly phenology patterns within the Southern Hemisphere, is important as the need to predict the associated impacts on plants because of climate change has become imperative in our ever-changing world. The IPCC report (Allan et al., 2021) predicts that, irrespective of the emissions scenarios modelled, global surface temperatures are anticipated to increase. Other climatic factors are subsequently anticipated to change in relation to increasing surface temperatures, e.g., increases in the frequency and intensity of extreme weather conditions (e.g., heat waves, frost events, heavy precipitation, and/or drought conditions in some areas as well as reductions in snow cover and permafrost) are expected (Allan et al., 2021). Furthermore, with increasing temperatures, the global water cycle will be impacted, with predicted changes in variability and intensity of precipitation events. At a more local scale, model simulations predict that southern Africa will experience an increase in temperatures, including an increase in annual heatwaves and the frequency of very hot days, with a decrease in the number of cold days and cold extremes (Allan et al., 2021, Rotter et al., 2021). Associated with the increasing temperatures, southern Africa is likely to experience lower precipitation levels and decreased soil moisture (Erasmus et al., 2022, Allan et al., 2021). As climatic drivers change in accordance with climate change, they bring about associated changes in fruiting phenology patterns which has implications at the level of the ecosystem.

Based on the above, it is anticipated that the fruiting patterns of fleshy-fruited tree species will be affected by warmer summer temperatures that may be experienced under climate change, while the effect on dry-fruited species will not be as marked. Despite this, under hotter and dry conditions, the fitness of dry-fruited species is likely to be affected through resultant impacts on the amount and/or quality of the seeds produced as well as the fate of the dispersed seeds. Furthermore, the associated decreases in precipitation levels predicted under climate change (Allan et al. 2021) are likely to negatively impact the fruiting phenology of fleshy-fruited tree species (e.g., resulting in changes in fruiting patterns or decreased crop yields because of insufficient moisture needed for fleshy-fruit development). Such changes in phenology have implications across ecosystems; not only in the reproductive output of the trees, but also for the dispersal of the trees (especially when they are dependent on animals for dispersal), and for frugivores that rely on fleshy fruits as a source of food. For example, in South Africa, changes in fruiting phenology of fleshy-fruited tree species of the genera *Afrocaprpus* and *Podocarpus* have implications for the endemic, endangered Cape Parrot (*Poicephalus robustus*) (Hart, Grieve & Downs, 2013). Variation in the availability of *Afrocarpus* and *Podocarpus* fruits affects the parrot's movement patterns (Wirminghaus et al., 2001). Annual bird surveys of forest fragments have shown that parrots are sometimes absent in forest fragments (Downs, 2011, Downs, Pfeiffer & Hart, 2014) during periods in which *Afrocarpus* and *Podocarpus* trees have not fruited (i.e., during periods of mast fruiting) (Silvertown, 1980, Wirminghaus et al., 2001). Furthermore, changes to the fruiting phenology of fleshy-fruited species, may have implications for migratory birds; peak fruiting typically occurs when migratory bird species arrive (Thompson & Willson, 1979). Alterations in the availability of fruits may thus impact bird diversity and abundance as well as affect the fitness of the plant species that rely on bird dispersers.

As climate change continues and the ability to better predict associated ecological changes in plant communities is needed, herbarium data are expected to become an increasingly important resource for use in analysing plant responses to changing climates (Jones & Daehler, 2018). Here we show that herbarium data, although haphazardly collected, can be used to infer spatial patterns of phenology over large scales. In regions with long histories of herbarium collections, they have also been used to assess temporal changes in plant phenology (e.g., Zohner & Renner, 2014, Park & Schwartz, 2015, Rawal et al., 2015, Lima et al., 2021). The use of herbarium data to inform long-term, broad scale data bases has previously been criticised (Lamoureux, 1973, Jones & Daehler, 2018); for example, specimens collected may not necessarily have been collected during their peak flowering or fruiting periods, thus potentially biasing potential explanation (Lamoureux, 1973). Furthermore, biases in spatial, temporal, trait, phylogenetic, and collector biases amongst herbarium specimen samples exist (Daru, Van der Bank & Davies, 2018). Despite this criticism, recent studies have shown the practical application of using such data to infer on ecological components including, phenological changes, broad scale species distributions, coevolved plant-pollinator systems, and phylogenetic relationships, among others (Robbirt et al., 2011, Greve et al., 2016, Jones & Daehler, 2018, Kosanic et al., 2018). The benefit of using herbarium data is that some of the innate biases (e.g., collector biases and plant selection choice) of herbarium data can be overcome with the use of appropriate statistical analyses (Daru, Van der Bank & Davies, 2018). Furthermore, the large sample sizes provided by herbarium collections and the use of mean fruiting times rather than absolute fruiting day can yield valid conclusions (Bertin, 2015). As digitization efforts drastically improve access to collections, our access to such long-term and large-scale databases increases.

Appendix A

TABLE A1 Table of the 58 species, and their families, included in this study. The table also indicates whether species possess dry (n = 29) or fleshy fruits (n = 29), and the number of records for each species within the relevant herbaria.

Family	Species name	Fleshy/Dry	No. records
Anacardiaceae	*Harpephyllum caffrum* Bernh. ex Krauss.	F	23
Anacardiaceae	*Lannea discolor* (Sond.) Engl.	F	40
Anacardiaceae	*Searsia burchellii* (Sond. ex Engl.) Moffett.	F	44
Anacardiaceae	*Searsia chirindensis* (Barker) Moffett.	F	72
Anacardiaceae	*Searsia dentata* (Thunb.) Barkley.	F	182
Apocynaceae	*Acockanthera oppositifolia* (Lam.) Codd.	F	27
Aquifoliaceae	*Ilex mitis* Radlk.	F	113
Capparaceae	*Maerua caffra* Pax.	F	35
Celastraceae	*Maytenus acuminata* Loes.	F	54
Celtidaceae	*Celtis africana* Burm.	F	96
Celtidaceae	*Trema orientalis* Blume.	F	65
Erythroxylaceae	*Erythroxylum emarginatum* Thonn.	F	34
Euphorbiaceae	*Croton sylvaticus* Hochst.	D	89
Fabaceae	*Adenopodia spicata* Prescl.	D	51
Fabaceae	*Albizia harveyi* Fourn.	D	21
Fabaceae	*Bauhinia galpinii* N.E. Br.	D	80
Fabaceae	*Bauhinia petersiana* Bolle	D	16
Fabaceae	*Bauhinia tomentosa* L.	D	36
Fabaceae	*Bolusanthus speciosus* (Bolus) Harms	D	20
Fabaceae	*Calpurnia aurea* (Aiton) Benth.	D	134
Fabaceae	*Dalbergia armata* E. Mey.	D	83
Fabaceae	*Dalbergia obovata* E. Mey.	D	66
Fabaceae	*Elephantorrhiza burkei* Benth.	D	37
Fabaceae	*Erythrina humeana* Spreng.	D	30
Fabaceae	*Erythrina lysistemon* Hutch.	D	34
Fabaceae	*Faidherbia albida* (Delile) A. Chev.	D	15
Fabaceae	*Ormocarpum trichocarpum* (Taub.) Engl.	D	67
Fabaceae	*Pterocarpus angloensis* DC.	D	67
Fabaceae	*Pterocarpus rotundifolius* (Sond.) Druce.	D	40
Fabaceae	*Senegalia ataxacantha* (DC.) Kyal. & Boatwr.	D	189
Fabaceae	*Senegalia burkei* (Benth.) Kyal. & Boatwr.	D	150
Fabaceae	*Senegalia caffra* (Thunb.) P.J.H. Hurter & Mabb.	D	298
Fabaceae	*Senegalia nigrescens* (Oliv.) P.J.H.Hurter	D	57
Fabaceae	*Senegalia senegal* Britton.	D	52
Fabaceae	*Vachellia borleae* (Burtt Davy) Kyal. & Boatwr.	D	38
Fabaceae	*Vachellia davyi* (N.E.Br.) Kyal. & Boatwr.	D	62
Fabaceae	*Vachellia erioloba* (E.Mey.) P.J.H. Hurter	D	35
Fabaceae	*Vachellia grandicornuta* (Gerstner) Seigler & Ebinger	D	30

Family	Species name	Fleshy/Dry	No. records
Fabaceae	*Vachellia luederitzii* (Engl.) Kyal. & Boatwr. var. *retinens* (Sim) & Kyal. & Boatwr.	D	45
Fabaceae	*Vachellia robusta* (Burch.) Kyal. & Boatwr. subsp. *robusta*	D	142
Icacinaceae	*Apodytes dimidiata* E. Mey. ex Arn. subsp. *dimidiata*	F	81
Malvaceae	*Sterculia rogersii* N.E.BR	D	42
Meliaceae	*Ekebergia capensis* Sparmm.	F	42
Myricaceae	*Morella pilulifera* (Rendle) Killick	F	25
Myricaceae	*Morella serrata* (Lam.) Killick	F	82
Myrtaceae	*Syzygium cordatum* Hochst. Ex C. Krauss subsp. *cordatum*	F	49
Ochnaceae	*Ochna natalitia* (Meisn.) Walp.	F	81
Olacaceae	*Ximenia caffra* Sond. var. *caffra*	F	68
Pittosporaceae	*Pittosporum viridiflorum* Simms.	F	77
Rhamnaceae	*Rhamnus prinoides* L. Hér	F	202
Rosaceae	*Prunus africana* (Hook.F.) Kalkman	F	32
Rutaceae	*Clausena anisata* (Willd.) Hook. F. ex Benth. var. *anisata*	F	46
Rutaceae	*Vepris lanceolata* (Lam.) G. Don	F	42
Rutaceae	*Vepris reflexa* I. Verd.	F	30
Rutaceae	*Zanthoxylum capense* (Thunb.) Harv.	F	91
Rutaceae	*Zanthoxylum davyi* (I. Verd.) P.G.Waterman	F	21
Sapindaceae	*Hippobromus pauciflorus* (L.f.) Radlk.	F	36
Sapotaceae	*Sideroxylon inerme* L. subsp. *inerme*	F	50

TABLE A2 Correlation matrix for nine environmental variables considered as predictor variables in this study. Nine variables were initially selected: minimum temperature of the coldest month (MTCM), precipitation seasonality (PSEAS), temperature seasonality (TSEAS), potential evapotranspiration (PET), solar radiation (Solar), average wind speed (Wind), precipitation of the driest quarter (PDQ), precipitation of the wettest quarter (PWQ), and temperature of the warmest quarter (TWQ). If two variables had a *correlation coefficient* greater than 0.75 (in bold), one was excluded from the analysis. Retained variables are italicised in the table.

MTCM	PSEAS	TSEAS	PET	*Solar*	*Wind*	*PDQ*	*PWQ*	*TWQ*	Variable
	-0.09	-0.71	0.73	-0.65	-0.37	0.27	0.08	0.70	*MTCM*
		0.21	0.25	-0.16	-0.67	**-0.84**	0.37	0.20	PSEAS
			-0.21	0.74	0.24	-0.51	-0.47	-0.03	TSEAS
				-0.43	-0.54	-0.19	-0.15	**0.87**	PET
					0.54	-0.19	-0.51	-0.27	*Solar*
						0.50	-0.41	-0.43	*Wind*
							0.07	-0.21	*PDQ*
								-0.30	*PWQ*
									TWQ

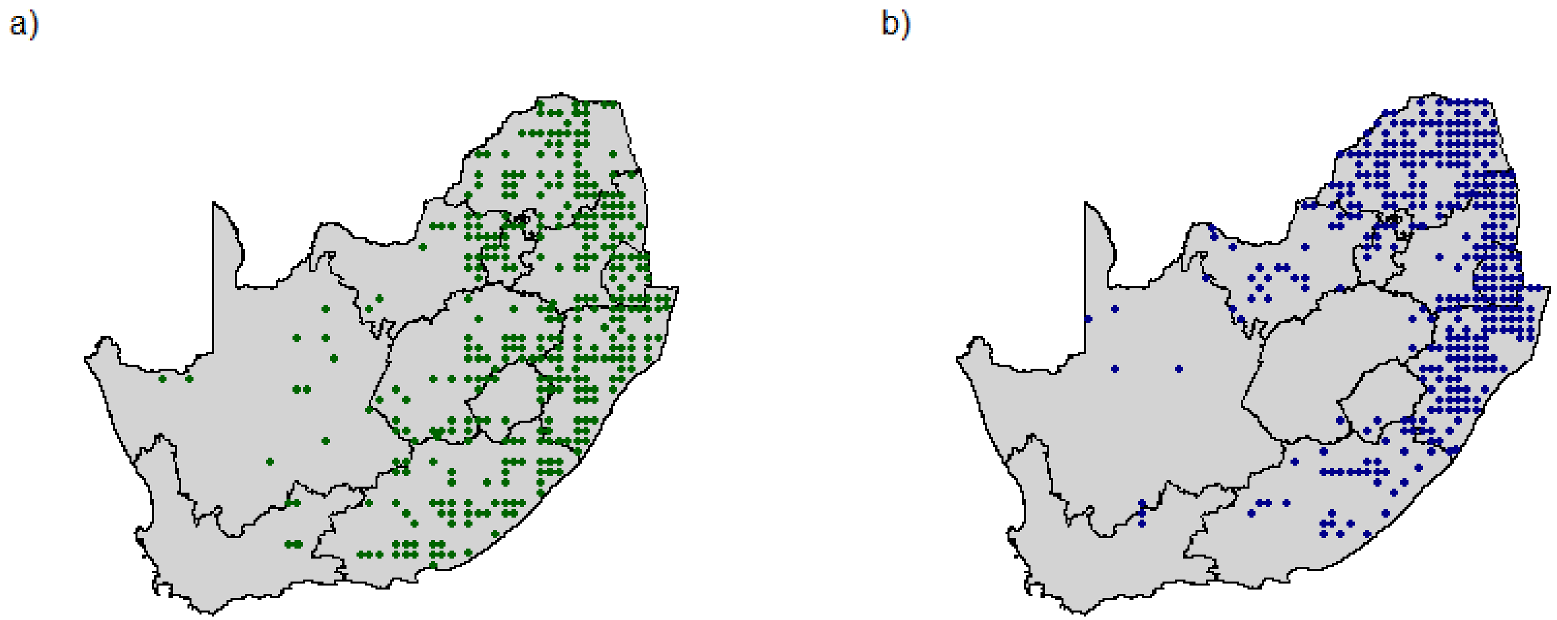


FIGURE A1 Maps of the locality records of all herbarium specimens used in this study for a) the 29 fleshy-fruited tree species (n = 1877 records), and b) the 29 dry-fruited species (n = 2065 records) in the summer rainfall regions of South Africa.

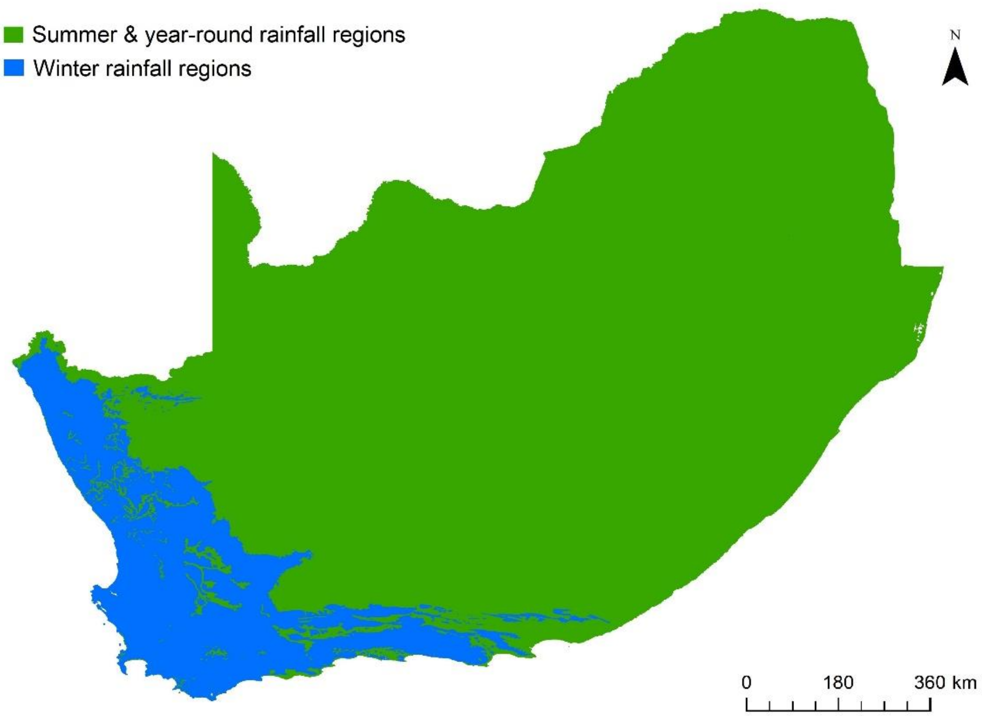


FIGURE A2 Map of South Africa illustrating summer rainfall regions (including savanna, grassland, thicket, and Nama Karoo biomes as well as forest patches of year-round rainfall patterns) vs. winter rainfall regions (which include the fynbos and succulent Karoo biomes). Map created in Arc GIS using biome data from Mucina & Rutherford (2006).

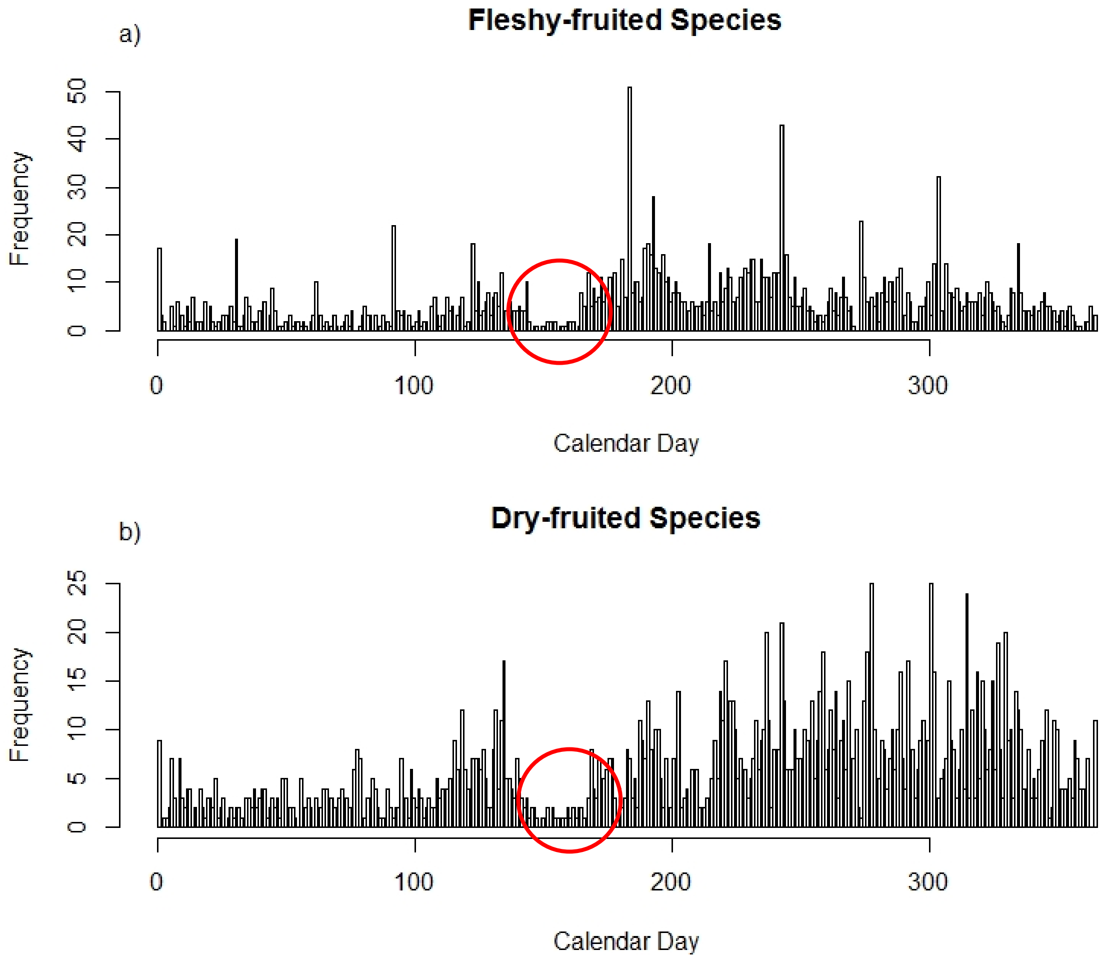


FIGURE A3 Histogram illustrating the frequency of herbarium vouchers per calendar day for a) fleshy-fruited species, and b) dry-fruited species. Phenology was quantified as day of the year, i.e., 1 represents 1 January. The histogram revealed a gap in fruiting between the end of May and beginning of June (illustrated in the red circles above). Therefore, for analyses, the fruiting day of each specimen was calculated as the Julian day after June 1.

TABLE A3 The average variable contribution of different environmental variables for fleshy-fruited *vs* dry-fruited tree species. Variable importance was determined using random forest regressions. For each species, the average variable importance (given as a percentage) is given for the following variables: MTCM (mean temperature of the coldest month), TSEAS (temperature seasonality), PDQ (mean precipitation of the driest quarter), TWQ (mean temperature of the wettest quarter), and Solar (Solar radiation).

Variable	**Average variable contribution**				
	Dry-fruited species	**Fleshy-fruited species**	**df**	**t-value**	**p-value**
MTCM	11.10 ± 8.66	15.78 ± 7.82	53.568	2.100	**< 0.05**
TSEAS	16.38 ± 6.76	14.01 ± 9.96	55.210	1.069	> 0.05
PDQ	14.74 ± 7.45	13.25 ± 7.66	59.654	0.623	> 0.05
TWQ	14.15 ± 7.41	13.32 ± 9.33	58.855	0.014	> 0.05
Solar	13.26 ± 5.80	15.51 ± 9.12	53.454	-1.600	> 0.05

TABLE A4 The relative variable importance of different environmental variables to the timing of fruiting of each of the 58 species investigated. Variable importance was determined using random forest regressions. The relative variable importance of mean temperature of the coldest month (MTCM), temperature seasonality (TSEAS), precipitation of the wettest quarter (PWQ), precipitation of the driest quarter (PDQ), Temperature of the warmest quarter (TWQ), solar radiation (solar) and wind speed (Wind) was averaged across the species to get an indication of mean variable contribution. The mode fruiting day of each species is also included in the table.

Fruit type	Species	Mode fruiting day	MTCM	TSEAS	PDQ	TWQ	Solar
Fleshy	*Acokanthera oppositifolia*	26	10.22	20.08	17.38	7.60	13.77
Fleshy	*Apodytes dimidiata*	69	13.90	13.20	19.30	13.26	13.27
Fleshy	*Celtis africana*	267	15.93	12.63	16.89	12.51	15.28
Fleshy	*Clausena anisata*	333	20.22	9.50	10.64	9.75	26.76
Fleshy	*Ekebergia capensis*	330	1.54	5.53	15.55	4.90	19.28
Fleshy	*Erythroxylum delagoense*	342	22.37	18.29	1.34	8.23	20.75
Fleshy	*Erythroxylum emarginatum*	15	9.37	17.94	26.15	13.09	7.77
Fleshy	*Harpephyllum caffrum*	42	14.92	15.76	17.40	10.83	12.08
Fleshy	*Hippobromus pauciflorus*	342	19.03	21.27	17.96	21.85	2.84
Fleshy	*Ilex mitis*	72	4.70	16.13	9.55	13.27	10.11
Fleshy	*Lannea discolor*	279	9.96	16.87	17.01	14.43	10.06
Fleshy	*Maerua cafra*	285	4.87	6.79	24.09	20.27	5.27
Fleshy	*Maytenus acuminata*	94	15.35	30.92	5.29	17.77	4.67
Fleshy	*Morella pilulifera*	254	17.24	22.78	10.44	3.17	12.17
Fleshy	*Morella serrata*	94	38.85	13.44	9.60	7.62	12.22
Fleshy	*Ochna natalitia*	276	4.03	23.23	4.72	20.55	11.63
Fleshy	*Pittosporum viridiflorum*	75	7.08	16.07	22.32	12.52	14.97
Fleshy	*Prunus africana*	234	4.18	19.86	21.75	28.98	18.71
Fleshy	*Rhamnus prinoides*	69	12.46	15.23	13.52	9.51	16.43
Fleshy	*Searsia burchellii*	244	0.07	21.33	19.36	7.25	11.97
Fleshy	*Searsia chirindensis*	344	10.42	10.51	14.33	26.92	6.72
Fleshy	*Searsia dentata*	316	6.06	25.45	27.60	9.25	13.98
Fleshy	*Sideroxylon inerme*	16	4.23	34.33	4.20	24.00	7.57
Fleshy	*Syzygium cordatum*	345	8.48	14.55	14.44	14.79	21.98
Fleshy	*Trema orientalis*	106	9.73	16.89	13.94	4.93	4.62
Fleshy	*Vepris lanceolata*	74	29.04	13.36	11.34	4.17	8.58
Fleshy	*Vepris reflexa*	273	2.67	6.00	17.77	2.74	5.93
Fleshy	*Ximenia caffra*	333	0.67	8.35	29.26	15.57	10.21
Fleshy	*Zanthoxylum capense*	61	10.00	12.28	8.57	27.31	8.40
Fleshy	*Zanthoxylum davyi*	61	5.30	12.90	0.58	7.60	19.88
Dry	*Adenopodia spicata*	19	11.10	16.38	14.74	13.15	12.26
Dry	*Albizia harveyi*	232	13.87	10.82	14.78	10.84	15.34
Dry	*Bauhinia galpinii*	10	12.24	10.40	18.66	11.55	12.07
Dry	*Bauhinia petersiana*	359	11.20	7.93	26.84	7.61	22.73

Fruit type	Species	Mode fruiting day	MTCM	TSEAS	PDQ	TWQ	Solar
Dry	*Bauhinia tomentosa*	9	28.21	13.46	7.75	12.12	7.11
Dry	*Bolusanthus speciosus*	9	7.39	25.15	16.85	3.52	20.32
Dry	*Calpurnia aurea*	193	11.00	1.77	22.56	27.24	14.08
Dry	*Croton sylvaticus*	121	20.77	14.32	17.89	10.24	6.99
Dry	*Dalbergia armata*	296	13.00	0.83	8.47	18.61	44.62
Dry	*Dalbergia obovata*	4	5.93	21.18	7.85	1.81	23.52
Dry	*Elephantorrhiza burkei*	30	2.12	28.85	28.19	8.67	20.76
Dry	*Erythrina humeana*	50	16.23	14.95	18.91	13.69	11.93
Dry	*Erythrina lysistemon*	277	15.20	11.28	17.47	11.52	8.29
Dry	*Faidherbia albida*	327	14.10	24.10	2.99	35.40	1.54
Dry	*Ormocarpum trichocarpum*	35	13.15	16.24	5.39	16.22	13.24
Dry	*Pterocarpus angolensis*	190	2.12	27.61	12.76	5.48	2.38
Dry	*Pterocarpus rotundifolius*	68	21.92	3.99	11.94	34.52	23.60
Dry	*Senegalia ataxacantha*	101	16.66	6.84	10.37	8.74	21.36
Dry	*Senegalia burkei*	55	20.23	14.80	9.53	17.14	12.45
Dry	*Senegalia caffra*	94	8.42	24.57	22.60	11.90	9.43
Dry	*Senegalia nigrescens*	299	13.44	14.65	17.58	7.54	18.50
Dry	*Senegalia senegal*	114	11.17	32.12	22.73	3.98	4.75
Dry	*Sterculia rogersii*	229	23.72	8.02	18.08	12.32	21.41
Dry	*Vachellia borleae*	55	21.13	30.31	2.76	3.39	7.69
Dry	*Vachellia davyi*	88	26.59	7.45	6.71	16.26	31.99
Dry	*Vachellia erioloba*	30	23.88	2.12	0.28	27.29	19.50
Dry	*Vachellia grandicornuta*	62	19.54	0.85	6.70	12.91	5.79
Dry	*Vachellia luederitzii*	113	22.48	32.48	11.75	0.83	20.22
Dry	*Vachellia robusta*	45	26.32	0.88	20.06	30.44	21.31

CHAPTER 3

The role of deterministic succession during forest development within a southern African savanna

THE ROLE OF DETERMINISTIC SUCCESSION DURING FOREST DEVELOPMENT WITHIN A SOUTHERN AFRICAN SAVANNA

Abstract

Woody encroachment can lead to a switch from open savannas to dense woodlands or forests. This has implications for both the composition of ecological communities and the provision of ecosystem services such as nutrient cycling and grazing capacity. The patterns and underlying drivers responsible for woody encroachment are not fully understood. Here, we investigate the underlying determinants of bush clump formation (a form of encroachment) in a South African savanna and explore whether bush clump succession is driven by deterministic (i.e., predictable changes in species composition) or stochastic (i.e., random) processes. Specifically, we test (1) whether the similarity in species composition of saplings and trees differs among small and large clumps, (2) which environmental factors are driving succession, (3) if forest specialization of tree and sapling species within bush clumps increases with the successional gradient, and 4) if functional traits of trees change with clump succession. Similarity in species composition between saplings in small clumps and trees in large clumps was higher than similarity between trees in small clumps and trees in large clumps. Furthermore, temperature, soil moisture, relative humidity and light intensity difference were related to changes in species composition along the successional gradient. As expected, forest specialization of trees increased with increasing clump area indicating that late-successional bush clumps have more forest-type species. The proportion of fleshy-fruited tree species did not increase with an increase in bush clump size, however, the proportion of fleshy-fruited sapling species significantly decreased as clump size increased. In contrast to expectation, the average maximum height of trees did not increase as bush clump area increased. The directional changes of species found along the successional gradient suggest a deterministic process of succession driven by changes in local environmental conditions during clump formation.

Introduction

Woody encroachment, i.e., the increase in density of indigenous woody cover within grassy ecosystems, is a major concern globally (Archer et al., 2017b). Associated changes in tree-grass ratios modify the composition of ecological communities (Ratajczak, Nippert & Collins, 2012) and the provision of ecosystem services (e.g. nutrient cycling and grazing capacity; Asner et al., 2004) and are thought to be the result of a combination of both local and global drivers (Wigley, Bond & Hoffman, 2010, Skowno et al., 2017). Local drivers of woody encroachment include altered land-use practices and management (e.g. changes in fire and herbivory management; O'Connor & Chamane, 2012), whereas increased atmospheric carbon dioxide concentrations are thought to be a major driver at the global scale (O'Connor, Puttick & Hoffman, 2014).

Although encroachment is generally viewed as the densification of woody species, it can also occur through the formation of bush clumps (i.e., dense clumps of woody species) which subsequently expand in size (O'Connor & Chamane, 2012). This succession often starts with the establishment of a founder tree which then facilitates the establishment of other species (Bews, 1917, Barnes & Archer, 1996, Dean, Milton & Jeltsch, 1999). The succession of these clumps is unusual in that they do not develop following a disturbance as postulated by the definition of succession, i.e., the sequential change in species composition following a disturbance that results in the abrupt losses of biomass or ecological structure (Wardle, Walker & Bardgett, 2004, Prach & Walker, 2011). However, these clumps do occur where natural disturbance factors (i.e. fire suppression and decreased herbivory) have been reduced. In this example, successional procceses thus occur following the removal of natural (vegetation-driving) disturbance, which in itself is a form of disturbance. Bush clumps have been recorded from various localities in southern Africa, West Africa, and Texas (USA) (e.g. Bews, 1917, Mordelet, Abbadie & Menaut, 1993, Archer, 1995, Northrup et al., 1995, Hester, Scogings & Trollope, 2006, O'Connor & Chamane, 2012), where they are usually initiated by a single woody species (except Bews, 1917).

Two underlying processes, namely deterministic and stochastic, are recognized in succession (Dent, DeWalt & Denslow, 2013, Dini-Andreote et al., 2015). Deterministic succession involves a directional change in species composition which is driven by environmental conditions that allow establishment and persistence (Peterson & Carson, 2008, Dent, DeWalt & Denslow, 2013). In deterministic succession, factors such as site conditions, species sorting mechanisms and disturbance intensity may directionally influence the trajectory of succession (Meiners et al., 2015, Chang & Turner, 2019). Thus, species benefit from each other, forming characteristic associations of species rather than random species associations (Liautaud et al., 2019). For instance, along a forest successional gradient, species composition can change predictably due to increases in soil moisture as the canopy of a forest becomes denser (Schönbeck et al., 2015). Accordingly, the sapling composition of early successional stages may be similar to that of the adult composition in later successional stages as these saplings ultimately grow to become adult trees in later successional stages (Dent, DeWalt & Denslow, 2013). Furthermore, tree composition during early successional changes can be expected to be different from that of the sapling community in later successional stages, indicating poor establishment of early successional species in later successional stages (Dent, DeWalt & Denslow, 2013). In contrast, stochastic succession as an inherent probabilistic biological process, is influenced by less predictable factors such as random chance events, the availability of colonisers in the surrounding landscape, or unique conditions during disturbance events (Chase & Myers, 2011, Zhou et al., 2014). For example, processes that govern a species' ability to disperse into an area, and thus species availability, are largely random (Meiners et al., 2015). Such processes can lead to changes in species composition that are not strongly associated with the environmental conditions at a particular site (Dini-Andreote et al., 2015).

One result of deterministic succession in bush clumps would be that older bush clumps are dominated by late-successional forest species (Jarvel & O'Connor, 1999, O'Connor & Chamane, 2012). As light levels decline during succession (Montgomery & Chazdon, 2001), shade-intolerant species should disappear and shade-tolerant (i.e., forest) species increasingly dominate in old (i.e., large) bush clumps (O'Connor & Chamane, 2012). Moreover, old bush clumps should differ in other microclimatic conditions from young bush clumps, e.g., maximum air temperature and irradiance may be lower while humidity may be higher in old vs. young bush clumps (Jarvel & O'Connor, 1999). Such changes in microclimate during bush clump succession can reduce the establishment of herbaceous species (Archer, 1995), reduce the flammability of vegetation and provide a suitable environment for fire-intolerant (forest) species to establish. Hence, bush clump succession and associated changes in microclimate are likely to favour forest species which can be expected to establish in later stages of succession.

Another prediction of deterministic bush clump succession is that more specialized species will colonize, survive, and dominate in old, large clumps. For instance, plant species may be specialized in terms of their climatic or habitat niche breadths (Dolédec, Chessel & Gimaret-Carpentier, 2000), i.e. the range of (micro-)climatic and habitat conditions they can tolerate. The level of specialization across species in a community can thus provide insights into whether different successional stages are associated with the presence of particular plant groups (e.g., forest specialists). Measures of habitat breadth (Barnagaud et al., 2012) would indicate the ability of a species to survive in a number of different ecosystems (e.g., savannas or forests), and whether species that come at later stages of succession are unable to tolerate a wide range of habitat conditions compared to early-successional species. Therefore, it can be expected that bush clump succession leads to an increase of forest specialists and a decrease of species with wide habitat niches (Christensen & Peet, 1984, Palmer & Dixon, 1990).

Studies on bush clumps have suggested that succession of woody species within bush clumps occurs through directional change (Bews, 1917, Archer et al., 1988, Archer, 1990, O'Connor & Chamane, 2012). However, most studies (except O’Connor & Chamane, 2012) have neither empirically tested this nor have they systematically compared the association between multiple environmental factors and different successional trajectories (Meiners et al., 2015). Hence, elucidating whether the pattern of species turnover is deterministic or stochastic can inform on the drivers and processes of bush encroachment across space and time.

If environmental filtering processes are at play during bush clump succession, then it can be expected that functional traits (i.e., the physiological, morphological, behavioural, or phenological characteristics that are related to the fitness and performance of an organism (Violle et al., 2007)) will change consistently as environmental conditions change in accordance with changing successional stages. Indeed, uniform trends are expected between the traits associated with early successional and late successional species (Raevel, Violle & Munoz, 2012). Identifying whether functional traits change over succession allows us to infer on the community assembly processes at play during succession. This information also aids in our understanding of how traits will change across succession under the inflluce of global change drivers.

Here, we investigate the successional patterns associated with the development of bush clumps within a South African open savanna. Woody encroachment increases tree-grass ratios in savannas and can lead to a transition into forest. Under encroachment, savanna species, both woody and herbaceous, eventually disappear (Ratajczak, Nippert & Collins, 2012), and productivity and function of the landscape changes (O'Connor, Puttick & Hoffman, 2014). We test whether species composition changes with clump size, how multiple environmental factors in bush clumps relate to changes in species composition, and whether habitat specialisation of species is more dominant in large bush clumps. Specifically, we test whether (1) similarity between saplings of small bush clumps and trees of large bush clumps is higher than the similarity between trees of small bush clumps and trees of large bush clumps, indicating deterministic succession (Dent, DeWalt & Denslow, 2013), (2) changes in species composition between bush clumps are accompanied by changes in microclimatic conditions, namely temperature, relative humidity, soil moisture, and light availability (Dent, DeWalt & Denslow, 2013), (3) species composition changes towards more forest-type species as clumps get larger at the expense of savanna-type founder individuals, (4) species with narrow habitat breadth are more common in old or large bush clumps (Palmer & Dixon, 1990), (5) if functional traits, namely proportion of fleshy-fruited species and maximum tree height, of trees change with clump succession. Our study provides novel insights into how multiple environmental variables accompany species turnover during succession of South African bush clumps which can inform management of woody encroachment and conservation of savannas and grasslands.

Methods

Study site

Our study was conducted in Buffelskloof Nature Reserve (25º19’22.21” S, 30º29'15.41” E), in NE South Africa (Fig. B1a, Appendix B). This reserve is approximately 1500 ha with an altitude ranging between 1000 and 1800 m.a.s.l., and experiences warm, wet summers, and cold, dry winters with periodic frost events. The mean annual precipitation of the reserve is approximately 1270 mm (Burrows & Burrows, 2003) and the mean annual temperature of the nearest city, Lydenburg, averages 16.3ºC (Climate-data.org, 2019). The reserve was proclaimed in 1980 around a 10 km long, 300–800 m wide forested valley (Fig. B1b, Appendix B). Much of the grasslands and savannas surrounding the reserve have been afforested with pines. The first pine plantations in the area were planted in the 1950s and have contributed to the current fire management of the area. Before proclamation of the reserve, the areas in and around the valley were burned annually during April–May to protect the surrounding plantations. Since the establishment of the reserve, a two-year fire rotation has been employed with burning during May and early June (John Burrows pers. comm.). The geology of the reserve consists largely of sedimentary and subordinate volcanics of the Transvaal Supergroup. Three major biomes (and vegetation types) are represented in the reserve: forest (Northern Afrotemperate Forest), grassland (Lydenburg Montane Grassland) and savanna (Lydenburg Thornveld) (Mucina & Rutherford, 2006). Savannas are open in structure, with trees in a matrix of grasses. Within the savannas of this reserve, there is evidence of recent woody thickening (Haddad, 2011) which often occurs through the formation of bush clumps, i.e. associations of one or more large woody individuals (> 1.2 m; hereafter referred to as ‘trees’) with woody saplings (< 1.2 m; hereafter referred to as ‘saplings’) growing beneath the canopy of the trees and separated from other such clumps by grassy vegetation (Fig. B1 c & d, Appendix B). Several herbivores can be found in the reserve, including Chacma baboons *(Papio ursinus)* and various antelope (e.g., greater kudu (*Tragelaphus strepsiceros*), common duiker (*Sylvicapra grimmia*), red duiker (*Cephalophus natalensis*), mountain reedbuck (*Redunca fulvorufula*) and oribi (*Ourebia ourebi*)).

Vegetation Sampling

Sampling was carried out between 2015 and 2017 (July-August 2015, January, April-May, July 2016, January, March, and August 2017). The trees in the clumps are mostly evergreen. While small saplings were detected, no evidence of seedling germination (e.g., cotyledons) was found. Most small saplings appeared to be in a ‘stunted’ sapling stage, which can last for several decades until suitable conditions allow for rapid growth into mature trees (Antos, Guest & Parish, 2005). Therefore, season of sampling is unlikely to have influenced species composition.

We chose 40 clumps in the reserve. A stratified random sampling was used, i.e., a range of sizes were represented, but selection within different size grouping was random). Clump size was determined by measuring the length and breadth of each clump (to the nearest 10 cm) using a measuring tape and calculating its area as an ellipse. The smallest clump was defined as a single tree (> 1.2 m) beneath which woody vegetation (< 1.2 m) was present. Across the reserve, the number of small and intermediate size bush clumps outnumber very large clumps; as such, there are a greater number of smaller sized clumps than there are large clumps. Within each clump, all tree species (i.e., species listed in Coates Palgrave (2002)) were identified to species level.

The circumference of each tree (defined as individuals > 1.2 m) was recorded at 30 cm above the ground using a sewing tape measure (to the nearest mm). The measurement height of 30 cm was selected as the clumps are often too dense to consistently measure diameter at breast height. Multithemed trees were measured, and the circumference averaged. Additionally, a count of the number of saplings (defined as individuals < 1.2 m) of each species was made per clump. The 1.2 m cut-off to distinguish between saplings and trees was chosen, which is in the range of other studies that have differentiated between saplings and trees in forests (Janse-Ten Klooster, Thomas & Sterck, 2007). This cut-off is lower than that for savanna trees (2 - 4 m, Higgins, Bond and Trollope (2000)): bush clump saplings would have been exposed to lower, or no, flames and/or because savanna trees grow faster to escape the fire trap; also, a higher cut-off would have resulted in too few trees for comparing sapling and tree assemblages between small and large clumps. We assumed that the largest tree(s) (in circumference) in the bush clumps was (were) the founder tree(s) (i.e., the initial tree around which the bush clump established). This assumption carries two possible forms of uncertainty (O'Connor & Chamane, 2012). First, founder individuals may have died. Hence, a search for old stumps was also performed; none were found; thus, it was assumed that the largest tree in the clump was the founder. Second, different trees might have different growth rates, and the largest tree in a bush clump may thus not be the founder individual. However, growth rates of tree species in our study area are not known. It was not if >1 tree was the founder, i.e., if several large (founder) trees were present. The trunks of the founders were always considerably larger than those of other trees in the bush clumps.

Basal area was estimated for each tree stem (for multi-stemmed trees, the area was calculated per stem), using the formula $A = C^2 / 4\pi$, where A is basal area and C is the circumference of the stem measured 30 cm from the tree base. Total woody basal area per clump was calculated by summing the areas of all stems and was used as a proxy for bush clump maturity. In addition, a measure of tree and sapling species richness (number of species), and a count of trees (trees > 1.2m), were calculated for each clump.

Environmental Data

Temperature, relative humidity, soil moisture and light intensity difference were measured in each clump. Temperature and relative humidity measurements were recorded using Maxim iButton dataloggers that were placed in the center of clumps from 21 November 2018 to 29 March 2019. Of the 40 iButtons, 17 were hygrochrons (measuring both temperature and relative humidity), whereas the remaining 23 iButtons were thermochrons (measuring temperature only). While humidity was not recorded in all clumps, the 17 hygrochrons were placed in a range of clump sizes to measure the range and variability of humidity across the successional gradient (Table B1, Appendix B). All iButtons were programmed to capture data at 60-minute intervals at a 0.0625°C resolution. Four humidity loggers were faulty or got lost. Soil moisture was recorded for each clump using a FieldScout TDR 300 portable soil moisture meter (Spectrum Technologies, Inc., Plainfield, IL, USA) on 19 and 20 January 2016.

For soil moisture, four readings were taken beneath the canopy of each clump (one reading in each quarter of the clump). Average, maximum, and minimum soil moisture was calculated per clump. Light intensity difference was recorded using a ceptometer (Accu-PAR LP-80, Decagon Devices, Pullman, WA, USA) in May 2019. Four light readings were recorded both inside and outside the clumps. The difference in light intensity between inside and outside of a bush clump was then averaged and used as a measure of light intensity difference. These reading give an indication of light inception into the bush clumps. All readings were taken between 9h00 and 15h00 on cloud-free days.

Statistical Analyses

To test the assumption that bush clump size could be used as a proxy for age, three separate generalized linear regression models (GLMs) were used to investigate the relationship between bush clump area and a) species richness (fitted using a Poisson distribution with a log link), b) woody basal area (fitted with a Gaussian distribution with an identity link), and c) the total number of trees (fitted with a Poisson distribution with a log link). We expected that species richness, woody basal area, and the total number of trees would increase with an increase in clump size and thus clump maturity.

To compare similarity of sapling and tree species composition between large and small clumps we identified the 10 smallest clumps and the 10 largest clumps as ‘small’ and ‘large’ clumps, respectively. The Morisita-Horn index, which is robust to uneven sampling (Magurran, 2013), was used to quantify similarity in species composition between small and large clumps. The Morisita-Horn similarity index was calculated for each combination of large and small clumps. We tested if the similarity in species composition between trees-in-large-clumps and saplings-in-small-clumps was greater than the similarity between trees-in-large-clumps and trees-in-small-clumps. These two sets of similarity indices were compared between small and large clumps using a Welch two-sample t-test (Welch 1947).

To test whether environmental variables accompanied the change in species composition with succession, we tested whether, for the 30 largest bush clumps, differences in similarity with the 10 smallest clumps could be explained by environmental conditions in the largest clumps. We expected that increased dissimilarity of large bush clumps with small bush clumps would be accompanied by directional changes in the microclimate. Initially, similarity in species composition between all combinations of the 10 smallest and the 30 largest bush clumps was calculated using the Morisita-Horn index of similarity. For every large bush clump the similarity with the 10 smallest clumps was averaged, providing 30 data points (one for each of the 30 largest bush clumps). We then tested whether this average similarity index of the small bush clumps with each of the 30 largest bush clumps could be explained by mean and minimum temperature, range in relative humidity, minimum soil moisture (the lowest value identified out of each of the 4 measures taken per clump) and light intensity difference of the 30 largest bush clumps (Table B2, Appendix B). As the number and identity of the 30 largest bush clumps with measures of temperature (n = 27), relative humidity (n = 13), soil moisture (n = 30), and light intensity difference (n = 30) differed (Table B1, Appendix B), four univariate GLM models were run. Models were fitted with a quasi-binomial distribution with a logit link as the response variable was bound between zero and one and over-dispersed (Zuur et al., 2009).

An index of habitat preference for each species was developed using habitat descriptions from several southern African tree field guides (Coates Palgrave, 2002, Schmidt, Lotter & McCleland, 2002, Van Wyk & Van Wyk, 2013). The habitat index ranged from 1 (open habitat species) to 8 (closed habitat species) (Table B4, Appendix B). Species were classified as forest species when recorded in field guides as occurring in one of the following habitat types: forest, mist-belt forest, evergreen forest, afromontane forest, coastal forest, sand forest, riverine forest, and montane forest. In total, 23 species (21.9%) were classified as forest species (Table B4, Appendix B).

To test whether the proportion of a) founder tree species decreased, and b) forest tree species increased with increasing clump size, we fitted beta regression models (with a Gaussian distribution and an identity link) using the proportion of founder/forest tree species per bush clump as a response variable and bush clump size as predictor variable.

To test whether forest specialization were more common in large bush clumps, a community-weighted mean of forest specialization was calculated for each bush clump using the equation: $\sum_{i=1}^{s} \mathrm{P}i\ x\ \mathrm{FS}i$, where s is species richness, Pi is the proportion of species i and FS_i is the forest specialization value for species i (Table B4, Appendix B). High values represent bush clumps with a higher community-weighted mean showing a higher degree of forest specialisation. GLMs (fitted with a Gaussian distribution and an identity link) were used to test if the community-weighted mean of forest specialization increased with bush clump size. Analyses were repeated (separately) for both trees and saplings.

To test whether there was a difference in average forest specialization across the clump gradient, mean forest specialization for species of the 10 smallest clumps, the 10 largest clumps and of surrounding savanna species was calculated. Savanna species were categorized as those species growing in a grassland matrix with no woody species growing beneath their canopy in the study site, based on *ad hoc* observations. These species were also described as being found in closed and open woodlands in the habitat preference index. Identification as savanna trees was also confirmed by expert opinion (John Burrows pers. comm.). One-way ANOVA with Tukey post-hoc tests were used to assess whether the community-weight mean for forest specialization differed between small clumps, large clumps, and the savanna habitat. Analyses were run separately for trees and saplings.

Habitat breadth was calculated for each species by summing the number of habitat classes (from the habitat preference index; Table B3/4, Appendix B) for which the species was described. This value was used as an indication of habitat specialization with species ranging from specialists (habitat breadth = 1; occur in only one habitat class) to generalists (habitat breadth = 8; occur in only all 8 habitat classes). This was used to calculate a measure of community-weighted mean of tree species habitat breadth using the equation: $\sum_{i=1}^{s} = Pi\ x\ HBi$, where s is species richness, P*i* is the proportion of species and HB*i* is the habitat breadth for species *i* (Table B4, Appendix B).

To assess whether species in large bush clumps possessed narrower habitat breadths, GLMs (fitted with a Gaussian distribution and an identity link) were used to test if the community-weighted mean of tree species habitat breadth (response variable) changed with bush clump size (predictor variable). We expected that old, large bush clumps would show a greater proportion of habitat specialists. Additionally, we compared the habitat specialization of savanna species (not considered in the above analysis) with the habitat specialization of trees in small and large bush clumps. For this, the range of habitat breadth values for species of trees in the ten small bush clumps, the ten large clumps and the surrounding savanna species were calculated. One-way ANOVA, followed by Tukey post-hoc tests, were used to assess whether species habitat breadth of trees was significantly different between small bush clump species, large bush clump species and savanna species. One-way ANOVA and Tukey post-hoc tests were repeated to assess whether species habitat breadth of saplings was significantly different between small bush clump species, large bush clump species and savanna species.

To identify which species were associated with early and late successional stages, boral analysis, which is a parametric approach to the fourth root corner problem, was run. This method employs multivariate latent variable models and allows for non-normally distributed response variables (Hui, 2016). Using this method, we quantified the position of species along the successional gradient (i.e., the likelihood of where each species is likely to be found along the successional gradient) while also accounting for unexplained correlations between sapling abundance and clump basal area. Thus, sapling species abundance was regressed against bush clump basal area using beta-distributed errors while also compensating for between-group correlations by using two latent variables (Hui, 2016).

I tested whether two functional traits, namely proportion of fleshy-fruited species and maximum tree height, of BC trees change with clump succession. I tested: whether the proportion of fleshy-fruited tree species, and the proportion of fleshy-fruited sapling species increased with increasing clump size using fitted beta regression models (fitted using a Poisson distribution with a log link). The proportion of fleshy-fruit tree/sapling species per bush clump were used as a response variable and bush clump size as predictor variable. To test the assumption that the average maximum height of trees within a bush clump would increase with bush clump size, a GLM with a Gaussian distribution with a log link was fitted.

All analyses were conducted in R, version 3.5.1 using packages: *vegan* (Oksanen et al., 2007), *corrplot* (Wei et al., 2017), *car* (Fox et al., 2012), *Boral* (Hui, 2016), and *hdi* (Dezeure et al., 2015).

Results

A total of 105 tree species (totalling 21,471 woody individuals) were identified across the 40 bush clumps, of which 24 (22.9%) were identified as contributing founder species (Table B3, Appendix B). All 105 species occurred at least once as trees (> 1.2 m), whereas only 92 species were recorded as saplings (< 1.2 m) across the clumps. Bush clump area ranged from 10 m^2 to 1343 m^2 (mean = 266 m^2, SE = 347.7 m^2). Total basal area per bush clump varied between 0.2 m^2 and 30.2 m^2 (mean = 5.5 m^2, SE = 7.4 m^2). The total number of trees per bush clump ranged between one and 350 (median = 14), and saplings between four and 3,503 (median = 131). The average distance between bush clumps and the forested valley was 188 m (SE = 91.2). As expected, with an increase in bush clump area, species richness (R^2 = 0.68, *F*(38,39) = 79.74, *P* = 7.191e-11; Fig. 3.1a), basal area (R^2 = 0.82, *F(*38,39) = 170.81, *P* = 1.233e-15; Fig. 3.1b) and the number of trees (R^2 = 0.76, *F*(28,39) = 205.88, *P* = 2.2e-16; Fig. 3.1c) increased (Table B5, Appendix B). We are confident in our assumption that bush clump size could be used as a proxy for bush clump maturity.

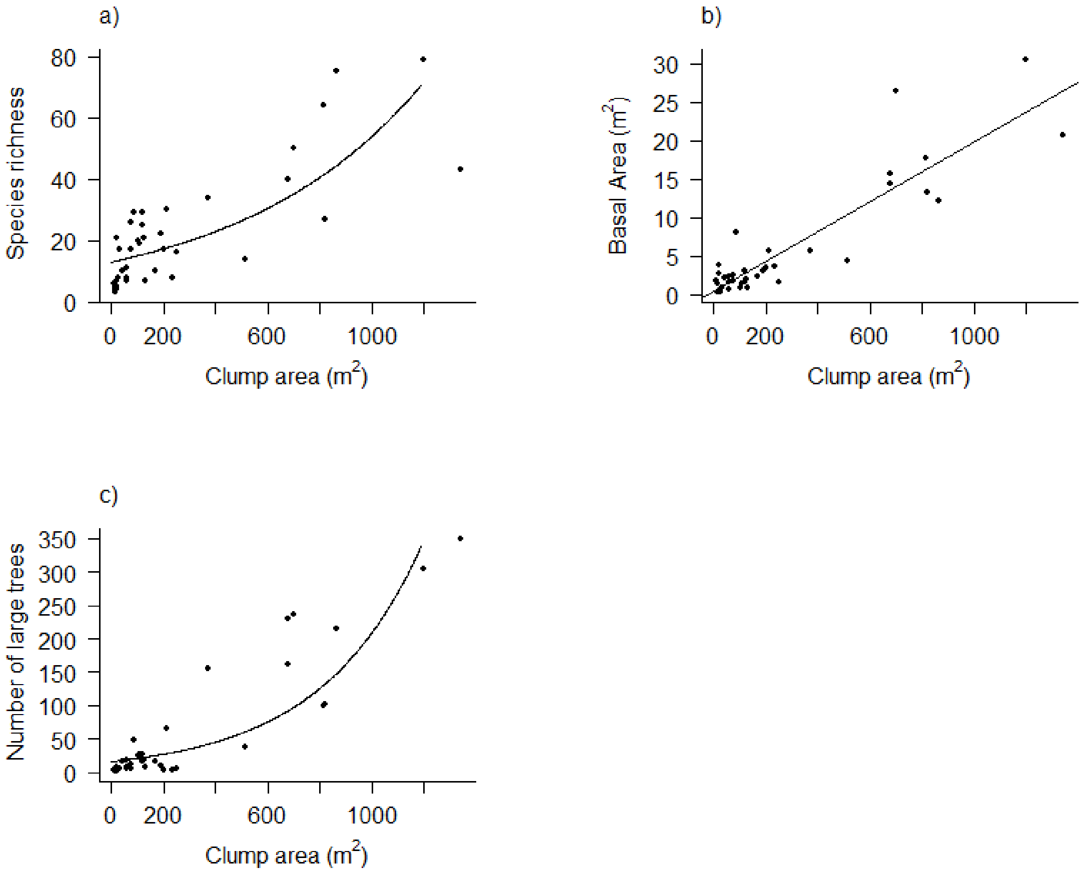


FIGURE 3.1 Results from generalised linear models testing the relationships between bush clump area and (a) species richness (R^2 = 0.68), (b) basal area (R^2 = 0.82), and (c) the number of large trees within each bush clump (R^2 = 0.76).

As expected, the species composition of trees in large bush clumps more closely resembled the species composition of saplings in small bush clumps than the composition of trees in small bush clumps (*t* = 9.29, *P* = 5.004e-09; Fig. 3.2b).

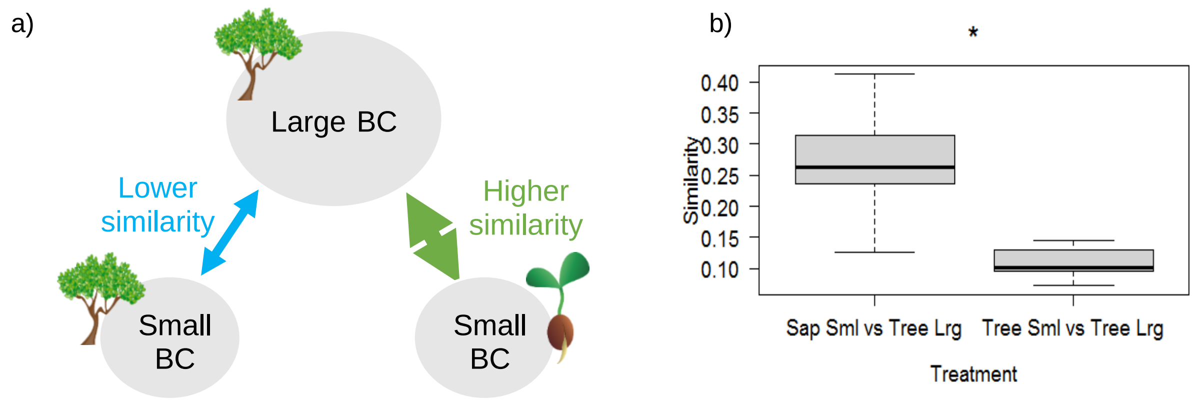


FIGURE 3.2 For systems undergoing deterministic succession, it could be expected that a) the similarity of adult tree species composition of large bush clumps more closely resembles similarity of sapling composition in small bush clumps than that of adult tree composition in small bush clumps. (b) Boxplots illustrating the similarity in species composition (calculated as the Morisita-Horn similarity index) between different sized bush clumps at Buffelskloof Private Nature Reserve, South Africa. As expected, the similarity of the adult tree composition of large bush clumps more closely resembles that of saplings in small bush clumps than that of adult trees in small bush clumps. The boxplots illustrate the lower (Q1) and upper (Q3) quartiles. The plots also illustrate the mean and median observation for similarity. Abbreviations: Sap = sapling; sml = small; lrg = large, BCs = bush clumps.

Changes in species composition similarity between the largest bush clumps and the small bush clumps were predicted by changes in all measured environmental variables (Fig. 3.3; Table B6, Appendix B). Similarity with the smallest bush clumps decreased (i.e. species composition of large bush clumps became more dissimilar with small clumps) as mean temperature decreased ($R^2 = 0.10$, $F(25, 26) = 3.14$, $P = 4.60\text{e-}02$) (Fig. 3.3a), minimum temperature increased ($R^2 = 0.25$, $F(25, 26) = 9.36$, $P = 5.00\text{e-}03$) (Fig.3.3b), the range of relative humidity decreased ($R^2 = 0.13$, $F(11, 12) = 1.892$, $P = 4.30\text{e-}02$) (Fig. 3c), minimum soil moisture increased ($R^2 = 0.12$, $F(28, 29) = 4.525$, $P = 4.10\text{e-}02$) (Fig. 3.3d), and the difference in light intensity difference increased ($R^2 = 0.20$, $F(28, 29) = 8.17$, $P = 8.00\text{e-}03$) (Fig. 3.3e).

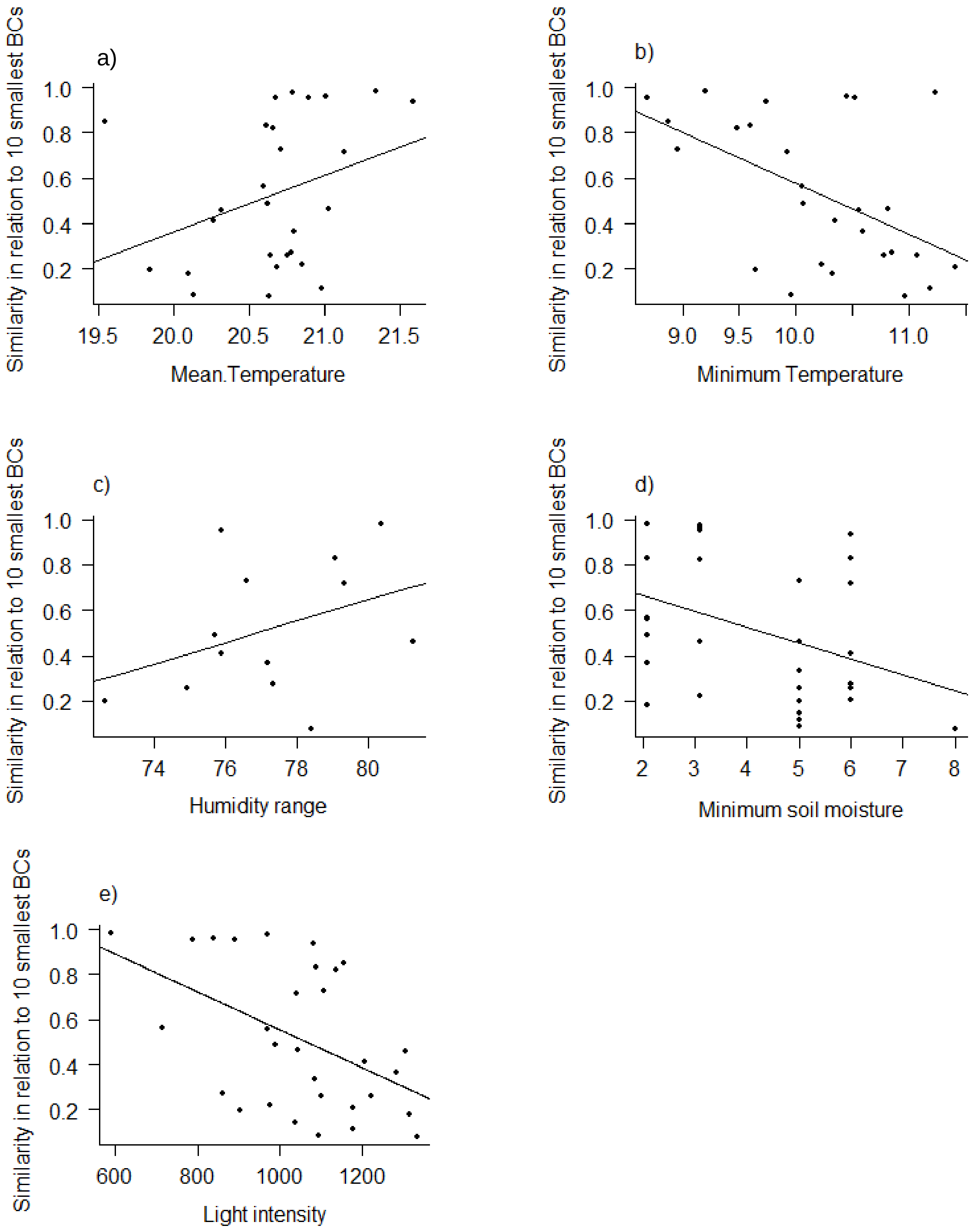


FIGURE 3.3 Partial residual plots illustrating the relationships between environmental variables and similarity in species composition. Similarity is quantified as the average Morisita-Horn index of similarity in species composition between each of the 30 largest bush clumps with the 10 smallest bush clumps. Similarity was used as a response variable and environmental variables (mean and minimum temperature, the range of relative humidity, minimum soil moisture and light intensity difference) as predictors. The panels show how similarity in tree species composition is related to a) mean temperature (R^2 = 0.10), (b) minimum temperature (R^2 = 0.25), (c) range of relative humidity (R^2 = 0.13), (d) minimum soil moisture (R^2 = 0.12), and (e) light intensity difference (R^2 = 0.20). The y-axis can be

interpreted as small bush clumps illustrating high similarity to the 10 smallest bush clumps (high similarity values on the y-axis) whereas large bush clumps would share low similarity with the 10 smallest bush clumps (low similarity values on the y-axis). BCs = bush clumps.

The proportion of forest species significantly increased with an increase in bush clump size ($R^2 = 0.15$, $z = 4.41$, $P = 1.03e\text{-}05$; Fig. 3.4a; Table B7, Appendix B), while the proportion of founder species decreased ($R^2 = 0.61$, $z = 4.33$, $P = 1.48e\text{-}05$; Fig. 3.4b; Table B7, Appendix B). Furthermore, the community-weighted mean of a) tree forest specialization ($R^2 = 0.22$, $F(38,39) = 10.88$, $P = 2.12e\text{-}03$; Fig 3.5a; Table B8, Appendix B) and, b) sapling forest specialization ($R^2 = 0.10$; $F(38,39) = 4.24$, $P = 4.63e\text{-}02$; Fig 3.5b; Table B8, Appendix B) increased with bush clump size. Tree forest specialization did not significantly differ between small bush clumps, large clumps and savanna trees ($F(2, 199) = 2.34$, $P = 9.90e\text{-}02$) (Fig. 3.5c).

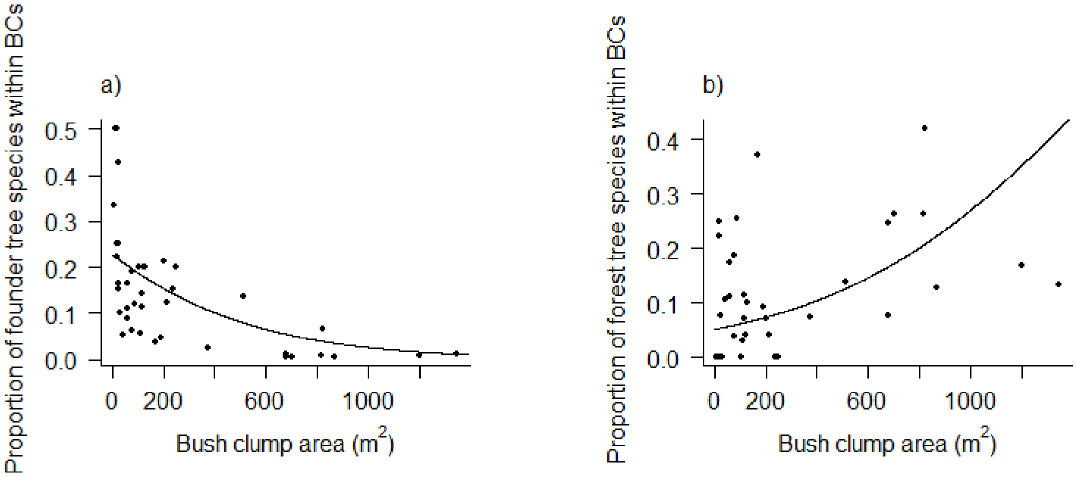


FIGURE 3.4 Relationship between bush clump area and (a) the proportion of founder tree species ($R^2 = 0.61$), and (b) the proportion of forest tree species ($R^2 = 0.15$). Founder trees were identified as those species that most likely initiated a bush clump whereas forest species were identified using field guides. BCs, bush clumps.

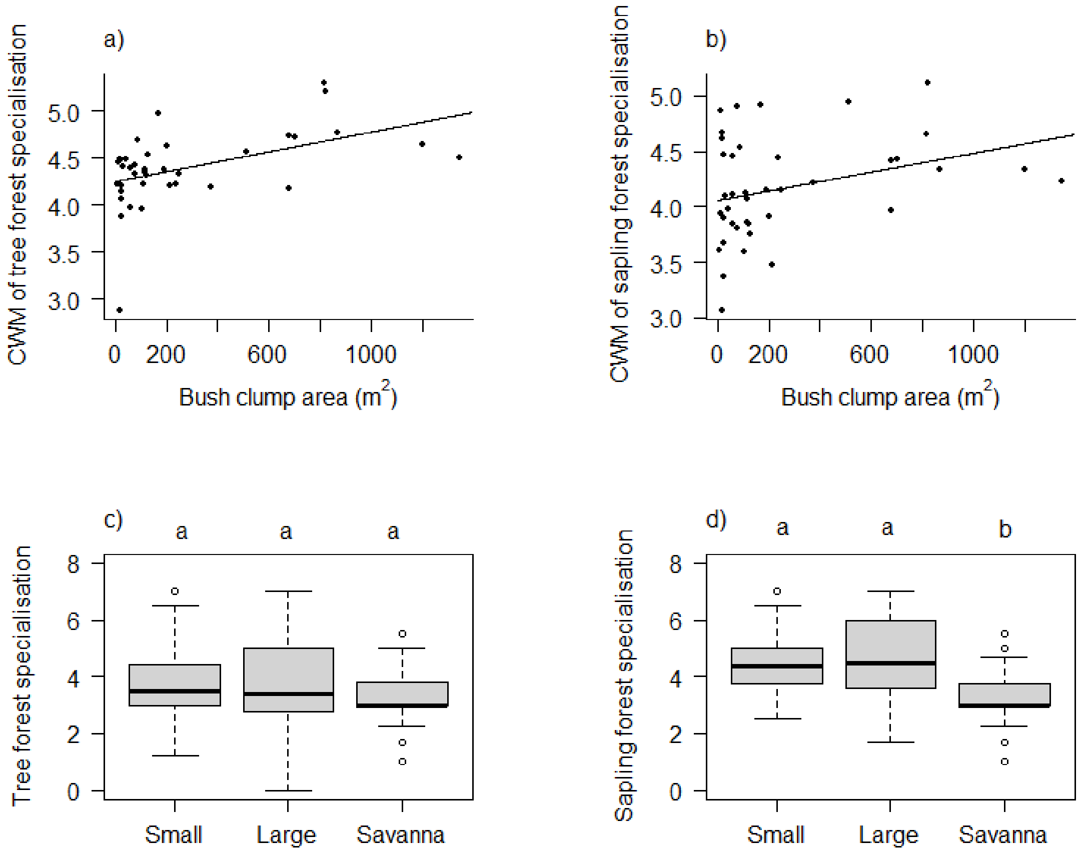


FIGURE 3.5 Forest specialization of species in different sized bush clumps. (a) Results of a generalized linear model illustrating how the community-weighted mean of forest specialization of trees changes with bush clump size (R^2 = 0.22). (b) Changes in the community-weighted mean of forest specialization of saplings with bush clump size as derived from a generalized linear model (R^2 = 0.10). (c) Boxplots showing forest specialization of trees in small bush clumps, large bush clumps and in the surrounding savanna, respectively. (d) Boxplots showing forest specialization of saplings in small bush clumps, large bush clumps and in the surrounding savanna, respectively. The boxplots illustrate the lower (Q1) and upper (Q3) quartiles. The plots also illustrate the mean observation for forest specialization. Different letters represent significant differences. Data falling outside of the Q1-Q3 range are plotted as outliers. Abbreviations are as follows: Small = small bush clumps; large = large bush clumps; Savanna = surrounding savanna.

Species with narrow habitat breadths were expected to be more common in large clumps. However, the community-weighted mean of habitat breadth of both trees (R^2 = 0.03, *F*(38,39) = 0.15, *P* = 6.98e-01; Table B8, Appendix B) and saplings (R^2 = 0.03, *F*(38,39) = 1.26, *P* = 2.68e-01; Table B8, Appendix B) showed no relationship with bush clump size. The mean habitat breadth of trees (*F*(2, 198) = 2.69, *P* = 7.00e-02) and saplings (*F*(2, 191) = 1.61, *P* = 2.04e-01) did not differ between small bush clumps, large bush clumps and the savanna group. The average habitat breadth of trees within the bush clumps was 4.505 (± 1.367), indicating that many species are generalist species that can withstand a variation of habitat types.

The Boral analysis indicated where species occurred along the bush clump successional gradient (Table B3). Examples of species identified as savanna species included *Tarchonanthus trilobus* (-1.129) and *Vangueria infausta* (-0.562), whereas examples of forest species included *Keetia gueinzii (*0.326) and *Pavetta gracifolia* (0.362).

It is evident that across Buffelskloof Private Nature Reserve, fleshy-fruited species are dominant. Of the different categories of tree species (founder species vs. bush clump constituents), fleshy fruited species were the most common, though the proportion of fleshy-fruited species was higher for bush clump species than for founder species (Figure 3.6).

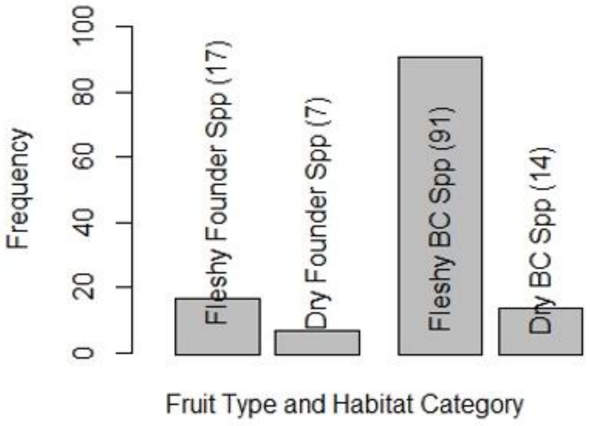


FIGURE 3.6 Frequency of fleshy- vs dry-fruited species represented by the different tree habitat categories, namely founder species and bush clump constituents. "Spp" stands for species. The frequency of each fruit type represented within each habitat category is given in brackets.

The proportion of fleshy-fruited tree species did not increase with an increase in bush clump size (R^2 = 0.01, z = 0.005, P = 0.996; Fig. 3.7a, Table 1), while the proportion of fleshy-fruited sapling species significantly decreased as clump size increased (R^2 = 0.12, z = 4.33, P = 0.011; Fig. 3.7b, Table B9).

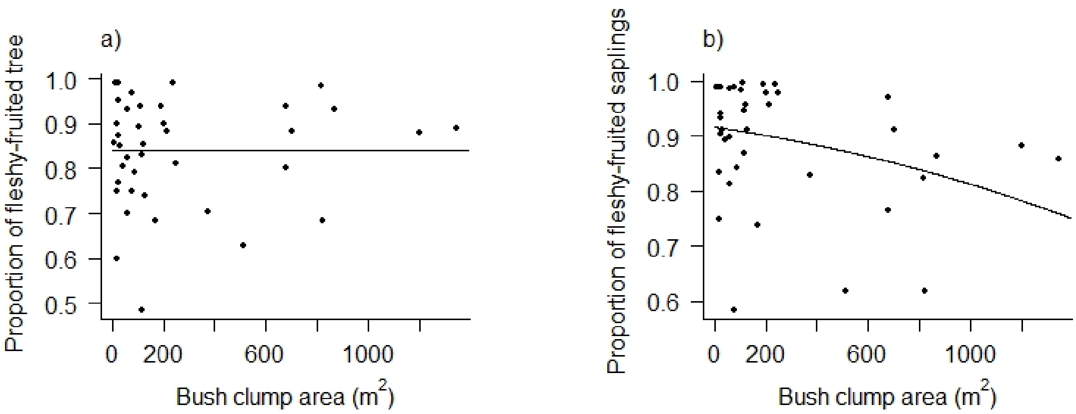


FIGURE 3.7 Relationship between bush clump area and (a) the proportion of fleshy-fruited tree species (R2 = 0.01), and (b) the proportion of fleshy-fruited sapling species (R2 = 0.12).

In contrast to expectation, the average maximum height of trees did not increase as bush clump area increased (R^2 = 0.012, *F*(38,39) = 121.94, P = 0.502; Fig. 3.8, Table B10).

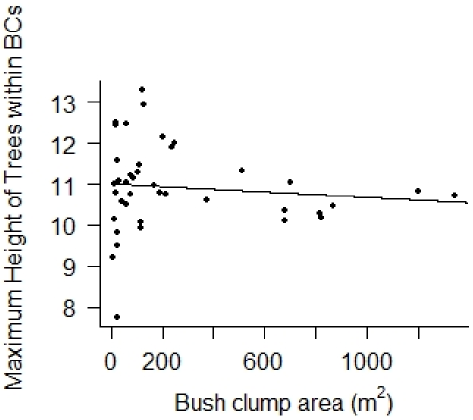


FIGURE 3.8 Results from generalised linear model testing the relationship between bush clump area and the average maximum height of tree species within a clump (R2 = 0.012).

Discussion

Our results suggest that woody encroachment within Buffelskloof Private Nature Reserve is initiated by the establishment of a founder individual which then facilitates the establishment of other species, resulting in a directional change towards forest-type species in larger and older bush clumps. This change in species composition is apparently driven in part by alterations in microclimatic environmental conditions as the bush clump develops and vegetation thickens. Furthermore, as species composition changes, functional traits associated with these species (e.g., canopy traits) change which further influences changes within the microclimate of the clumps (e.g., see Charles-Dominique, et al., 2018). Within Buffelskloof Private Nature Reserve, these clumps tend to culminate in closed vegetation community, anagolous to a forest system. The likely drivers of these clumps within the reserve include the loss of large herbivores within the area, lower intensity fires (local drivers associated with altered land use practices) as well as altered atmospheric CO_2 levels (likely global driver).

The similarity in species composition between saplings of small bush clumps and trees of large bush clumps was higher than the similarity between trees of small bush clumps and trees of large bush clumps, suggesting that saplings arising from the seed bank of small bush clumps grow to become the large trees in large bush clumps. This is an indication of deterministic succession. Whether a successional trajectory follows a directional path can be affected by factors such as dispersal constraints, site conditions, and disturbance intensity (Cramer, 2007, Norden et al., 2009, Meiners et al., 2015, Chang & Turner, 2019). In particular, a barrier to dispersal or variation in dispersal ability (Dent, DeWalt & Denslow, 2013) may lead to spatial aggregation, increasing dissimilarity in species composition between adjacent sites. However, this does not seem to apply within this study system. Here, the Afrotemperate forest and savanna biomes exist in close proximity (average distance between each of the 40 bush clumps and the forest edge was 188 ± 91 m with a range of 363 m) and most bush clump species are fleshy-fruited (Jamison et al., 2017), suggesting an endozoochoric dispersal mechanism (Sinnott-Armstrong et al., 2018). Therefore, dispersal from the forest (seed source) to founder trees, which provide perches and shade for avian and mammalian (e.g., baboon) dispersers, is unlikely to be prevented. Seeds that germinate beneath the canopy of founder trees then lead to further expansion of the clumps (Bews, 1917, O'Connor & Chamane, 2012).

Our study highlights the importance of multiple environmental factors for the deterministic development of bush clumps within a savanna system as changes in species composition were accompanied by changes in microclimate (temperature, relative humidity, soil moisture) and light availability. Larger clumps had lower mean temperatures and higher minimum temperatures. Warmer temperatures increase seedling growth rates, which can allow seedlings to escape the fire trap more rapidly (Wakeling, Cramer & Bond, 2012). Bush clumps also had a regulating effect on humidity, i.e., variability in humidity decreased with clump size, and this was associated with a change in species composition. Higher stability in humidity reduces evapotranspiration rates beneath the canopy while simultaneously increasing the moisture content (Jarvel & O'Connor, 1999). Moreover, increased soil moisture in larger clumps, possibly related to decreased evaporation under denser canopies in large clumps (Zhu et al., 2013), favours the establishment of forest trees (Pastor & Post, 1986). Lastly, lower light intensity differnece, as found in larger bush clumps, is an important compositional driver during succession as late-successional species, which usually possess tough, long-lived leaves that efficiently utilize light and are slow-growing and shade-tolerant, are best suited to such conditions (Bazzaz & Pickett, 1980, McCulloh et al., 2011). Thus, the change in community composition of the bush clumps is characterized by those species that can reach the bush clump, establish and persist under the particular environmental and ecological conditions of the clumps (Peterson & Carson, 2008).

Changes in these environmental drivers with increasing bush clump size suggest that directional changes in species composition in bush clumps are brought about by autogenic processes (Archer et al., 1988, O'Connor & Chamane, 2012); changes in the microclimate of the bush clumps form a positive feedback system allowing the persistence and expansion of the clumps. Early successional species establish poorly in late successional stages where resources have been altered (Pacala & Rees, 1998) by the bush clump canopy. Instead, early successional species are replaced with late successional species which are adapted to new levels of resources such as reduced light intensity (Pacala & Rees, 1998). Therefore, species composition moved towards more forest-type species as clumps got larger.

While many bush clump studies subjectively infer deterministic succession (Bews, 1917, Archer et al., 1988, Archer, 1990), few empirically test this process (though see O'Connor & Chamane, 2012). Our study shows empirical evidence for directional change in species composition with succession, even in a system where the potential tree species pool is large (the 1500 ha reserve supports 216 woody species, see Buffelskloof Nature Reserve (2020)). Additionally, our study system differed from most others (except Bews (1917)) in that the clumps were initiated by several species rather than a single species (Table B3, Appendix B). While founder trees grew in a matrix of grasses, several founder species were not typical savanna species but rather forest edge species (Table B3, Appendix B). Nevertheless, founder trees were not associated with termite mounds, rocky areas, or any other features that apparently promote the establishment of these trees. Thus, the specific factors allowing trees to establish in a grassy matrix remain to be understood (but see, e.g., Flake et al. 2021). Additionally, what drives tree seedlings to establish under these species and not under most ‘true’ savanna species in the landscape (e.g., *Pterocarpus angolensis*, *Combretum molle*, and *Heteropyxis natalensis*) remains unknown. Possible reasons for this may be attributed to the following: 1) these “true” savanna species are less favoured as perches by fruit dispersing vertebrates which leads to less dispersal of seeds under these individuals, 2) the microclimate conditions under these species are less suitable for seedling establishment and survival than that compared to founder species, and 3) these species may produce a germination inhibitor that prevents other species from establishing under the canopy (as is postulated for *Pterocarpus angolensis* (John Burrows pers. comm.).

The average habitat breadth of species in bush clumps showed no trend with succession. We suggest that this is because savanna species are also specialists. Savanna systems, like other grassy ecosystems, have distinct suites of species that are adapted to the unique conditions and disturbances that are integral to savanna ecosystems (Bond & Parr, 2010). This also supports the result that several species can be ranked according to the stage of succession in which they are most likely to occur (Table B7, Appendix B). It is likely that across bush clump succession stages (e.g., small clumps vs large clumps and savanna trees vs forest trees), most species are specialists, but each habitat (i.e., small vs large clump) contains a mix of strategies resulting in an average habitat breadth across the successional gradient. Although the bush clumps within Buffelskloof Private Nature Reserve culminated in forest species, elucidating on forest expansion, it should be noted that not all bush clumps are associated with forest expansion. Indeed, bush clumps can often develop on fire refugia such as termite mounds and/or rocky outcrops, although this was not the case for our study system (O’Connor et al., 2012, Aide et al., 2023).

Forest–savanna boundaries are generally determined by natural disturbances (e.g., fire and herbivory) characteristic of savanna biomes but absent from forest biomes (Hoffmann, Orthen & Franco, 2004). In the absence, or reduced frequency or intensity of these disturbances, the savanna biome can switch to forest (Sankaran, Ratnam & Hanan, 2008). Adaptations of savanna trees, e.g., deciduousness, thick bark, resprouting mechanisms, allow them to persist within disturbance-driven savannas (Joubert, Smit & Hoffman, 2012). In comparison, forest trees are generally fire-sensitive and less resistant to water stress (Hoffmann, 2000, Hoffmann, Orthen & Franco, 2004). Consequently, forest saplings are scarcely found within savannas (Hoffmann et al., 2012). However, within the sheltered microclimate of a bush clump, forest trees are protected from fire and can outcompete savanna saplings as they have denser foliage (Hoffmann et al., 2012) and are more shade tolerant (Montgomery & Chazdon, 2001). We propose that 1) there is a suppression of flammable grasses within the clumps thus reducing the incidence of fire beneath the clump canopy (e.g., Charles-Dominique, et al., 2018), and/or 2) that the low flammability of trees compared to grasses keeps fire out of bush clumps and lowers fire intensity at the edge of bush clumps (O'Connor & Chamane, 2012), thus enabling bush clump persistence, and, in the case of infrequent or cool fires, expansion and concomitant species have turnover within the sub-canopy of the bush clumps. Once forest species have established, development towards canopy closure is faster than if only savanna species were present (Hoffmann et al., 2012) because forest trees have higher leaf area, which translates into denser crowns (Gotsch et al., 2010) and reduced light levels (Schönbeck et al., 2015).

It was expected that the proportion of fleshy-fruited species (trees and saplings) would increase as bush clump size increased. However, the proportion of fleshy-fruited tree species did not change significantly with succession, whereas the proportion of fleshy-fruited sapling species decreased as bush clump size increased. The increase in dry-fruited species as clump size increased may be related to their dispersal mechanisms. Many dry-fruited species are dispersed by animals, especially vertebrates (Howe & Smallwood, 1982, Wheelwright, 1985). As clumps get larger, they may be more frequented by animals (especially vertebrates) that use these areas as a refuge. This increase in animal activity may increase the abundance and diversity of dry-fruited species within the canopy of the bush clumps. The increase in dry-fruited species is attributed to an increase in two species in particular, namely Senegalia ataxacantha and Dalbergia armata. The forest specialisation values for these species were 4 and 6.5 respectively (Table B3), i.e., Senegalia ataxacantha is a generalist and Dalbergia armata is forest specialist with a liane growth form, preferring closed habitats. The favourable microclimate beneath the bush clump canopy enables the germination and establishment of these species within the clumps. As competition for light increases, particularly within environments in which light is a limiting factor, the maximum height of trees was expected to increase with succession (Vile, Shipley & Garnier, 2006, Navas et al., 2010). However, within the bush clumps, maximum tree height showed no trend as clump size increased.

As competition for light increases, particularly within environments in which light is a limiting factor, the maximum height of trees is expected to increase with succession (Vile, Shipley & Garnier, 2006, Navas et al., 2010). However, within the bush clumps, maximum tree height showed no trend as clump size increased.

Environmental filtering exerts pronounced pressure on the selection of functional traits displayed in plant communities; different abiotic conditions require varying sets of traits to establish and persist in a particular environment (Cornwell & Ackerly, 2010). Therefore, as succession progresses and abiotic (and biotic) conditions change, species can be replaced by others whose traits enable them to be better adapted to the environmental conditions that are experienced at the various stages of succession (Huston & Smith, 1987, Douma et al., 2012b, Prach & Walker, 2020). Thus, it was expected that functional traits would change consistently over succession. The lack of consistency in trait change here elucidates on whether consistent trends occur across successional patterns and whether these trends can be used to infer on community assembly processes.

As approximately 25% of the Earth’s land surface is comprised of savanna biomes, a better understanding of how woody encroachment proceeds is of global importance (Wigley, Bond & Hoffman, 2010, Parr et al., 2012, Chapin, Sala & Huber-Sannwald, 2013, Stevens et al., 2017). Woody encroachment alters the species composition and therefore significantly contributes to biodiversity degradation in savanna ecosystems. Deterministic succession is often seen as a process leading to a “climax” system (Horn, 1974, Guariguata & Ostertag, 2001, Nuñez, Chazdon & Russo, 2019). In our case, the “climax system” (forest) replaces an ancient landscape with unique diversity and important ecosystem services and biodiversity (Greiner, Gordon & Cocklin, 2009). Therefore, in this case, management methods should incorporate natural disturbances (such as frequent and hot fires) that minimize opportunities for the environmental conditions associated with the climax system to occur. With such management interventions, savannas could be conserved, and the characteristic biodiversity of these ecosystems can be maintained.

Appendix B

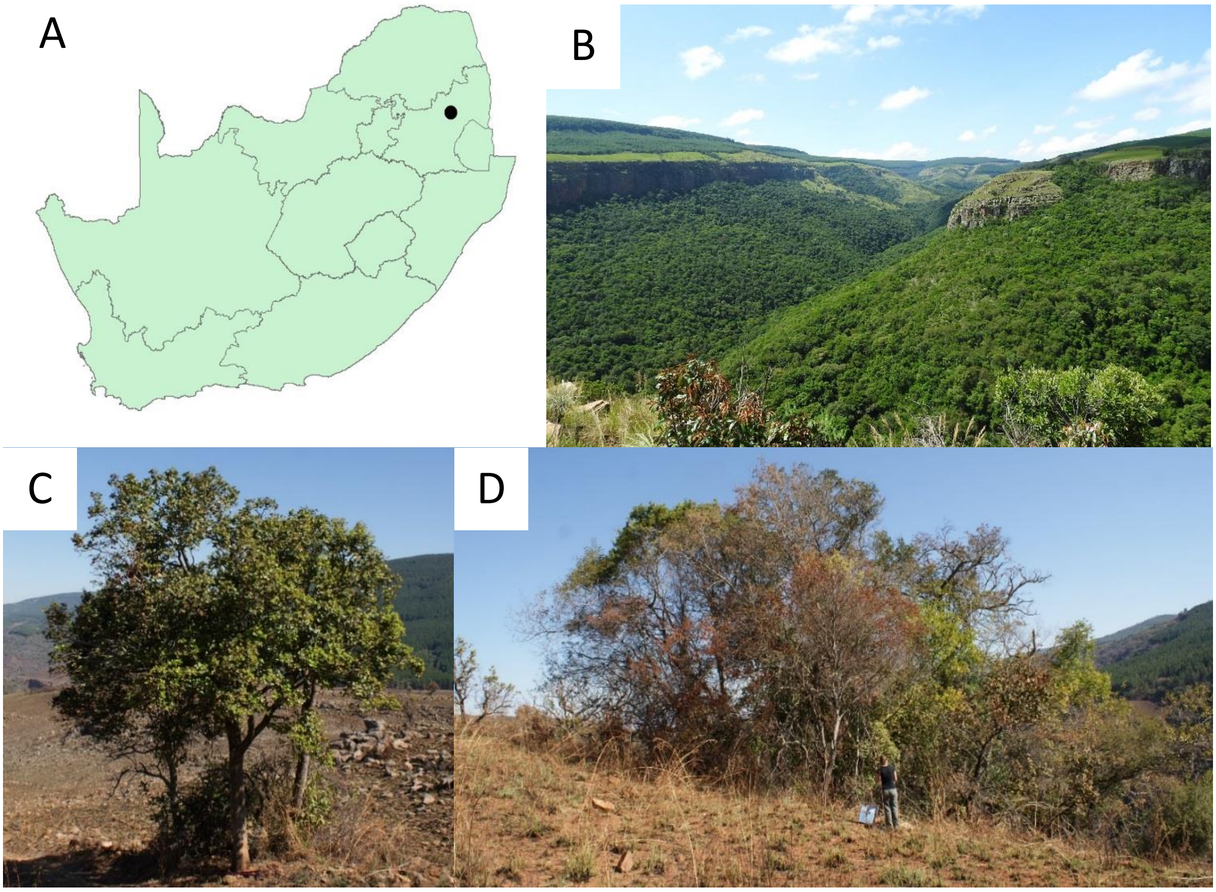


FIGURE B1. Images of a) a map illustrating where Buffelskloof Private Nature Reserve (black dot) is located in South Africa, b) the study site (including a section of the indigenous forested valley surrounded by grassy vegetation types), c) a small bush clump (approximately 61.827 m^2), and d) a large bush clump (approximately 1342.999 m^2) found at Buffelskloof Private Nature Reserve. Bush clumps surveyed in this study ranged in size from 10.053 m^2 to 1342.999 m^2.

Table B1 Table indicating which environmental variables were collected for each bush clump. A tick indicates that the respective environmental variables were measured for that clump, whereas a cross indicates that data (e.g., an ibutton) was recorded as faulty or lost on collection.

Bush clump	Basal Area (m^2)	Temperature	Relative humidity	Soil moisture	Light intensity Difference
BC01	2.398	✓		✓	✓
BC02	0.315	✓		✓	✓
BC03	0.782	X		✓	✓
BC04	2.299	✓		✓	✓
BC05	1.330	X		✓	✓
BC06	1.384	✓	✓	✓	✓
BC07	3.505	X		✓	✓
BC08	4.459	✓	✓	✓	✓
BC09	1.526	✓		✓	✓
BC10	2.382	✓		✓	✓
BC11	0.360	✓		✓	✓
BC12	2.605	✓	✓	✓	✓
BC13	5.635	✓		✓	✓
BC14	1.673	✓		✓	✓
BC15	0.440	✓	✓	✓	✓
BC16	2.953	✓	✓	✓	✓
BC17	0.246	✓		✓	✓
BC18	20.403	✓	✓	✓	✓
BC19	2.050	✓	✓	✓	✓
BC20	13.160	✓		✓	✓
BC21	0.330	✓	✓	✓	✓
BC22	15.514	X		✓	✓
BC23	5.524	✓	✓	✓	✓
BC24	1.800	✓		✓	✓
BC25	0.815	✓		✓	✓
BC26	0.598	✓	✓	✓	✓
BC27	26.070	✓		✓	✓
BC28	3.098	✓	✓	✓	✓
BC29	7.988	✓	✓	✓	✓
BC30	14.177	✓	✓	✓	✓
BC31	1.883	✓		✓	✓

Bush clump	Basal Area (m^2)	Temperature	Relative humidity	Soil moisture	Light intensity Difference
BC32	30.221	✓		✓	✓
BC33	17.524	✓	✓	✓	✓
BC34	0.235	✓	✓	✓	✓
BC35	1.293	✓		✓	✓
BC36	3.368	✓		✓	✓
BC37	12.038	✓	✓	✓	✓
BC38	3.691	✓		✓	✓
BC39	1.603	✓		✓	✓
BC40	1.613	✓	✓	✓	✓

TABLE B2 Pearson's correlation coefficients between environmental variables used to test if the average similarity index of each bush clumps was associated with environmental conditions of the bush clumps. For temperature, relative humidity and soil moisture, the mean, range, maximum, minimum and coefficient of variation were calculated. Light intensity differncewas calculated as the difference in light intensity difference between inside and outside of a bush clump. Maximum relative humidity was excluded from analyses as all ibuttons reached a maximum humidity of 100%. Shaded cells indicate variables that were retained for analyses.

		Soil moisture					**Light intensity**	**Temperature**					**Relative humidity**			
		Range	Mean	Maximum	Minimum	Coefficient of variation	Difference	Range	Mean	Maximum	Minimum	Coefficient of variation	Range	Mean	Minimum	Coefficient of variation
Soil moisture	Range	1	0.41	0.64	0.09	0.55	-0.01	-0.14	0.15	-0.03	0.67	-0.10	0.07	0.06	-0.07	0.05
	Mean	0.41	1	0.94	0.92	-0.4	0.31	-0.11	0.27	-0.04	0.41	0.12	-0.28	0.05	0.28	-0.24
	Maximum	0.64	0.94	1	0.82	-0.14	0.18	-0.15	0.22	-0.06	0.52	0.05	-0.14	0.02	0.14	-0.16
	Minimum	0.09	0.92	0.82	1	-0.59	0.33	-0.07	0.19	-0.08	0.01	0.23	-0.35	-0.04	0.35	-0.35
	Coefficient of variation	0.55	-0.4	-0.14	-0.59	1	0.51	0.15	-0.01	0.17	0.10	-0.04	-0.08	-0.18	0.08	0.10
Light intensity	Difference	-0.01	0.31	0.18	0.33	0.51	1.00	-0.03	0.16	0.04	0.45	-0.26	-0.11	0.06	0.11	-0.18
Temperature	Range	-0.14	-0.11	-0.15	-0.07	0.15	-0.03	1	0.43	0.98	-0.51	0.78	0.20	-0.45	-0.20	0.19
	Mean	0.15	0.27	0.22	0.19	-0.01	0.16	0.43	1	0.51	0.19	0.44	-0.06	-0.15	0.06	-0.10
	Maximum	-0.03	-0.04	-0.06	-0.08	0.17	0.04	0.98	0.51	1	-0.35	0.72	0.21	-0.42	-0.21	0.18
	Minimum	0.67	0.41	0.52	0.01	0.10	0.45	-0.51	0.19	-0.35	1	-0.6	0.04	0.27	-0.04	-0.11
	Coefficient of variation	-0.10	0.12	0.05	0.23	-0.04	-0.26	0.78	0.44	0.72	-0.6	1	-0.14	-0.37	0.14	-0.02
Relative humidity	Range	0.07	-0.28	-0.14	-0.35	-0.08	-0.11	0.20	-0.06	0.21	0.04	-0.14	1	-0.66	-1	0.89
	Mean	0.06	0.05	0.02	-0.04	-0.18	0.06	-0.45	-0.15	-0.42	0.27	-0.37	-0.66	1	0.76	-0.77
	Minimum	-0.07	0.28	0.14	0.35	0.08	0.11	-0.20	0.06	-0.21	-0.04	0.14	-1	0.76	1	-0.89
	Coefficient of variation	0.05	-0.24	-0.16	-0.35	0.10	-0.18	0.19	-0.10	0.18	-0.11	-0.02	0.89	-0.77	-0.89	1

NOTE: We tested if the average similarity index calculated between each large bush clump and the ten smallest bush clumps (see Methods) was associated with the environmental conditions (temperature, relative humidity, soil moisture and light intensity difference) of the respective large bush clump. We hypothesized that both measures of central tendency, extremes and variation in environmental conditions could affect successional gradients (O'Connor & Chamane, 2012). Therefore, the mean, range, maximum, minimum and coefficient of variation of temperature, relative humidity and soil moisture were calculated. Because only one mean measure of light intensity difference was calculated, no measures of central tendency, extremes and variation were considered for this variable. Environmental measures had different sample sizes due to limited availability of hygrobuttons (humidity) and damaged or lost ibuttons (temperature: n = 27, relative humidity: n = 13, soil moisture: n = 30, light intensity difference: n = 30). A correlation matrix of the mean, median, range, coefficient of variation, minimum and maximum for temperature, relative humidity and soil moisture and light intensity difference was generated to test for collinearity amongst these variables (Table B2). After excluding highly correlated variables ($r > 0.7$), the variables that remained and thus used in further analyses were: mean and minimum temperature, the range of relative humidity, minimum soil moisture and light intensity.

TABLE B3 List of tree species and their habitat preferences in the Buffelskloof Private Nature Reserve, South Africa. Depicted in the table are forest specialization values and habitat breadths calculated for each of the species (compare Table B4). Founder species were identified as those species that initiated a bush clump. Forest species were classified according to field guides as those species that only occurred in forest-type habitats. An asterisk (*) indicates whether the species was identified as a savanna species (i.e., not found in either the bush clumps or forested valley of the reserve but rather within the surrounding grassy matrix between bush clumps) and/or found within the 40 bush clumps (BCs) sampled in this study. Median Boral values indicate the results from the Boral analysis that was implemented using the sapling data (see Figure B2). As such only species that were found as saplings and present in more than 10 clumps) have values presented. More negative numbers indicate a preference for younger bush clumps, whereas more positive values indicate a preference for more mature bush clumps. Species are ranked based on where they are most likely be found along the successional gradient; thus, species most likely to be found in larger bush clumps (which have larger associated basal areas) are expected to be more 'forest' type species, whereas species most likely to be found in the smaller bush clumps (with smaller associated basal areas) are expected to be more savanna type species.

Species	**Forest specialization**	**Fleshy-/ Dry-fruited**	**Habitat breadth**	**BC species**	**Founder species**	**Forest species**	**Median Boral values**
Acalypha glabrata	4.67	Fleshy	5	*			
Allophylus africanus	5	Fleshy	5	*			
Aloe arborescens	2.67	Fleshy	5				
Aloe marlothii	3	Fleshy	5				
Annona senegalensis	3.5	Fleshy	6				
Apodytes dimidiata	4	Fleshy	4	*			0.128
Berchemia zeyheri	3	Fleshy	5	*			
Brachylaena rotundata	3	Dry	5				
Brachylaena transvaalensis	4.5	Dry	4	*			
Canthium inerme	4	Fleshy	4	*			0.030
Canthium mundianum	5	Fleshy	5	*			0.108
Carissa bispinosa	5	Fleshy	3	*			0.200
Cassinopsis ilicifolia	6.5	Fleshy	6	*		*	
Cassipourea gerrardii	6.5	Fleshy	6	*		*	
Celtis africana	3.86	Fleshy	1	*			0.063
Cephalanthus natalensis	5	Fleshy	5	*	*		
Chaetachme aristata	4.4	Fleshy	3	*			

Species	**Forest specialization**	**Fleshy-/ Dry-fruited**	**Habitat breadth**	**BC species**	**Founder species**	**Forest species**	**Median Boral values**
Chionanthus foveolatus subsp. *foveolatus*	6.5	Fleshy	6	*		*	
Choristylis rhamnoides	6.5	Fleshy	6	*		*	
Clausena anisata	5.67	Fleshy	5	*			
Clerodendrum glabrum	4	Fleshy	3	*			
Combretum erythrophyllum	3.5	Dry	6				
Combretum kraussii	5.67	Dry	5	*	*		0.148
Combretum molle	3	Dry	5	*	*		0.056
Combretum zeyheri	3	Dry	5	*	*		
Coptosperma supra-axillare	3.75	Fleshy	4				
Crotolaria capensis	5.5	Dry	6				
Crypolepis oblongifolia	3.33	Dry	5	*			
Cryptolepis cryptolepioides	1.67	Dry	5	*			
Cussonia natalensis	3	Fleshy	5	*			
Cussonia paniculata var. *sinuata*	3	Fleshy	5				
Cussonia spicata	3.75	Fleshy	4	*	*		
Cyathea dregei	3	Dry	6				
Dalbergia armata	6.5	Dry	6	*		*	0.190
Dichrostachys cinerea subsp. *africana*	3.5	Dry	6				
Diospyros lycioides subsp. *guerkei*	3.5	Fleshy	5	*			
Diospyros lycioides subsp. *sericea*	3.5	Fleshy	4				
Diospyros whyteana	3.33	Fleshy	5	*			0.153
Dombeya pulchra	4.33	Dry	5	*			
Dombeya rotundifolia	3.5	Dry	6	*			
Dovyalis lucida	7	Fleshy	7	*		*	
Dovyalis zeyheri	3.75	Fleshy	4	*			
Ehretia rigida	2.67	Fleshy	5	*			
Ekebergia pterophylla	5	Fleshy	5	*	*		0.037

Species	**Forest specialization**	**Fleshy-/ Dry-fruited**	**Habitat breadth**	**BC species**	**Founder species**	**Forest species**	**Median Boral values**
Empogona lanceolata	4	Fleshy	2	*			
Englerophytum magalismontanum	5	Fleshy	5	*	*		0.078
Erythrina lysistemon	3.5	Fleshy	4				
Erythroxylum delagoense	2.83	Fleshy	2	*			
Erythroxylum emarginatum	6	Fleshy	5	*		*	
Euclea crispa subsp. *crispa*	3	Fleshy	3	*	*		0.090
Euclea natalensis subsp. *natalensis*	4	Fleshy	1	*			0.234
Eugenia natalitia	7	Fleshy	7	*	*		
Euphorbia cooperi	3	Fleshy	5				
Euphorbia ingens	3	Fleshy	5				
Faurea rochetiana subsp. *speciosa*	2.33	Dry	5				
Faurea saligna	3	Dry	5	*	*		
Ficus burkei	3	Fleshy	5	*			
Ficus glumosa	3	Fleshy	5				
Ficus ingens	2.25	Fleshy	4				
Ficus salicifolia	3	Fleshy	5				
Ficus sur	4.5	Fleshy	4	*	*		
Grewia occidentalis	5	Fleshy	3	*			0.101
Gymnosporia buxifolia	3	Fleshy	1	*			
Gymnosporia harveyana	5.5	Fleshy	4	*		*	
Halleria lucida	4.2	Fleshy	3	*			
Harpephyllum caffrum	7	Fleshy	7	*		*	
Heteromorpha arborescens var. *abyssinica*	3.75	Dry	4	*			
Heteropyxis natalensis	4.25	Dry	4	*	*		
Hippobromus pauciflorus	6	Fleshy	5	*			0.171
Hyperacanthus amoenus	4.67	Fleshy	5				
Ilex mitis	7	Fleshy	7	*		*	

Species	**Forest specialization**	**Fleshy-/ Dry-fruited**	**Habitat breadth**	**BC species**	**Founder species**	**Forest species**	**Median Boral values**
Indigofera swaziensis	2.67	Dry	5				
Keetia gueinzii	6.5	Fleshy	6	*		*	
Lannea discolor	3	Fleshy	5				
Lopholaena coriifola	1.67	Fleshy	5				
Maerua cafra	5	Fleshy	5	*			
Maesa lanceolata	3.6	Fleshy	3	*	*		
Maytenus peduncularis	6	Fleshy	6	*		*	0.118
Maytenus undata	4.4	Fleshy	3	*			
Mimusops obovata	5.33	Fleshy	5	*			
Morella microbracteata	3	Fleshy	6				
Morella pilulifera	2.67	Fleshy	5	*			
Morella serrata	3	Fleshy	6				
Mundulea sericea	3	Fleshy	5				
Myrsine Africana	4	Fleshy	3	*			0.105
Nuxia congesta	3.2	Fleshy	3				
Obetia tenax	3	Fleshy	5				
Ochna holstii	5	Fleshy	5	*		*	0.248
Ochna natalitia	2.75	Fleshy	4	*			0.069
Olea europaea subsp. *africana*	3	Fleshy	5				
Osyris lanceolata	4	Fleshy	3	*			
Pappea capensis	3.33	Fleshy	5	*			
Pavetta cooperi	4.5	Fleshy	6	*			0.238
Pavetta edentula	3	Fleshy	5				
Pavetta eylesii	3	Fleshy	5				
Pavetta gardeniifolia var. *subtomentosa*	3	Fleshy	5	*			0.165
Pavetta gracilifolia	3	Fleshy	3	*			
Peddiea africana	6.5	Fleshy	5	*		*	

Species	**Forest specialization**	**Fleshy-/ Dry-fruited**	**Habitat breadth**	**BC species**	**Founder species**	**Forest species**	**Median Boral values**
Peltophorum africanum	3.5	Dry	6				
Phylica paniculata	3.75	Dry	4				
Pittosporum viridiflorum	4.5	Fleshy	2	*			0.076
Pleurostylia capensis	6	Fleshy	5	*			0.231
Protea caffra subsp. *caffra*	2.5	Fleshy	6				
Protea gaguedi	2.25	Fleshy	4				
Protea roupelliae subsp. *roupelliae*	1.67	Fleshy	5	*			
Psychotria capensis	5	Fleshy	4	*			0.129
Psydrax obovata subsp. *Elliptica*	6	Fleshy	6	*			
Ptaeroxylon obliquum	4.67	Fleshy	5				
Pterocarpus angolensis	3	Fleshy	5				
Pterocelastrus echinatus	5	Fleshy	5	*	*		0.092
Pterocelastrus rostratus	4.5	Fleshy	6	*		*	
Rhamnus prinoides	6.5	Fleshy	6	*		*	
Rhoicissus rhomboidea	6.5	Fleshy	6	*		*	
Rhoicissus tomentosa	6.5	Fleshy	6	*		*	
Rhoicissus tridentata subsp. *cuneifolia*	3.75	Fleshy	4	*			
Rhus (Searsia) chirindensis	4.5	Fleshy	2	*	*		0.104
Rhus (Searsia) dentata	4.4	Fleshy	3	*			0.042
Rhus (Searsia) lucida	6.5	Fleshy	6	*	*		0.098
Rhus (Searsia) pentheri	2.5	Fleshy	4	*	*		0.109
Rhus (Searsia) pyroides var. *gracilis*	3.6	Fleshy	3	*	*		
Rhus (Searsia) rehmanniana subsp. *rehmanniana*	3	Fleshy	4	*			
Rhus (Searsia) tumulicola var. *meeuseana*	1	Fleshy	6				
Rhus (Searsia) tumulicola var. *tumulicola*	2.67	Fleshy	5				
Robsonodendron eucleiforme	6.5	Fleshy	6	*	*		

Species	**Forest specialization**	**Fleshy-/ Dry-fruited**	**Habitat breadth**	**BC species**	**Founder species**	**Forest species**	**Median Boral values**
Rotheca myricoides	3.33	Fleshy	5	*			
Rothmannia capensis	5	Fleshy	5	*		*	
Schefflera umbellifera	6.5	Fleshy	6	*		*	
Schrebera alata	5	Fleshy	4	*			
Scolopia mundii	4.33	Fleshy	5	*			0.093
Scolopia zeyheri	4.4	Fleshy	3	*			0.146
Scutia myrtina	6.5	Fleshy	6	*		*	
Secamone alpinii	6	Fleshy	5	*			
Senegalia ataxacantha	4	Dry	3	*	*		0.096
Senegalia caffra	2.8	Dry	3				
Solanum giganteum	3.33	Fleshy	2	*			
Strychnos henningsii	4	Fleshy	4	*			
Strychnos madagascariensis	4.67	Fleshy	5				
Strychnos spinosa	4.5	Fleshy	4				
Syzygium cordatum	4.2	Fleshy	3	*	*		0.169
Tarchonanthus trilobus	3.8	Dry	3	*	*		
Tricalysia capensis var. *transvaalensis*	7	Fleshy	7	*		*	
Trimeria grandifolia	6.5	Fleshy	6	*			
Vachellia karroo	2.33	Fleshy	5				
Vachellia nilotica subsp. *kraussiana*	3.5	Dry	6				
Vachellia sieberiana subsp. *woodiana*	2.33	Dry	5				
Vangueria infausta	3.5	Fleshy	4	*	*		
Vepris reflexa	3	Fleshy	5				
Ximenia caffra	3	Fleshy	5	*			
Zanthoxylum capense	3.75	Fleshy	4	*			0.117
Ziziphus mucronata	4	Fleshy	3	*	*		

FIGURE B2 Results of a generalized linear model illustrating the relationship between the median basal area output (generated from a Boral analysis) and the forest specialization values of saplings that were found to be present in more than 10 bush clumps (R^2 = 0.08, *F*(32,33) = 2.785, *P* = 1.05e-01).

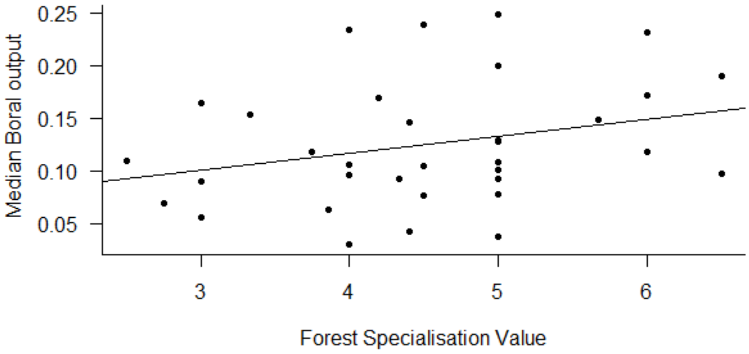


TABLE B4 An eight-class habitat gradient classification ranging from closed habitats (values close to 8) to open habitats (values close to 1). Characteristic terms used in field guide descriptions are provided for each habitat class (Coates Palgrave, 2002, Schmidt, Lotter & McCleland, 2002, Van Wyk & Van Wyk, 2013). Each tree species (compare Table B3) was scored on the habitat class/es they were reported in the literature. For species occurring in several different habitat classes, an average forest specialization score was calculated as the mean class for which the species was described (Table B3).

Habitat	Ordered gradient	Field guide descriptions
Forest	8	Mist-belt Forest, evergreen forest, Afromontane Forest, coastal forest, riverine forest, montane forest
Wooded crevices	7	Forest margins, wooded gullies/ kloofs/ ravines
Thicket	6	Riverine fringe thicket, coastal thicket/ dune bush, sand dunes/ coastal scrub, valley bushveld, Albany thicket, coastal bush
Closed woodland (mesic)	5	Thornveld, moist bushveld, bushveld, Jesse bush, low altitude woodlands
Open woodland (arid)	4	Grassy woodlands, wooded grassland, open woodland/bushveld, dry woodlands, wooded grasslands, high altitude woodlands
Rocky areas in otherwise shurbland, woodland or grassland	3	Rocky ridges, including termite mounds, mountain slopes and hillsides *Please note: rocky ridges can have quite dense woody vegetation, even in grassland areas
Open shrubland	2	Low scrub (taller forms to be placed under thicket), karroid scrub
Grasslands	1	Montane grasslands, high-altitude grasslands, grassy hillsides/mountain slopes, Highveld grassland, plateau, coastal grasslands

TABLE B5 Results of univariate generalized linear models testing the relationship between bush clump area and a) species richness (log-transformed), b) basal area, and c) the number of large trees within each bush clump. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = not significant.

	Estimate	**Std Error**	**t-value**	**R^2 value**	**p-value**
Species richness ~ Area	0.045	0.005	8.930	0.68	***
Basal area ~ Area	0.012	0.001	13.053	0.88	***
Total trees ~ Area	0.003	0.001	58.32	0.76	***

TABLE B6 Results from generalized linear models testing if environmental variables influenced the change in species composition over succession. Similarity was calculated as follows: the Morisita-Horn index of similarity in species composition between each of the 10 smallest bush clumps was calculated and averaged. This average was then compared to the similarity between each of the remaining 30 bush clumps. Similarity was used as a response variable and environmental variable measures (mean and minimum temperature, the range of relative humidity, minimum soil moisture and light intensity difference inside and outside of clumps) were used as predictor variables. NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; and *** = $p < 0.001$.

		Estimate	**Std Error**	**t-value**	**R^2**	**p-value**
Temperature	Mean	1.061	0.637	1.665	0.10	*
	Minimum	-1.004	0.361	-2.778	0.25	*
Humidity	Range	0.198	0.150	1.320	0.13	*
Soil moisture	Minimum	-0.291	0.143	-2.037	0.12	*
Light intensity difference	Range	-0.004	0.001	-2.632	0.20	**

TABLE B7 Results of beta regression models (fitted with a Gaussian distribution and log link) testing the relationships between a) the proportion of founder species across different sized bush clumps, and b) the proportion of forest species across different sized bush clumps. NS = not significant; * = p < 0.05; ** = p < 0.01; and *** = p < 0.001.

	Estimate	Std Error	t-value	R^2 value	p-value
Proportion founder species ~ Area	-0.002	0.001	-5.624	0.61	***
Proportion forest species ~ Area	0.002	0.001	4.072	0.15	***

Table B8 Results of a generalized linear model testing the relationships between a) the community-weighted mean of species forest specialization of trees with bush clump area, b) the community-weighted mean of species specialization of saplings with bush clump area, c) the community-weighted mean of habitat breadth of trees with bush clump area and d) the community-weighted mean of habitat breadth of saplings with bush clump area. NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; and *** = $p < 0.001$.

	Estimate	Std Error	t-value	R^2 value	p-value
Tree specialisation ~ Area	-0.0005	0.0001	-3.299	0.22	**
Sapling specialisation ~ Area	-0.0004	0.0002	-2.060	0.10	*
Tree habitat breadth ~ Area	-0.0002	0.0002	-1.030	0.03	NS
Sapling habitat breadth ~ Area	-0.0003	0.0002	-1.124	0.03	NS

TABLE B9 Results of beta regression models (fitted using a Poisson distribution with a log link) testing the relationships between a) the proportion of fleshy-fruited tree species across different sized bush clumps, and b) the proportion of fleshy-fruited sapling species across different sized bush clumps. NS = not significant; * = p < 0.05; ** = p < 0.01; and *** = p < 0.001.

	Estimate	**Std Error**	**t-value**	**R^2 value**	**p-value**
Proportion fleshy-fruited tree species ~ Area	0.003	0.005	0.01	0.996	NS
Proportion fleshy-fruited sapling species ~ Area	0.003	-2.532	0.12	0.114	*

TABLE B10 Results of univariate generalized linear model testing the relationship between bush clump area and the average maximum height of tree species within each bush clump. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, NS = not significant.

	Estimate	**Std Error**	**t-value**	**R^2 value**	**p-value**
Maximum Height ~ Area	-0.001	0.001	-0.677	0.012	NS

CHAPTER 4

Do plant functional traits show consistent trends across succession? A systematic review

DO PLANT FUNCTIONAL TRAITS SHOW CONSISTENT TRENDS ACROSS SUCCESSION? A SYSTEMATIC REVIEW

Abstract

Understanding successional trajectories and community assembly processes is a major objective of plant ecology. Indeed, without a clear understanding of the drivers of succession, our ability to predict how species assemblages regenerate after disturbance remains difficult. Plant functional traits, i.e., the physiological, morphological or phenological characteristics that are related to the fitness and performance of plants, can reveal the underlying mechanisms that drive species turnover across successional gradients. Trait-based approaches prove advantageous as they allow for comparisons to be drawn between the driving mechanisms of succession in different ecosystems and vegetation types. In this systematic review, I conducted a search (using the Scopus search engine) for scholarly papers, books and book chapters on how functional traits change with succession. Using the data collected, I identified six of the most frequently studied traits (namely specific leaf area (SLA), plant height, seed mass, leaf nitrogen content (LNC), photosynthetic rate/capacity and plant life span) and established the direction in which each of these functional traits changed as succession progressed. A null model approach was used to assess whether the direction of trait change with successional gradient (i.e., increase, decrease, hump-shape or valley-shape) was consistent across studies. A null model approach was also used to test for biases in growth form, geography, and vegetation type in which trait-based successional studies were conducted. Across successional gradients SLA, LNC, and photosynthetic rate/capacity decreased, whereas plant height, seed mass, and plant life span increased. Clear biases in trait studies across successional gradients were observed: woody communities were studied more often than herbaceous and combined woody and herbaceous communities; studies were biased towards Europe; and most studies were conducted in forest systems, with other biomes being consistently underrepresented. This systematic review also highlighted that aboveground traits are better represented in trait studies than belowground traits. While soft traits (i.e., morphological, or anatomical traits) are often considered to be surrogates for hard traits (i.e., physiological

traits, are used to capture a particular function of a plant), many hard traits are still in need of soft trait surrogates. Differences in the frequency of trait categories (i.e., whole-plant, leaf, stem, reproductive) investigated was also evident, with research focus directed particularly towards whole-plant traits (e.g., plant height and life span) and leaf traits (e.g., SLA, LNC and photosynthetic rate). Given that traits from different organs within a plant are postulated to be coordinated within a species allowing for adaptive changes across environmental gradients, there is a critical need to investigate how traits vary across gradients to test predictions of the plant economic spectrum (PES) for coordinated variation across axes; it is vital that the types of traits measured represent several dimensions of the PES. Our ability to generalise how traits will change with succession, over broad vegetation types and geographic regions, is thus limited to forest systems and Europe. Future research should focus on underrepresented geographic regions (i.e., within Africa) and, perhaps more importantly, vegetation types (e.g., grasslands), to improve our overall understanding of trait change, and to incorporate traits that represent different aspects of plant function.

Introduction

Understanding successional trajectories and community assembly processes is a major objective of plant ecology (Walker & del Moral, 2009, Douma et al., 2012b). Indeed, without a clear understanding of the drivers of succession, our ability to predict how species assemblages regenerate after disturbances (that result in the abrupt losses of biomass or ecological structure) remains difficult (Prach & Walker, 2011). Successional trajectories cannot be predicted from measures of species diversity and composition alone (Zhou et al., 2014, Norden et al., 2015). Indeed, how species diversity and composition changes with succession does not necessarily link assembly processes with ecological function (Piqueray et al., 2015). Plant functional traits, i.e., the physiological, morphological or phenological characteristics that are related to the fitness and performance of plants (Violle et al., 2007), can reveal the underlying mechanisms that drive species turnover across successional gradients (McGill et al., 2006). The advantage of using a trait-based approach over measuring only the taxonomic composition of species assemblages is that the driving mechanisms of succession in different ecosystems and vegetation types become comparable and universal trends can be elucidated (Díaz, Noy-Meir & Cabido, 2001, Kahmen & Poschlod, 2004, Piqueray et al., 2015).

Environmental filtering exerts pronounced pressure on the selection of functional traits displayed in plant communities; different abiotic conditions require varying sets of traits to establish and persist in a particular environment (Cornwell & Ackerly, 2010). Therefore, as succession progresses and abiotic (and biotic) conditions change, species can be replaced by others whose traits enable them to be better adapted to the environmental conditions that are experienced at the various stages of succession (Huston & Smith, 1987, Douma et al., 2012b, Prach & Walker, 2020). In such instances, it should be possible for the functional traits of individual plants to be scaled up to infer on broader community dynamics (Prach & Walker, 2020). If such environmental processes are at work, it should be possible for community assembly processes and mechanisms to be predicted from plant functional traits (Violle et al., 2007, Schleicher, Peppler-Lisbach & Kleyer, 2011, Chang & Turner, 2019, Prach & Walker, 2020).

A major goal within the field of vegetation ecology is to understand how functional traits shift with succession. Several expectations for how functional traits change with succession have been proposed; for example, during early succession, in which disturbance rates are high, specific leaf area (SLA) tends to be high (Grime, 1979). High SLA values typically correspond to a high competitive ability because of high mass-based photosynthetic ability (Grime, 1979). Canopy height is expected to increase with succession as competition for light increases, particularly within environments in which light is a limiting factor (Vile, Shipley & Garnier, 2006, Navas et al., 2010). Similarly, average seed size is expected to increase with forest succession because large seed sizes promote high seedling longevity (Moles & Westoby, 2004). Leaf size may also increase with succession resulting in a stronger capacity to capture light to maximise carbon gains (Navas et al., 2010, Chen et al., 2021), whereas photosynthetic capacity is thought to decrease with succession due to lower light availability (Bazzaz, 1979). However, mixed results have also been reported (e.g. see Guariguata & Ostertag, 2001, Schneider et al., 2003, Khurana & Singh, 2004, Purschke et al., 2013). For example, contradictory results have been identified for traits such as SLA and leaf nitrogen content (LNC), in which the trends reported vary from an increase to a decrease or no identified trends over successional gradients (Navas et al., 2010, Uriarte et al., 2016, Boukili & Chazdon, 2017). To date there exists no comparative analysis on whether general rules exist for how or if functional traits can be used to consistently predict overall patterns of vegetation change related to succession (Douma et al., 2012b, Piqueray et al., 2015). Particularly, whether consistent trends exist across geographic regions, vegetation types, growth forms and disturbances are still unclear (Prach & Walker, 2020).

Theories postulating consistent plant ecological strategies and plant assembly patterns do exist. The plant economic spectrum (PES), which aims to integrate leaf, stem, and root traits to explain plant ecological strategies and patterns, conceptually conveys the organisational trade-offs that exist between resource acquisition and conservation (Wright et al., 2004, Díaz et al., 2016). PES postulates that traits from different organs within a plant should be coordinated within a species allowing for adaptive changes across environmental gradients (Díaz et al., 2016). For example, according to PES theory, within resource-rich environments, resource-acquisitive species, that have, for example, high SLA, high specific root length (SRL), high LNC and high root nitrogen concentrations and have traits associated with low tissue density (e.g., low leaf dry matter content (LDMC) and root tissue density) will be abundant, whereas in resource-poor environments resource-conservative species, with the opposite set of traits, will be abundant (Kramer-Walter et al., 2016). As such, there is a critical need to investigate traits across gradients to test predictions of the PES for coordinated variation across traits. To date there exists no comparative analysis on whether a general rule exists for how or if functional traits can be used to consistently predict overall patterns of vegetation change related to succession.

The aim of the review is to understand which functional traits have been studied in successional systems, and to identify consistencies and biases in such studies. More specifically, my objectives are to (i) establish if there are consistent trends in plant functional traits across successional gradients, and (ii) to assess whether existing studies investigating functional trait turnover across successional gradients show biases in the plant growth form (i.e., woody *vs* herbaceous plants *vs* both), geographic region, and vegetation types investigated. An in-depth search for relevant papers dealing with trait turnover in successional systems was conducted across the Scopus search engine. Within the search engines, a subset of search terms was used identify relevant papers, and all relevant data (e.g., which traits were investigated, growth forms studied, geographic regions studied, and vegetation type studied, amongst others) gleaned from the papers. Null models were generated to test if observed values for (i) functional traits, (ii) growth form, (iii) geographic regions, and (iv) vegetation type differed from random expectation. It is expected that that conservative traits will increase with succession, whereas acquisitive traits will decrease as succession progresses. Furthermore, it is expected that biases in the types of traits studied, growth forms, geographic regions, as well as the vegetation types investigated, will be apparent. By identifying the gaps in current research, we can provide an indication of the topics that future research should focus on. This is imperative if we are to better understand how communities change in the face of continuing global change.

Methods

Data collection

The systematic review was conducted in accordance with the preferred reporting style for systematic reviews and meta-analyses as per Moher et al. (2009) (Fig. C1, Appendix C). Only peer-reviewed scholarly papers, books and book chapters were considered. Unpublished data, theses, conference proceedings, technical reports and preprints were excluded. In total 3650 papers were found using the search criteria. All papers were screened for relevance to the topic of how traits change with succession using the following inclusion criteria: (i) only articles dealing with vascular plants in natural systems were included (European meadows with archeophytes were included; articles dealing with cultivated or non-vascular plants were excluded); (ii) only articles dealing with modern (non-paleontological) studies were included; (iii) only studies investigating interspecific, and not intraspecific, trait variation were included; (iv) only studies investigating terrestrial communities, including freshwater communities (e.g., mangroves, estuaries, everglades, swamps, mires, marshes, bogs, and wetlands) were included; oceanic communities were excluded; v) only studies investigating indigenous species were included; and lastly, vi) only comparative studies were considered. Studies on traits of single species or individual successional groups (e.g., only pioneer or only climax) were excluded.

A search was conducted using the Scopus search engine between January 2018 and June 2020 for scholarly papers, books and book chapters on how functional traits change with succession. The search terms used during the online search included: “plant*”, “tree*”, “woody”, “shrub*”, “herb*”, “functional”, “trait*”, “characteristic”, “succession”, “pioneer”, “climax”. Keywords used to exclude studies from the search included “agricul*”, “crop*”, “microb*”, “bacteria*”, “metabolism”, “animalia”, “animals”, “bryophyte”, “aves”, and “wetland”. The search was further limited to two subject areas (namely agriculture and environment) using “AGRI” and “ENVI” as keywords (see Appendix C for the script used during the Scopus searches). The search terms included matches in the abstracts, titles and keywords of English written papers published from 1980 until December 2019.

After screening, 199 articles remained. These papers all reported sufficient data pertaining to how traits change with succession (Fig. C1, Appendix C). For each paper, the following data were recorded (where provided): citation; year of publication; country and continent of study; biome/vegetation type in which the study was conducted (the following vegetation types were recorded: tundra, mangrove, montane, freshwater, semi-arid, mixed (i.e., combinations of several vegetation types), shrubland, Mediterranean, grassland, and forest vegetation types); the growth form (woody/herbaceous or both) of the plants; the study design (experimental or observational); successional stages investigated in the studies (e.g. early, mid or late successional stages); the disturbances preceding succession (e.g. logging, fire); the broad trait category investigated (leaf, stem, root, whole-plant, physiological or reproductive); and the traits investigated (e.g. SLA, leaf chlorophyll content).

For each study, the direction in which each functional trait changed as succession progressed was recorded. Trait values could increase with succession, decrease with succession, show a valley-shaped trend with succession, peak at intermediate levels of succession, or show no trend with succession. An indication of the proportion of studies (per trait) per observed trend (including studies that reported no effect) is provided in Table C2 (Appendix C). The ability to categorise traits based on patterns (i.e., increase, decrease, valley or peak) was generally easily achieved. For simplicity, only trait values reported to increase with succession, trait values reported to decrease with succession, trait values reporting a valley-shaped trend, and trait values that peaked at intermediate levels, were included in the analysis (thus traits that showed no trend over succession were excluded).

Data analysis

The screened studies were very heterogeneous and a lack of comparable data between them meant that a formal meta-analysis would be unfeasible. A qualitative synthesis was therefore undertaken.

A total of 398 traits (Table C1, Appendix C) were reported from the 199 papers. Several names and/or terms were often used to describe the same trait (e.g., SLA and leaf specific area (given as leaf area divided by dry weight) pertain to the same trait). In such instances, these terms were consolidated to allow more comparisons between fewer traits. The identified traits consisted of continuous data (including categorical data; an example of categorical data is the number of species with a seed dispersal mode, e.g., of zoochory).

Soft traits (i.e., morphological, or anatomical, which are used as proxies to infer on plant functions and strategies) are often considered to be surrogates for hard traits (i.e., physiological traits, which are used to capture a particular function of a plant). Because soft traits are more easily measured than hard traits, they are more frequently studied (Perez-Harguindeguy et al., 2016). The reported traits identified in the literature were scored as either "soft" or "hard" traits based on literature sources (Perez-Harguindeguy et al., 2016, e.g., Zhao, Ali & Yan, 2017, Belluau & Shipley, 2018, Zhang et al., 2020).

Random assemblages: functional traits

Only traits that had been scored in more than 20 studies were used for statistical analyses. Six traits met this criterion: SLA, plant height, seed mass, LNC, photosynthetic rate, and plant life span.

To establish if there were consistent trends in plant functional traits across successional gradients, random assemblages of trait (e.g., namely SLA, plant height, seed mass, LNC, photosynthetic rate, and life span) trends (e.g., increase, decrease, valley-shape, and peak) were created to test if the observed trait frequency (i.e., the frequency that a particular trait increased/decreased/illustrated a peak, or valley shape over succession) differed from random expectation. Using the randomizeR package (Uschner et al., 2018), a null model (of a 1000 replicates) was generated for each trait trend. The null model established a baseline pattern for each of the trait trends, to which the observed trait values was compared. The randomizeR package was used to generate 1000 random "assemblages", each consisting of N trends, where N = the number of studies with traits observed per trend. In the randomizations, the chance of each of the four trends (increase, decrease, valley and peak) being selected was weighted equally. Next, the 2.5% and 97.5% quantiles were determined for the frequency of *each* trend across the 1000 random assemblages generated. Observed values that fell above the 97.5% quantile were scored as being significantly larger than what is expected from random expectation; values that fell between the 2.5% and 97.5% quantile were scored as being not significantly different to random expectation, and values that fell below the 2.5% quantile were scored as being significantly smaller than what is expected from random expectation (Greve et al., 2008).

Random assemblages: biases in geographic region, growth form, and vegetation types

To test for geographic biases in trait studies across successional gradients, 1000 random assemblages were again generated. In this case, studies (N = the number of studies for which continent was assigned) were randomly appointed to each continent, weighted by the size of the continent. Next, the 2.5% and 97.5% quantiles were determined for the frequency with which studies were assigned to each continent across all randomisations. If the observed number of studies per continent was less or more frequent than the 2.5% and 97.5% quantiles respectively, then studies were considered to have been conducted less or more often than random respectively.

The same procedure was used to test for biases in the vegetation types and the types of growth forms in which trait studies across successional gradients have been conducted; however, in these randomisations, studies (N = the number of studies recording vegetation type or growth form) were randomly assigned to different vegetation types or growth, with vegetation types or growth forms being selected with equal frequency. Selection using equal frequency was applied as bins will be mores significant in representing the underlying distribution of the data trends. Please refer to the randomisations sample code provided in Appendix C.

Randomisations were run in R v.3.6.1 (R Development Core Team, 2022b), using the packages ‘randomizeR’ (Uschner et al., 2018) and ‘BSDA’ (Arnholt & Evans, 2017). Figures were generated in R v. 3.6.1 (R Development Core Team, 2022b) using the ‘base’ package (R Development Core Team, 2022a) and in ArcGIS 10.7.1 (ESRI, 2011).

Results

General patterns

A total of 398 functional traits were reported (Table C1; Appendix C). Most studies investigated a range of successional stages (namely early, mid, and/or late stages) indicating that, from a trait perspective, several successional stages were investigated, and most studies bridged across the different successional stages (Fig. 4.1b). Differences in the disturbance type associated with the succession varied considerably (Fig. 4.1d): agricultural practices and logging activities were the most frequently reported disturbances, with disturbances resulting from natural disasters and infrastructure development being the least frequently studied disturbance types. The number of studies investigating trait-based successional studies has increased over time (Fig. 4.1e). Whole-plant and leaf traits were the most frequently reported, whereas root traits were the least reported (Fig. 4.1f).

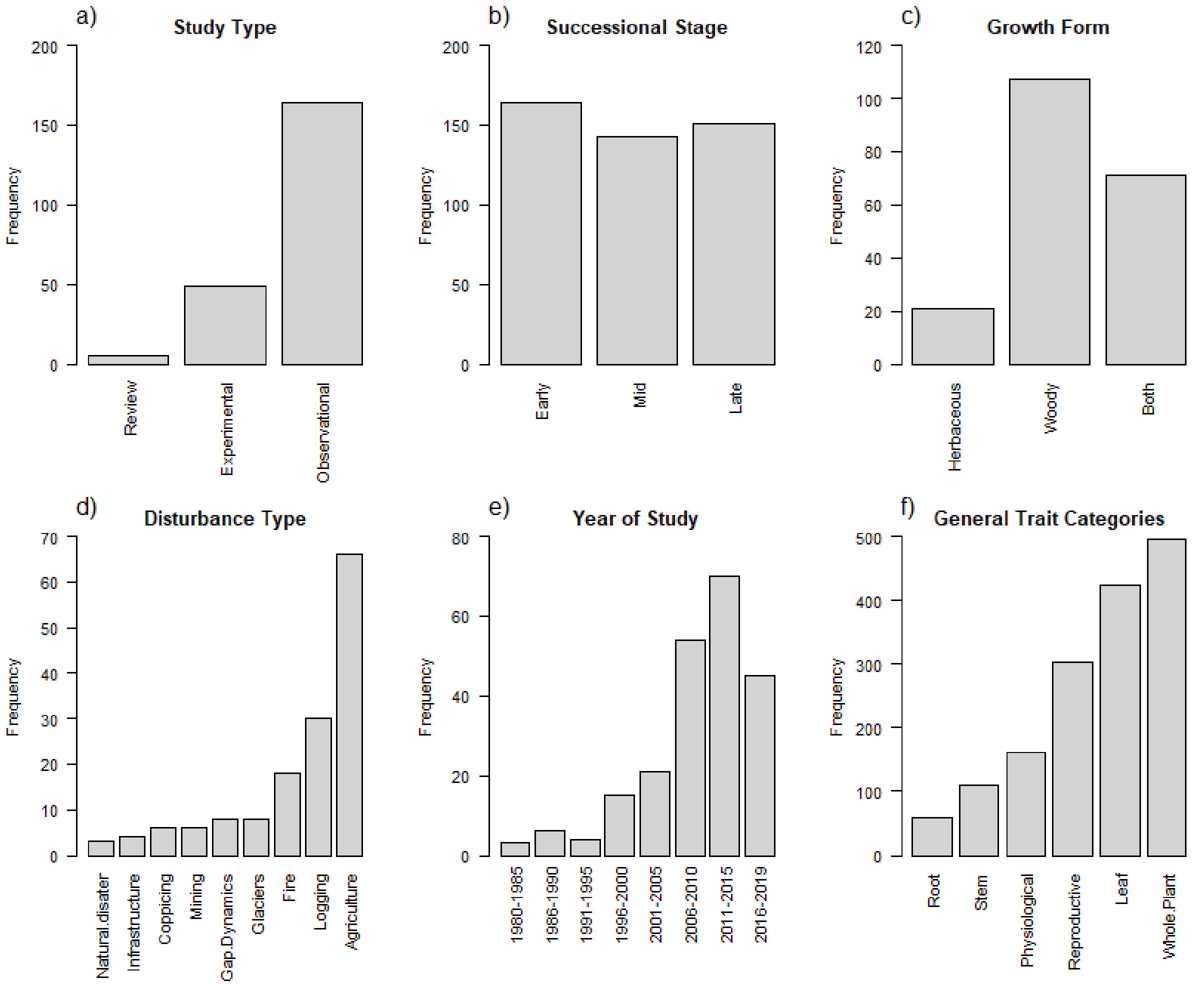


FIGURE 4.1 The frequencies of a) the types of studies, b) the successional stage reported, c) the type of growth forms (woody, herbaceous, or both) that have been studied, d) the disturbance types following which the successional studies were conducted, e) the year of publication, and f) the general trait categories that have been studied.

Frequently studied functional traits

Consistent trends in plant functional traits across successional gradients**,** which differed from random expectation, were observed for each of the six most common traits (Table 4.2; Fig. C2, Appendix C): (i) SLA decreased, (ii) plant height increased, (iii) seed mass increased, (iv) LNC decreased, (v) photosynthetic rate/capacity decreased and (vi) plant life span increased along successional gradients more than was expected from random (Fig. 4.2; Fig. C2, Appendix C).

TABLE 4.2 Results of the randomised trait assemblages indicating where the traits tested differed significantly from random expectation. Observed values that fell above the 97.5% quantile were scored as being significantly larger than what is expected from random expectation; values that fell above the 2.5% quantile and below the 97.5% quantile, were scored as being not significantly different to random expectation, and values that fell below the 2.5% quantile, were scored as being significantly smaller than what is expected from random expectation. Figure C2 (Appendix C) illustrates the random assemblages generated for each trait assemblage.

Trait	**Trait Pattern Observed**			
	Increase	**Decrease**	**Valley**	**Peak**
SLA	NS	Larger	Smaller	Smaller
Plant height	Larger	NS	Smaller	Smaller
Seed mass	Larger	Smaller	Smaller	Smaller
LNC	NS	Larger	Smaller	NS
Photosynthetic rate/photosynthetic capacity	Smaller	Larger	Smaller	Smaller
Plant life span	Larger	Smaller	Smaller	Smaller

Additional traits that were commonly reported included the proportion of seed dispersal types and of Raunkiaer life forms; however, different studies used different classifications of (1) seed dispersal type (e.g., biotic dispersal *vs* epizoochory) so that no one seed dispersal type was reported more than 20 times, and (2) Raunkiaer life form (e.g., therophyte, hemicryptophytes, amongst others) so that no one life form was reported more than 20 times (Table C1, Appendix C). Across the 199 peer-reviewed source material, the average number of times that each trait was reported was 2.533 (std = ± 4.133, min = 1, max = 41). Of the reported traits, 39 traits were classified as hard traits (16%) whereas the remaining traits were classified as soft traits (84%).

Geographic region

Bias in the geographic region investigated within trait-based successional studies was also apparent (Fig C3, Appendix C). Most studies were from Europe; several countries (e.g., Brazil, China, and France) received disproportionate amounts of research. The Middle East, Oceania, and Africa received the least amount of published research. Across the studies, the number of studies reported for Africa and North America were significantly smaller than expected from random, the number of studies reported for Asia, South America, and Oceania were not significantly different than expected from random, and the number of studies reported for Europe were significantly larger than expected from random (Fig. 4.2; Fig. C3, Appendix C).

Vegetation types

Bias in the vegetation type investigated within trait-based successional studies was also apparent (Fig. C4, Appendix C). Most trait-based successional studies have been conducted in forests; studies from all other vegetation types were underrepresented. Across the studies, it was found that: (i) the number of studies reported for most vegetation types (tundra, mangrove, montane, freshwater, semi-arid, mixed, and shrubland) was significantly smaller than expected from random, (ii) the number of studies reported within Mediterranean habitats and Grassland habitats were not significantly different than expected from random, and (iii) the number of studies reported within forests was significantly larger than expected from random (Fig. 4.2, Fig. C4, Appendix C).

Growth form

The types of growth forms studied (i.e., herbaceous, woody, or both) across the peer-reviewed studies consistently differed from random expectation (Fig. 4.1c; Fig. 4.2). Woody species (reported in 107 studies) were studied significantly more than expected from random expectation (Fig. C5, Appendix C), herbaceous species (reported in 21 studies) were consistently studied less frequently than expected from random (Fig. C5, Appendix C), and studies investigating both woody and herbaceous growth forms (reported in 71 studies) were not consistently studied less or more frequently than expected from random. This aligns with the findings that most studies have been conducted in forests (Fig. C4, Appendix C).

FIGURE 4.2 Results of the randomised trait assemblages indicating biases in the geographic region, vegetation types, and growth forms studied within trait-based studies. Values that fell above the 97.5% quantile, were scored as being significantly larger than what is expected from random expectation (shaded red), values that fell above the 2.5% quantile and below the 97.5% quantile, were scored as being not significant as they did not differ from random expectation (shaded green), and values that fell below the 2.5% quantile, were scored as being significantly smaller than what is expected from random expectation (shaded blue). Figures C3 – C5 (Appendix C) illustrate the random assemblages generated for each growth form, geographic region, and vegetation type.

Assemblage	**Over-represented**	**Not Significant**	**Under-represented**
Growth Form			
Both		🟩	
Herbaceous			🟦
Woody	🟥		
Geographic Region			
Africa			🟦
Asia		🟩	
Europe	🟥		
North America			🟦
Oceania		🟩	
South America		🟩	
Vegetation Type			
Forest	🟥		
Freshwater			🟦
Grassland		🟩	
Mangrove			🟦
Mediterranean		🟩	
Mixed			🟦
Montane			🟦
Semi-arid			🟦
Shrubland			🟦
Tundra			🟦

Discussion

Studies assessing trait changes during succession across a range of geographical regions have used a large number (398) of different traits; remarkably, only six of these (SLA, plant height, seed mass, LNC, photosynthetic rate/capacity and plant life span) were measured frequently (> 20 times). Standardising the traits investigated within successional trait-based studies is important, as having a subset of standardised traits (and associated standardised methods to measure such traits) allows for easy comparison with other trait values from studies from a variety of vegetation types, growth forms, and geographic regions. The ability to compare such patterns across spatial scales and spatial components should improve our understanding of successional trait trends, and our ability to infer on successional patterns.

Kattge et al. (2020) has previously illustrated a lack of completeness and representativeness of the types of traits utilised within the TRY plant trait database. Here, the authors found that commonly used traits were restricted to those that were commonly used in global vegetation and remote sensing models. Similarly, we identified a lack of consistency in the types of traits measured across trait-based successional studies. Traits in which a bias was reported and/or traits that were identified as being commonly studied in both the current review and Kattge et al. (2020) include plant growth form, woodiness, plant height, plant lifespan, SLA, LNC, and photosynthetic pathways. Furthermore, general geographic biases were recorded within both Kattge et al. (2020) and the current review; in both studies, Europe is well represented in the literature. The bias observed within trait-based studies may be attributed to the observation that commonly recorded traits are restricted to those used in global vegetation and remote sensing models (Kattge et al. 2020). Often the traits included in these statically intense models are more easily measured traits (e.g., SLA, LNC, plant height, amongst others).

The most commonly measured trait across all studies was SLA (Fig. 4.3). Specific leaf area is easily and inexpensively measured and can be used to infer whole plant growth, reproductive strategy, and plant life span (Perez-Harguindeguy et al., 2016, He et al., 2018). This inference is possible as SLA is correlated with traits of other plant organs, e.g., specific root length, relative growth rate, transpiration efficiency, and LNC, as postulated by PES (Wright et al., 2004, Nigam & Aruna, 2008, Reich, 2014, Perez-Harguindeguy et al., 2016). Specific leaf area was mostly found to decrease as succession progressed. A decrease in SLA suggests the replacement of fast-growing pioneer species that have high acquisition rates at early successional stages with slow growing, later successional species that exhibit high resource conservation and higher survival rates as succession progresses (Derroire et al., 2016).

Leaf nitrogen content and photosynthetic rate/capacity, both of which correlate positively with SLA, (Wright et al., 2004, Chen et al., 2020), consistently decreased with succession (Fig. 4.3). The positive correlation between photosynthetic rate/capacity and LNC is widely recognised (Evans, 1989). A decrease in LNC and photosynthetic rate/capacity can be attributed to a trade-off between fast growth rates achieved through increased photosynthetic capacity (because of high LNC); there is a conservation of what resources have been (slowly) acquired (Wright et al., 2004, Navas et al., 2010, Wilfahrt, Collins & White, 2014). High LNC at pioneer stages of succession suggest high photosynthetic rates/capacities which promote fast growth and the rapid acquisition of resources (Garnier et al., 2004, Derroire et al., 2016). In contrast, low LNC in later successional species suggest greater investment in stem growth, and in shade tolerance as photosynthetic rates decrease (Garnier et al., 2004, Craine, 2005).

Plant height increased as succession progressed (Fig. 4.3). Plant height is typically expected to increase with succession as increases in height improve the competitive ability for light during succession. Thus, taller plants benefit from increased light levels (Vile, Shipley & Garnier, 2006). Plant height is easily and inexpensively measured, making it a popular trait that is studied in a variety of research fields. However, the observed increase in plant height with succession may be attributed to the fact that most studies were conducted in forests; in other ecosystems this trend may not hold.

Plant life span also increased as succession progressed (Fig. 4.3); this relationship is expected because as succession progresses and the intensity of disturbance decreases (and thus the associated need for fast reproduction before plant death decreases), coupled with an increase in the intensity of interspecific competition (in which the advantage of greater plant size is favourable), increased life span is favoured (Vile, Shipley & Garnier, 2006).

Seed mass, an easily measured reproductive trait, was identified as one of the frequently studied traits associated with trait-based successional studies; it consistently increased as succession progressed (Fig. 4.3). Seed size during succession is related to a trade-off between producing more, smaller seeds (which increases the chances of seedling establishment during the early successional stages) *vs* producing fewer, larger seeds that are better suited to surviving the threats to seedling establishment (e.g., shade, drought, defoliation, and/or competition from already established plants later during successional stages (Leishman, 2001, Kahmen & Poschlod, 2004, Muller-Landau, 2010, Navas et al., 2010). Although a large body of literature exists within the field of plant reproduction, reproductive traits (especially hard traits), that mediate interactions in reproductive processes (e.g., between plants and their pollinators) are generally infrequently studied in community assembly processes.

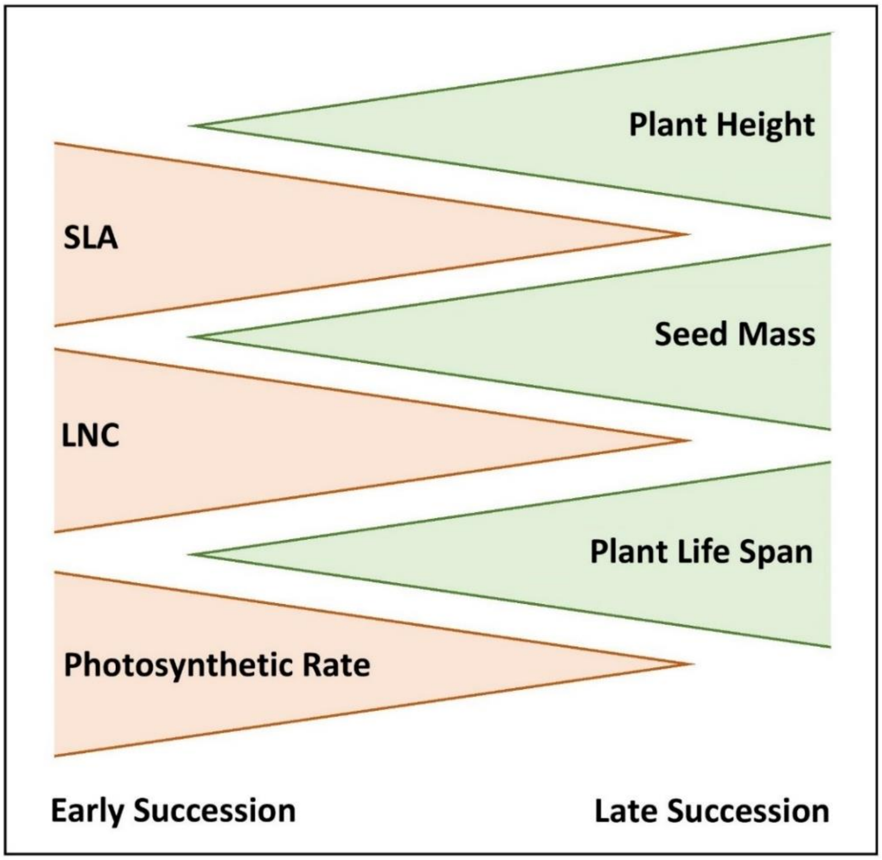


FIGURE 4.3 Schematic diagram illustrating the results generated from the randomised trait assemblages and whether traits increased with succession (green chevron) or decreased with succession (red chevron). The following trait patterns were observed: seed mass, plant height, and life span increased with succession (green chevrons), whereas SLA, LNC, and photosynthetic capacity decreased as succession progressed (red chevrons).

Differences in the frequency of trait categories (i.e., whole-plant, leaf, stem, root, physiological, and reproductive) investigated were evident (Fig. 4.2a). Research focus was found to be directed particularly towards whole-plant traits (e.g., plant height and life span) and leaf traits (e.g., SLA, LNC and photosynthetic rate). The whole-plant suite of traits (e.g., plant height and life span) and several leaf traits (including SLA and LNC) are amongst the easiest traits to measure in the field (Stahl et al., 2013), and they represent key plant responses to the environment, i.e., as postulated by PES (Perez-Harguindeguy et al., 2016). This bias toward resource-related traits has been illustrated previously (see Wigley et al., 2020). Similarly, Kattge et al. (2020) have previously illustrated a lack of completeness and representativeness of the types of traits utilised within the TRY plant trait database. Relatively few studies assessed the below-ground traits of plants, which is a general observation across traits studies (Maeght, Rewald & Pierret, 2013, Smit et al., 2013, Cabal, De Deurwaerder & Matesanz, 2021). This can be attributed to the (laborious) need to dig up plants which results in habitat disturbance and often the death of plants. Given the (recently) identified importance of below-ground processes for plant physiology and performance (Laliberté, 2017), there has been an increase in effort aimed at incorporating below-ground traits into plant functional strategy frameworks (Ávila-Lovera et al., 2022). A single axis of trait alignment between below-ground and above ground traits has yet to be established (Ávila-Lovera et al., 2022), especially as conflicting evidence of coordinated trait variation across below-ground and above-ground traits has been reported (Shen et al., 2019). Furthermore, many traits considered are not necessarily relevant to the functioning of some ecosystems; for example, the traits required in disturbance-driven ecosystems (e.g., grasslands and savannas) are underrepresented within the literature and are likely to comprise of a very different subset of traits than those postulated to be important for other ecosystems (e.g., non-disturbance driven forests) (Wigley et al., 2020).

As plants face various selection pressures during succession, an understanding of a diverse suite of plant traits, and how they change with succession is required. This is of particular concern given the impacts plant communities may experience because of global change factors. It is vital that the types of traits measured (e.g., stem, leaf, physiological, reproductive, root, and whole plant) represent several dimensions of the PES and are applicable to various ecosystems (i.e., disturbance-driven ecosystems vs. non-disturbance driven ecosystems). According to PES, (some) traits may be correlated with other traits across two distinct axes, resource acquisition and resource conservation (Shen et al., 2019). However, it is evident that more research into these coordinated dimensions needs to be conducted to improve our ability to infer on community dynamics, especially across ecosystems. This can be achieved by incorporating principles from the PES to identify useful dimensionality of plant traits within our ever-growing plant trait data sets (Laughlin, 2014). For example, reproductive traits coordinate themselves along their own axis (i.e., as per PES theory, these traits do not necessarily provide information related to other traits) (Shen et al., 2019) Thus, reproductive traits have often been overlooked; these traits are important to consider, and it is important that future studies investigate such traits so that a better understanding of the PES and associated community assembly patterns of plants can be ascertained.

Soft traits were more frequently reported than hard traits, an observation that has been noted previously (Cornelissen et al., 2003, Kattge et al., 2020, Zhang et al., 2020). This can be attributed to the need for specialised equipment and time-consuming and costly methods involved in obtaining these physiological measures associated with hard traits (Belluau & Shipley, 2018). While soft traits are correlates of hard traits (Cornelissen et al., 2003), many hard traits are still in need of soft trait surrogates (Cornelissen et al., 2003).

Differences in geographic region, growth form and vegetation type associated with functional traits

Although no topic can be "over-researched", when research outputs are considerably biased, conclusions may be drawn primarily from well-studied subjects and thus fail to represent patterns more broadly (Trimble & van Aarde, 2012). Here, it is evident that research output in terms of geographic regions, growth form, and vegetation type that trait-based successional studies investigate is unequal.

The research bias observed towards specific geographic areas has been illustrated across several ecological fields (e.g., climate change biology, invasive species research and conservation) (Pyšek et al., 2008, Trimble & van Aarde, 2012). The apparent research skew observed towards Europe is not uncommon, having been illustrated across several ecological fields (e.g., climate change biology, invasive species research and conservation) (Pyšek et al., 2008, Trimble & van Aarde, 2012). A disproportionate number of studies was recorded within Brazil, France, and China; however, these studies were not limited to local research groups but conducted by several different research groups. Studies from locations in North America and Africa were consistently reported less than expected from random expectation in this review. The underrepresentation of studies form Africa is not unexpected; it is well established that Africa has received much less research attention across several ecological topics than other geographic regions (e.g., Pyšek et al., 2008, Felton et al., 2009, Christie et al., 2019); in contrast, it was unusual that North America was underrepresented, however, this is likely the result of the in-depth forest ecology and vegetation science fields within Europe.

The bias towards forests over other vegetation types is common within the field of ecology (Felton et al., 2009, Trimble & van Aarde, 2012). It may on one hand be linked to Western perceptions on forests representing climax vegetation (Pausas et al., 2018, Vetter, 2020), thus, resulting in a disproportionate amount of research attention. Also, forests are species-rich ecosystems; the high species richness together with the associated social and economic value of forests may play a role in driving the observed bias of forests (Felton et al., 2009, Trimble & van Aarde, 2012). The plants in forests have economic value (i.e., timber) that puts them at a high risk of anthropogenic disturbance (e.g., deforestation) thus providing suitable model systems in which to study associated trait-based succession (Filotas et al., 2014). Furthermore, forests typically seem to follow a deterministic process of succession following disturbances (Dent, DeWalt & Denslow, 2013) which is often not as apparent in other vegetation types (Måren et al., 2018). Deterministic succession allows researchers to easily study and draw conclusions form the observed successional patterns. Given the strong bias to forest systems in this review, the general trends in plant traits observed with succession here (e.g., increase in height with succession) may not hold for all vegetation types. Thus, more studies are needed to elucidate how traits change with succession in different vegetation types.

The apparent bias towards studies that considered only woody species over those that considered only herbaceous species and considered both growth forms is probably linked to the bias observed towards forests, in which trees are the dominant growth form. The herbaceous layer provides integral ecological functions within many ecosystems, and while its importance and role have been highlighted more recently, the group remains underrepresented (Siebert & Dreber, 2019; Kattge et al., 2020). In some systems the herbaceous layer displays higher turnover rates than plants within other growth forms and strata, making it a particularly good model for use in trait-based studies (Gilliam, 2007).

Reducing bias in trait-based successional studies

The utility of traits to answer questions related to ecosystem change and assembly patterns has become apparent, especially in the face of global change (Navas et al., 2010, Chen et al., 2021). Furthermore, interpreting community assembly patterns in the face of global change has become challenging, albeit imperative. The growing evidence that differences in plant traits can be used to infer ecosystem processes such as succession has resulted in the need for 1) the use of consistent traits being measured across research fields, and 2) standardised ways in which to measure plant functional traits.

Only six of 398 traits identified from this review have been consistently used and reported in trait-based successional studies. The need to standardise across studies is of importance if comparisons are to be drawn to make generalisations on community assembly during succession, and/or in response to global change. Standardised methods have been developed and are available for a variety of traits (e.g., see Sack et al., 2010, Perez-Harguindeguy et al., 2016). With a growing body of research, there has been an increase in global trait databases (e.g., Wright et al., 2004, Díaz et al., 2007, Stahl et al., 2013, Jeliazkov et al., 2020, Kattge et al., 2020, Wigley et al., 2020), and trait handbooks to ensure standardised methodology (e.g., Perez-Harguindeguy et al., 2016, Wigley et al., 2020), further necessitating the need for stringent standardisations of measurement. The advantage of using standardised methods is that they allow for comparable data to address questions relating to ecosystem function and process at different scales and across different ecosystems. Although trait handbooks provide standardised methods for an array of functional traits, which traits are best to measure will always depend on the aims and types of questions investigated, as well as funding issues, and logistical and practical constraints (Trimble & van Aarde, 2012, Perez-Harguindeguy et al., 2016, Wigley et al., 2020). However, handbooks can be used as guides to help select appropriate traits and provide standardised methods in which to measure traits so that they are easily comparable with other such trait values from studies from a variety of vegetation types.

This systematic review has highlighted research gaps within the field of trait-based assembly patterns. Although only a subset of traits has been well studied, it is evident that some traits have the potential to predict patterns of change across successional gradients. Future research should focus on improving our overall understanding of succession-based trait change and to incorporate traits that represent different axes of plant function. Furthermore, additional focus should be placed on underrepresented geographic regions (e.g., Africa) and, perhaps more importantly, vegetation types (e.g., savannas). This is imperative if we are to better understand how communities change in the face of continuing global change.

Appendix C

Appendix Methods

The keyword syntax used during the Scopus search:

(TITLE-ABS-KEY(plant* OR tree* OR woody OR shrub* OR herb*) AND TITLE-ABS-KEY(functional OR trait* OR characteristic*) AND TITLE-ABS-KEY(succession OR pioneer OR climax) AND NOT TITLE-ABS-KEY(agricul*) AND NOT TITLE-ABS-KEY(crop*) AND NOT TITLE-ABS-KEY(microb*) AND NOT TITLE-ABS-KEY(bacteria*)) AND (LIMIT-TO (SUBJAREA,"AGRI") OR LIMIT-TO (SUBJAREA,"ENVI")) AND (EXCLUDE (EXACTKEYWORD,"Metabolism") OR EXCLUDE (EXACTKEYWORD,"Animalia") OR EXCLUDE (EXACTKEYWORD,"Bryophyta") OR EXCLUDE (EXACTKEYWORD,"Animals") OR EXCLUDE (EXACTKEYWORD,"Aves"))

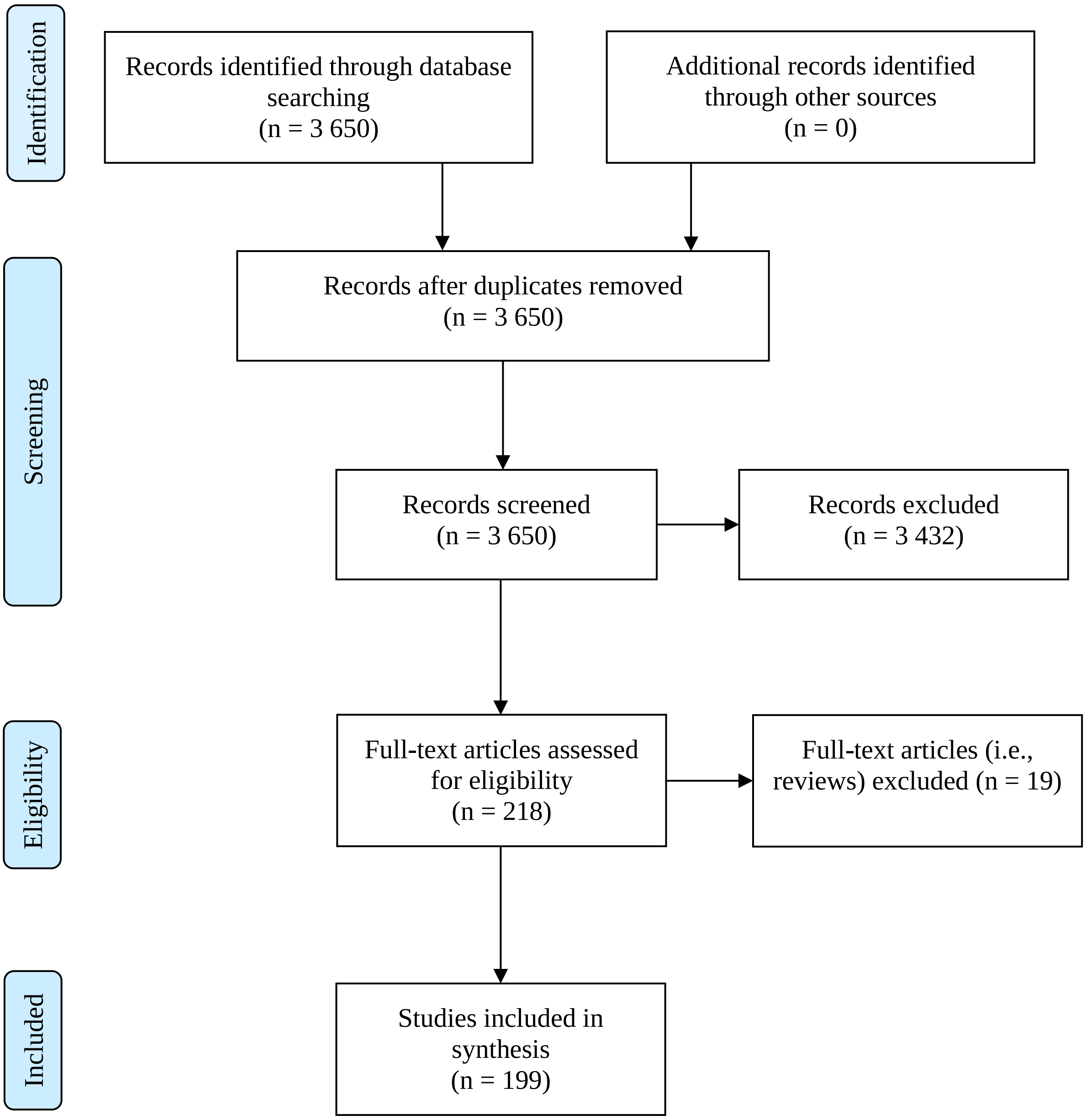


FIGURE D1 Flow diagram of the data selection process used in a systematic review. The diagram illustrates the criteria in which studies were initially identified and how studies were subsequently included or excluded for the purpose of the analysis. The above procedure is based on the 2009 PRISMA Flow Diagram, as described by Moher et al. (2009). The flow diagram illustrates how information was gathered at different stages of the systematic review. For more information, visit www.prisma-statement.org.

TABLE C1 A list of all the functional traits identified during the search for scholarly articles. Traits are listed as hard or soft traits. Soft traits are arranged by plant organ (e.g., leaf traits, stem traits, reproductive traits, crown traits, whole plant traits, and root traits). In cases where different terms were used to describe the same trait, these were grouped together (e.g., leaf specific area and leaf mass per area). Traits belonging to one broad category (e.g., different Raunkiaer life forms) are listed under their broad heading – indicated in italics (factor level). A tally of the total number of papers per trait category is also indicated in italics. The traits highlighted in bold were reported in more than 20 studies and thus included in the quantitative analysis. Studies that showed no relationship between traits and successional gradients are not included here (however traits that included interaction relationships (which were excluded for the purpose of analysis) are included). Some traits that are represented by categorical data have been grouped under a main trait category (i.e., factor, indicated in italics), bulleted points represented the factor levels that belong under the main trait factor. The total number of papers considering each trait type is also displayed in italics.

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
Soft Traits	
Leaf Traits	
Specific leaf area (SLA; leaf specific area; Leaf mass per area (LMA; inverse of SLA)	**45**
Leaf nitrogen content (LNC)	**30**
Leaf dry matter content (LDMC)	17
Leaf phosphorus (P) content	11
Leaf cell dimensions	*9*
• Leptophyll (< 25mm^2)	5
• Macrophyll (18 225-16 4025 mm^2)	1
• Mesophyll (4500-18 225 mm^2)	2
• Notophyll (2025-4500 mm^2)	1
Leaf thickness	9
Leaf area	6
Leaf carbon (C) content	6
Leaf carbon:nitrogen (C:N) ratio	3
Leaf carbon:phosphorus (C:P) ratio	1
Leaf carbon (C) isotopic composition	1
Leaf chlorophyl content	5
Leaf chlorophyl a:b ratio	2
Leaf life span	5
Leaf toughness	4
Leaf mass fraction (leaf dry mass/plant dry mass)	5
Leaf arrangement	*3*
• Dispersed/monolayered	3
• Clumped/multi-layered	2
Leaf compoundness	3

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
Leaf density/contacts	3
Leaf mass	3
Leaf nitrogen:phosphorus (N:P) ratio	3
Stomatal density	3
Leaf cellulose content	2
Leaf tannin:phenol content	2
Amount of air space in leaf	1
Guard cell length	1
Heat of combustion (ΔHC)	1
Herbivore susceptibility of leaves (i.e., low chemical defence) / Palatability/ foraging value	3
Leaf anatomy:mesomorphic	1
Leaf ascorbic acid content (AsA)	1
Leaf ash content	1
Leaf calcium (Ca) content	1
Leaf carotenoid content	1
Leaf coverage	1
Leaf δ15N content	1
Leaf length:width ratio (Leaf form)	1
Leaf glutathione content	1
Leaf length	1
Leaf lignin content	1
Leaf soluble sugar content	1
Leaf vein density	1
Leaf xeromorphy	1
Palisade parenchyma thickness	1
Palisade: spongy tissue ratio	1
Relative water content (RWC: 100% - LDMC)	1
Spongy parenchyma thickness	1
Stomatal pore index (SPI)	1
Reproductive Traits	
Seed dispersal	*26*
• Biotic	7
• Zoochory	7
• Epizoochory	3
• Endozoochory	2
• Avichorous (birds)	2
• Myrmecochorous (ants)	1

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
• Anthropochory (humans)	1
• Dyschory (by seeds collected and stored by animals)	1
• Abiotic	2
• Barochory (gravity)	1
• Hydrochory	1
• Autochory	4
• Anemochory (wind)	13
Seed mass	**26**
Pollination vector	*10*
• Biotic	2
• Insects	5
• Abiotic	3
• Spontaneous/self	3
• Wind	5
• Mixed	1
Flowering phenology	*4*
• Spring	1
• Summer	1
• Autumn	1
• Early	3
• Late	4
Seed size (length and/or width in mm)	7
Mating system	*2*
• Dioecious	2
• Self-sterility	2
• Autogamy	2
No. of seeds per ramet	5
Chasmogous flower colour	*1*
• White	1
• Unattractive (green or brown)	1
• Bright (red, yellow, or blue)	1
• Red/burgundy	1
• Greenish/ beige/cream	1
Seed bank longevity	*5*
• Short-term persistent	3
• Long-term persistent	5
• Transient	1
Floral type	*2*

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
• Tubular	1
• Gullet	1
• Flag	1
• Bell-funnel	1
• Inconspicuous	1
Flowering duration	3
Light requirement for germination	2
Flower size	2
No. of seeds per fruit	2
Seed length	2
Total mass of reproductive structures	2
Seedling emergence time	*1*
• All year	1
• Spring	1
Seedling type	*1*
• Phanerocotylar epigeal with foliaceous cotyledons (PEF)	1
• Cryptocotylar hypogeal with reserve storage or absorption cotyledons (CHR)	1
Seed bank location	*1*
• Soil	1
• Canopy	1
Seed phenology period	1
Recalcitrant seeds	1
Seed desiccation tolerance	1
Reproductive allocation (i.e., fraction of surplus energy allocated to reproduction as it increases in size)	1
Fruiting duration	1
Fruit mass	1
Fruit size	1
Corolla size (height and width)	1
Fruit colour: Green	1
Floral resources:pollen	1
Seed shape:spherical (as opposed to elongated)	1
Date of seed maturation	1
Seed volume	1
Seed dispersal distance	1
Germination temperature	1
Seed longevity	1

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
Nitrogen (N) content of seeds	1
Nitrogen (N) content of all reproductive organs	1
Root Traits	
Mycorrhizal species (presence/absence)	3
Root length	3
Root diameter	2
Root fibrousness	2
Root system type (presence/absence)	*2*
• Rhizomatous	1
• Stoloniferous	1
• Taproot	2
Arbuscular Mycorrhizal (AM) fungi colonization rate	2
Mycorrhiza type	*1*
• Vesicular arbuscular	1
• Ectomycorrhiza	1
Root hair length	1
Root hair incidence	1
Specific root length	1
Root tissue density	1
Additive Clonal growth organs (CGO) (presence/absence)	1
Horizontal aboveground rhizome	*1*
• Roots with adventitious buds	1
• Offspring tuber	1
Taproot persistence	*1*
• Not persistent	1
• Persistent	1
Root weight ratio	1
Number of root apices larger than 2mm	1
Taproot diameter: shoot base diameter ratio	1
Stem Traits	
Wood density (g/cm^3)	18
Wood specific gravity	5
Branching (canopy lateral spread)	4
Secondary growth	4
Vessel diameter	3
Vessel density	2
Vessel arrangement	*1*
• In diagonal and/or radial pattern	1

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
- In dendritic pattern	1
- Without patterns	1
Vessel perforation plates	*1*
- Scalariform perforation plates with ≤10 bars	1
- Scalariform perforation plates with 20–40 bars	1
- Reticulate, foraminate, and/or other types of multiple perforation plates	1
Wood porosity	*3*
- Ring-porous	1
- Semi-ring-porous	1
- Diffuse-porous	1
Stretch direction of branch	*1*
- Vertical	1
- Leaned	1
Vessel grouping	*1*
- Exclusively solitary	1
- In radial multiples of 4 or more	1
Growth ring boundaries	*1*
- Distinct	1
- Indistinct	1
Wood compression strength/Modulus of rupture	1
Specific stem length	1
Wood water content	1
Vessel fraction	1
Number of small stems	1
Number of large stems	1
Vessel length	1
Stem mass fraction (stem mass/total plant mass)	1
Sprout number (living shoots originating from the trunk)	1
Wood ray width	1
Vessel lumen fraction ratio	1
Branch weight ratio	1
% carbon isotope (C13) of wood cellulose	1
Whole Plant Traits	
Raunkiaer life form	*17*
- Therophytes	12
- Hemicryptophytes	12
- Micro- or nano-phanerophyte	3

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
• Mega- or meso-phanerophytes	10
• Phanerophytes	2
• Hemitherophyte	1
• Hydrophytes	3
• Geophytes	9
• Aerial parasite	1
• Chamaephytes	9
Growth form	*18*
• Non-tufted	1
• Forbs	12
• Ferns	2
• Trees	4
• Non-woodies	3
• Tufted	1
• Shrubs	5
• Graminoids	9
• Woody	9
Plant height	**28**
Plant life span	**26**
Relative growth rate (relative height growth rate; height gain)	17
Ecological strategy	*9*
• S-strategist	7
• R-strategist	5
• C-strategist	5
• CSR-strategist	1
• SC-strategist	1
• CR-strategist	1
Total plant biomass production	7
Root: shoot ratio (root mass fraction, dry root mass: dry plant mass)	2
Deciduousness	7
Regeneration mode	*4*
• Facultative Resprouter	3
• Facultative Seeder	1
• Obligate Seeder	2
• Obligate Resprouter	1
• Non-specific	1
Clonality	6
Fire response	*3*

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
- Unaffected (regains pre-fire status in first year after fire)	2
- Dispersal (does not resprout but recolonize area by seeds)	3
- Vegetative (resprout but require time to regain previous status after fire)	2
Morphological plasticity	5
Exotic status	5
Light requirement (light extinction)	*2*
- Shade tolerant	4
- Shade intolerant	4
- Mid-shade tolerant	1
Shade tolerance (first year survivorship in shade)	3
Principle means of reproduction, mostly by vegetative propagation	3
Drought tolerance	3
Clonal growth organs (CGO; presence/absence)	3
Foliage structure	*1*
- Erect stem	1
- Erect leafy stem	1
- Umbel-shaped stem	1
Basal area	3
Nitrogen (N) - fixing ability	*1*
- Present	1
- Absent	1
Principle means of reproduction	*2*
- Vegetative propagation possible but mostly by seeds	2
- Seeds only	2
Fire tolerance	2
Presence of dead leaves (shedding)	2
Multi-stemmed tree individual (presence/absence)	2
Nitrogen (N) requirements	2
Moisture requirement	*1*
- Dry	1
- Wet	1
Habitat naturalness	*1*
- Natural	1
- Semi-natural	1
Soil pH preference	*1*
- Neutral	1
- Acidic	1

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
Canopy structure	*2*
• Main part of phytomass along the stem	1
• Main part of phytomass near the ground	1
• Rosette or semi-rosette	2
Response to light intensity change: Modifying leaf mass	1
Etiolation index (related to the trait that enables a seedling to grow beneath closed canopy)	1
Vegetative mass	1
Vegetative mobility/ clonal growth	1
Grazing tolerance	1
Indeterminate growth height	1
Growth response in relation to Mycorrhizal fungi colonisation of the roots	1
Leaf angle from the horizontal plane	1
Recruitment rate	1
Plant age	1
Survival rate	1
Height of lowest branch	1
Maximum diameter at breast height (Dmax)	6
Vegetation layer	*1*
• Understory	1
Leaf coverage	1
Canopy height	1
Bud bank (presence / absence)	1
Sprouting primarily from central below-ground burl/lignotuber	1
Sprout-diffuse (Sprouting occurs from > 1 location)	1
Period of leaf loss	1
Frequent multiplication (Numerous ramets produced every year)	1
Spacer connectivity	*1*
• Long-term spacer connectivity between ramets	1
• Long-term connection between parent and offspring shoots	1
• Short-term spacer connectivity between ramets	1
Spacer between ramets length	1
Storage organs	1
Bud bank position	*1*
• In layer >10 cm, Perennial	1
• In layer 0-10 cm, Perennial	1
• In layer 0-10 cm, Seasonal	1
• In layer 0 cm, Perennial	1

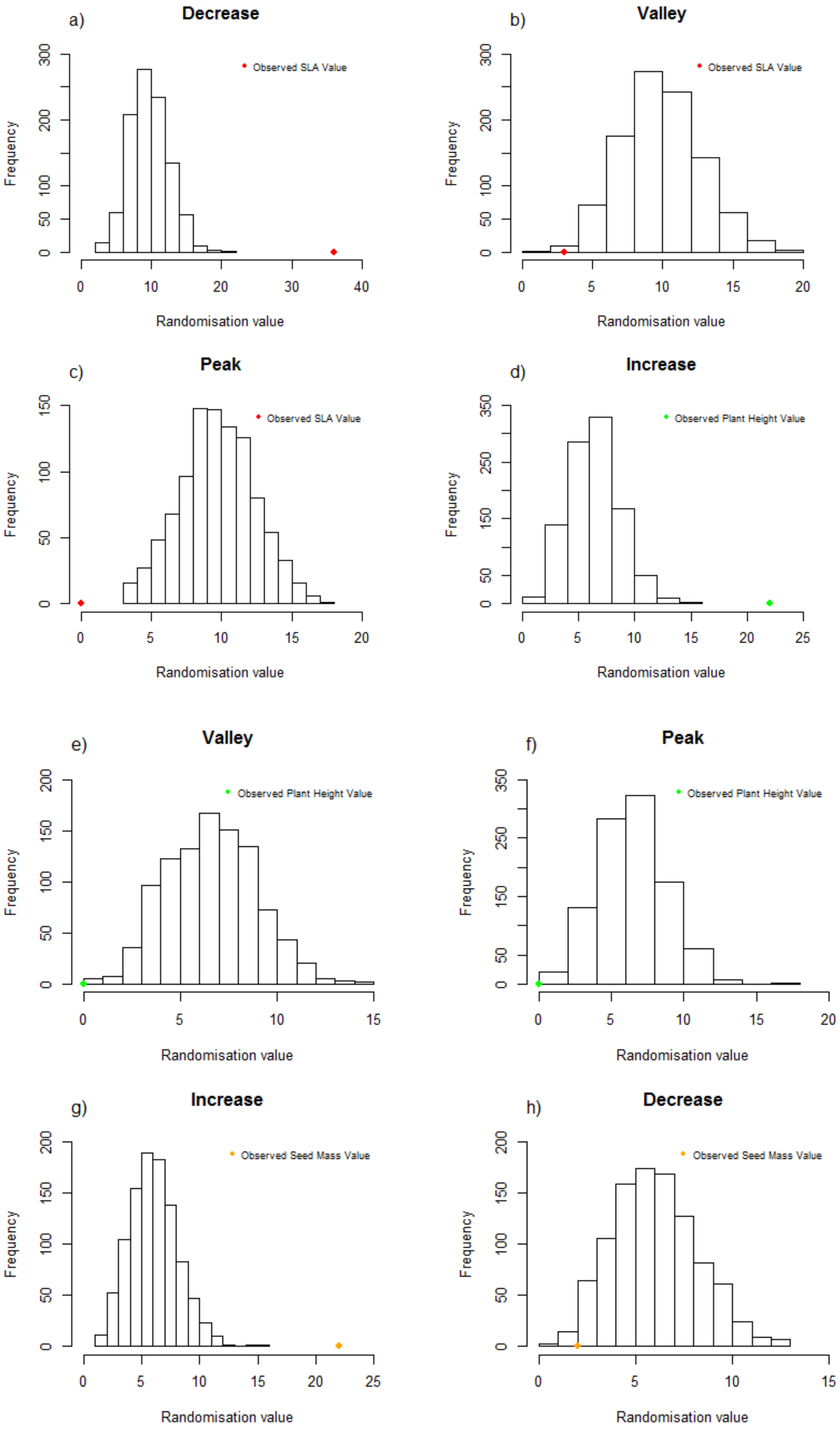
Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
• In layer 0 cm, Seasonal	1
• In layer 0 cm, Potential	1
• In layer 0 to -10 cm, Perennial	1
• In layer 0 to -10 cm, Seasonal	1
• In layer 0 to -10 cm, Potential	1
• In layer < -10 cm, Perennial	1
• In layer < -10 cm, Potential	1
Additive Clonal growth organs (CGO) (presence/absence)	*1*
• Horizontal aboveground rhizome	1
• Roots with adventitious buds	1
• Offspring tuber	1
Regenerative Clonal growth organs (CGO)	*1*
• Fragment of stem	1
• Roots with adventitious buds	1
Shoot cyclicity in Clonal growth organs (CGO)	*1*
• 1	1
• >2	1
Persistence of connection to Clonal growth organs (CGO)	*1*
• 1 year	1
• 2 years	1
N0. of offspring shoots/ parent shoot/ year in Clonal growth organs (CGO)	*1*
• <1	1
• 1	1
• 2-10	1
Lateral spread with rhizomes/runners/roots (presence/absence)	2
Lateral spread (m/year) in Clonal growth organs (CGO)	*1*
• <0.01	1
• 0.01–0.25	1
Secondary thickening in the clonal organ	1
Litterfall	1
Litter decomposability (characterizing the fast–slow growth continuum in plants)	1
Nitrogen (N) content of above-ground tissues	1
Crown Traits	
Crown area	1
Crown width	1
Crown depth/length	1
Crown radius	1

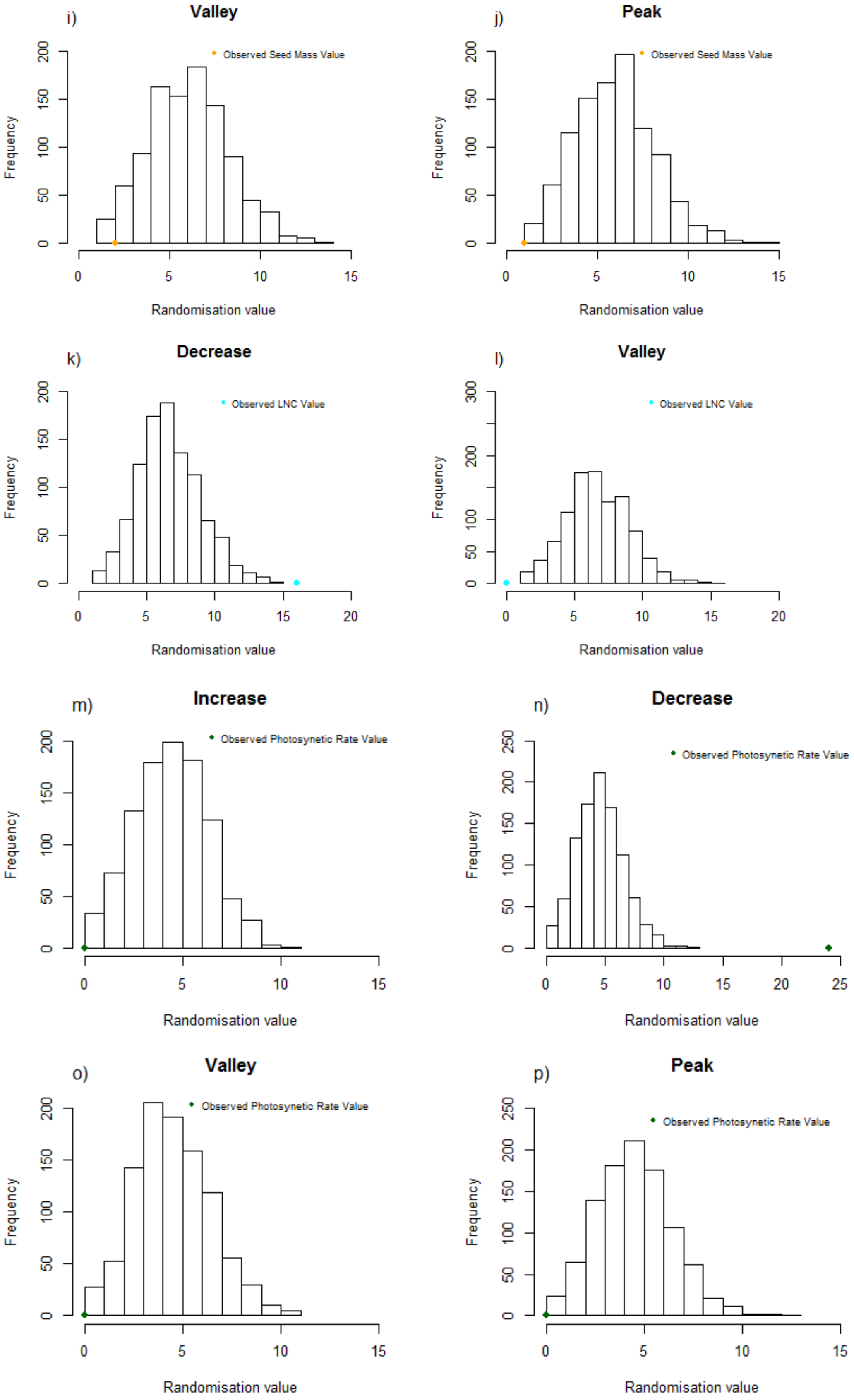
Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
Crown architecture	*1*
• Plagiotrophic	1
• Unbranched	1
• Orthotropic	1
Crown exposure	1
Hard Traits	
Photosynthetic rate/photosynthetic capacity	**20**
Stomatal conductance (gs)	6
Water use efficiency	5
Light compensation point (LCP)	5
Leaf specific hydraulic conductance (Kl)	4
Carbon dioxide (CO_2) assimilation rate	3
Transpiration rate	3
Leaf gas exchange rate (synonymous with photo-rate)	3
Daytime/dark respiration rate	3
Apparent quantum yield (AQY)	2
Sapwood specific hydraulic conductance (Ks)	2
Leaf carbon isotope discrimination (Δ)	2
Light saturation point (LSP)	2
Leaf water potential	2
Nitrogen fixation	2
Photosynthetic nitrogen-use efficiency (PNUE)	2
Recovery from photoinhibition	1
Leaf glutathione reductase (GR) activity	1
Lipid peroxidation	1
Leaf superoxide dismutase (SOD) activity	1
Glutathione (GSH): GSH + oxidized GSH (GSSG) ratio	1
Photosynthetic electron transport (Jmax)	1
Nonphotochemical quenching (NPQ)	1
Photorespiratory rate (Pr)	1
Maximum rate of carboxylation (Vcmax)	1
Hydraulic conductivity	1
Susceptibility to cavitation (embolism)	1
Apparent quantum efficiency (increase in growth rate with increasing irradiance)	1
Huver value (Hv)	1
Intercellular to ambient CO_2 concentration ratio (Ci/Ca)	1
Nitrogen uptake rate	1

Trait	**Total number of papers per trait category (subcategory numbers indicate the number of times the subcategory trait was reported in the papers)**
Leaf construction cost	1
Light-use efficiency (LUE)	1
Light-use efficiency adjustment ability	1
Triose phosphate utilisation rate (TPU)	1
Carboxylation efficiency (CE)	1
Photochemical reflectance index/leaf reflectance	1
Trunk and branch sap flux	1
Nitrate reductase activity	1

Table C2. Proportion of the trend values observed for each trait. No effect was excluded from the analyses.

Trait	**Trait Pattern Observed**				
	Increase	**Decrease**	**Valley**	**Peak**	**No effect**
LNC	0,282	0,410	0,000	0,077	0,231
SLA	0,176	0,471	0,044	0,000	0,309
Plant life span	0,828	0,069	0,000	0,000	0,103
Seed mass	0,561	0,049	0,049	0,024	0,317
Plant life span	0,828	0,069	0,000	0,000	0,103
Photosynthetic rate/photosynthetic capacity	0,000	0,800	0,000	0,000	0,200


a)
Decrease
Observed SLA Value
Frequency
0
50
100
200
300
0
10
20
30
40
Randomisation value
b)
Valley
Observed SLA Value
Frequency
0
50
100
200
300
0
5
10
15
20
Randomisation value
c)
Peak
Observed SLA Value
Frequency
0
50
100
150
0
5
10
15
20
Randomisation value
d)
Increase
Observed Plant Height Value
Frequency
0
50
150
250
350
0
5
10
15
20
25
Randomisation value
e)
Valley
Observed Plant Height Value
Frequency
0
50
100
150
200
0
5
10
15
Randomisation value
f)
Peak
Observed Plant Height Value
Frequency
0
50
150
250
350
0
5
10
15
20
Randomisation value
g)
Increase
Observed Seed Mass Value
Frequency
0
50
100
150
200
0
5
10
15
20
25
Randomisation value
h)
Decrease
Observed Seed Mass Value
Frequency
0
50
100
150
200
0
5
10
15
Randomisation value


i)
Valley
Observed Seed Mass Value
Frequency
0
50
100
150
200
0
5
10
15
Randomisation value
j)
Peak
Observed Seed Mass Value
Frequency
0
50
100
150
200
0
5
10
15
Randomisation value
k)
Decrease
Observed LNC Value
Frequency
0
50
100
150
200
0
5
10
15
20
Randomisation value
l)
Valley
Observed LNC Value
Frequency
0
50
100
200
300
0
5
10
15
20
Randomisation value
m)
Increase
Observed Photosynetic Rate Value
Frequency
0
50
100
150
200
0
5
10
15
Randomisation value
n)
Decrease
Observed Photosynetic Rate Value
Frequency
0
50
100
150
200
250
0
5
10
15
20
25
Randomisation value
o)
Valley
Observed Photosynetic Rate Value
Frequency
0
50
100
150
200
0
5
10
15
Randomisation value
p)
Peak
Observed Photosynetic Rate Value
Frequency
0
50
100
150
200
250
0
5
10
15
Randomisation value

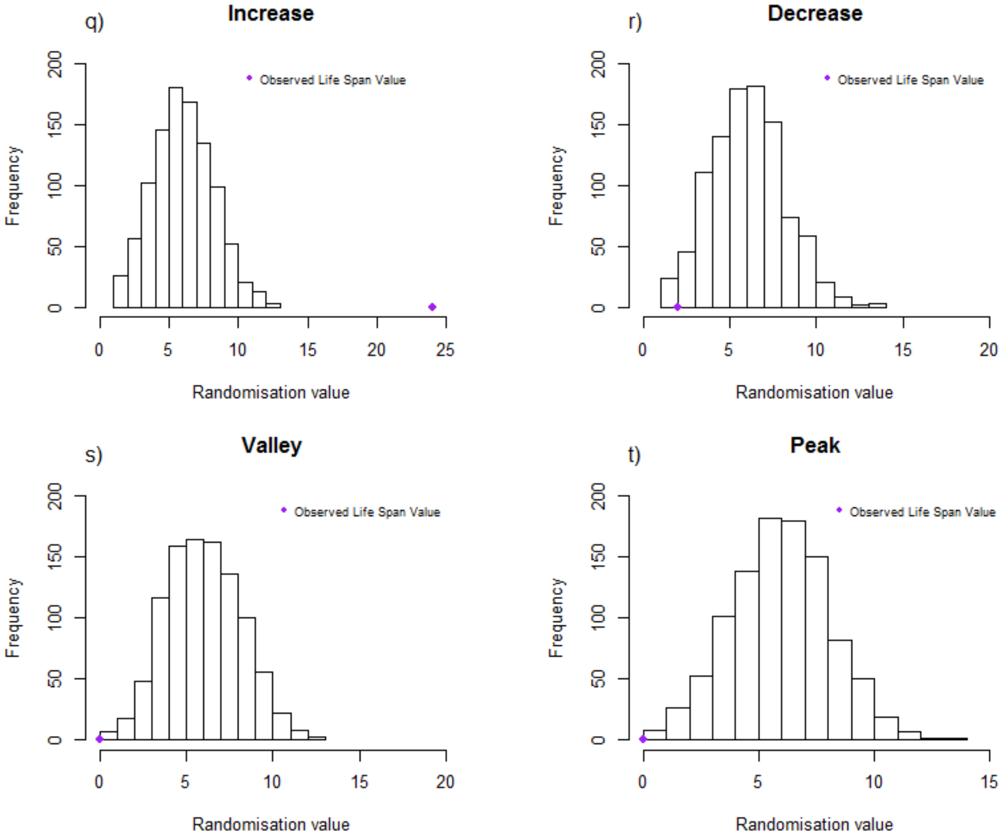


FIGURE C2 Results of the randomised trait assemblages indicating differences in the trait patterns (increase, decrease, valley or peak) observed for the six most frequently reported traits (SLA, plant height, seed mass, LNC, photosynthetic rate, and life span). Histograms represent the frequencies that each trait pattern was selected through assignment in 1000 randomisations. Only assemblages that differed from random expectation were included in the figure (Figure 4.3). The dots on each histogram represent the observed frequency of the respective trait. Different colours represent different traits; red = SLA, light green = plant height, orange = seed mass, cyan = LNC, dark green = photosynthetic rate, and purple = life span.

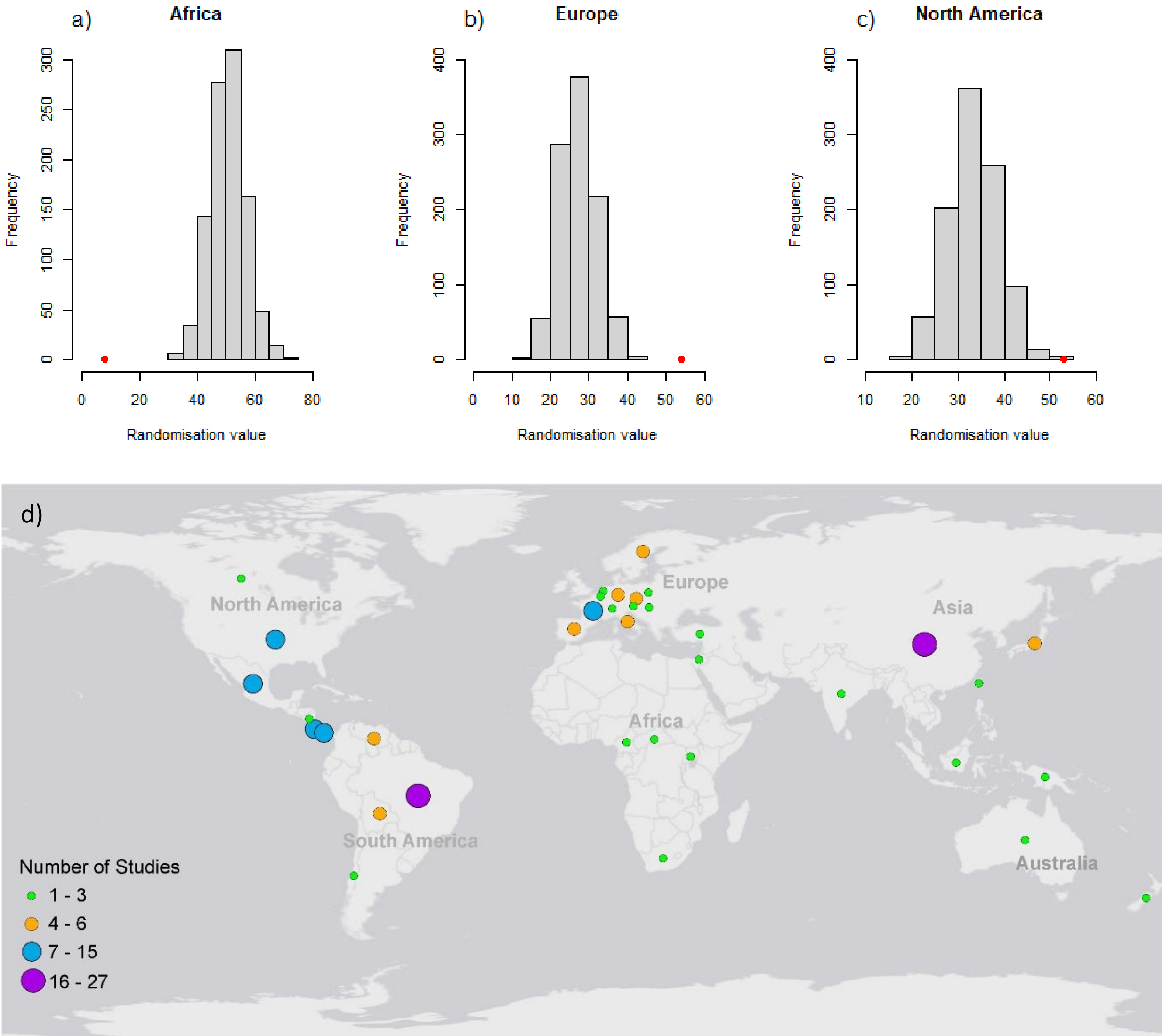


FIGURE D3 Results of the a-f) randomised trait assemblages indicating biases in the geographic region of trait-based studies. Histograms represent the frequencies that each geographic region was selected through assignment in 1000 randomisations. Randomisations were generated by weighing each region according to area of the continents. Significant assemblages were generated for the following regions: a) Africa, b) Europe, and c) North America. The red dots on each histogram indicate the observed frequency of studies reported for each geographic region across the included 199 trait-based studies. Table 4.2 indicates whether the observed number of studies reported for each region differed significantly from random expectation as generated by the randomisation; g) a map illustrating the number of studies investigating trait-based successional patterns plotted by country.

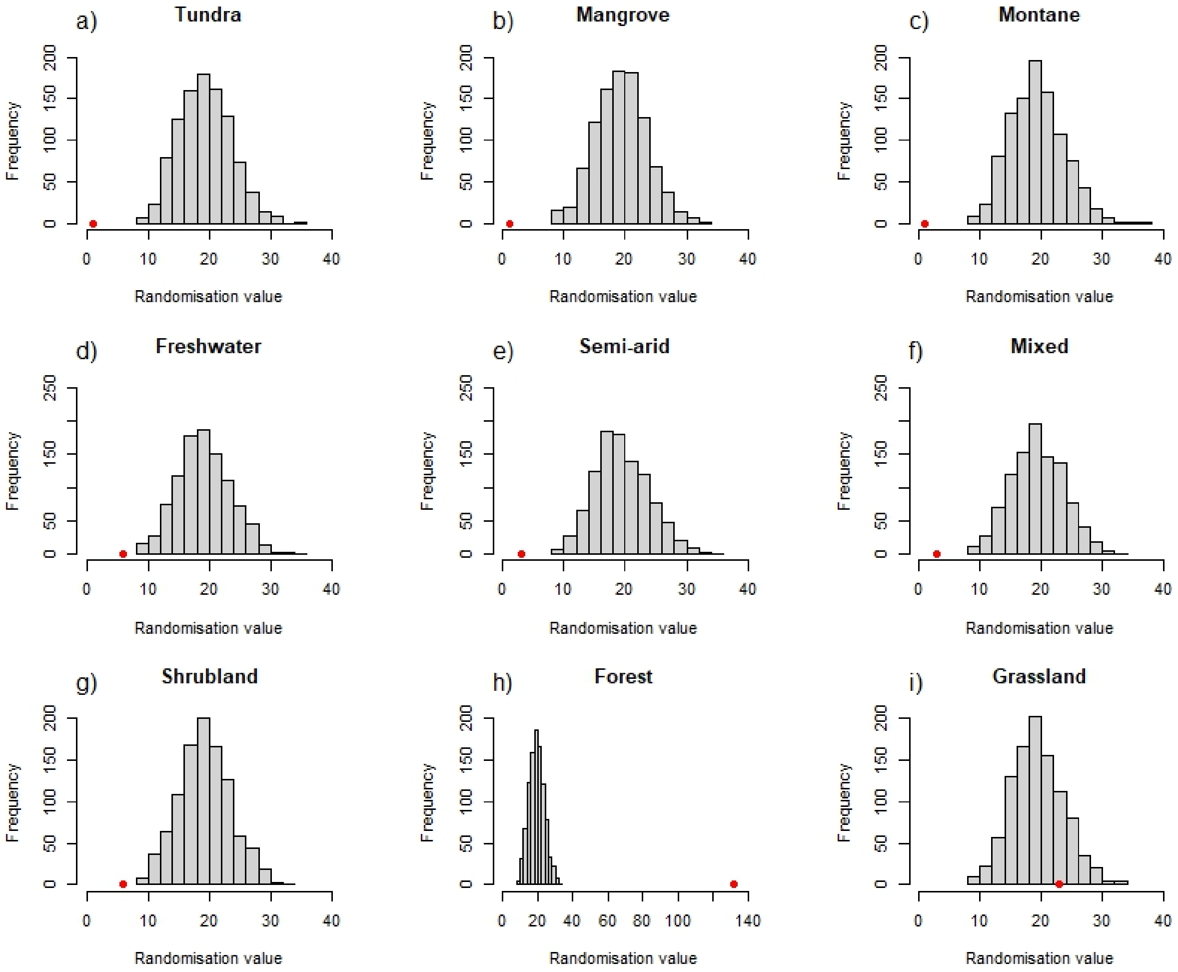


FIGURE D4 Results of the randomised trait assemblages indicating biases in the vegetation types represented in studies assessing trait changes with succession. Histograms represent the frequencies that each vegetation type was selected through assignment in 1000 randomisations. Randomisations for vegetation types were generated with equal weighing. Significant assemblages were generated for the following vegetation types: a) Tundra, b) Mangrove, c) Montane, d) Freshwater, e) Semi-arid, f) Mixed, g) Shrubland, and h) Forest. The red dots on each histogram indicate the observed frequency of studies reported for each vegetation type across the included 199 trait-based studies. Table 4.3 indicates whether the observed number of studies reported for each vegetation type differed significantly from random expectation.

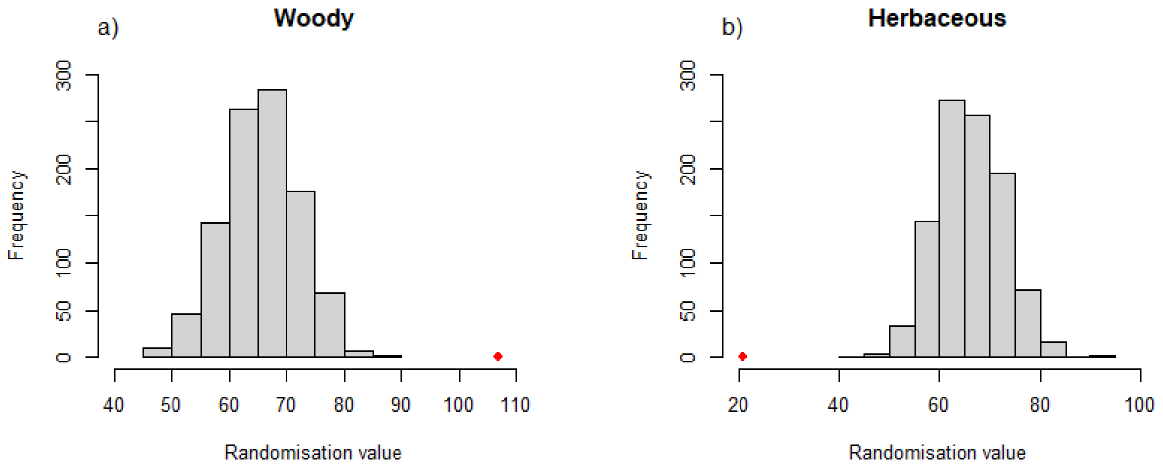


FIGURE D5 Results of the randomised trait assemblages indicating biases in the growth forms represented in studies assessing trait changes with succession. Histograms represent the frequencies that each growth form was selected through assignment in 1000 randomisations. Randomisations were generated with equal weighing for the different growth forms. Significant assemblages were generated for the following growth forms: a) Woody species, and b) herbaceous species. The red dots on each histogram indicate the observed frequency of studies reported for each growth form across the included 199 trait-based studies. Table 4.4 indicates whether the observed number of studies reported for each growth form differed significantly from random expectation.

Example Code

```
#### EXAMPLE CODE ####

#### Generation of random assemblages to test for consistent trends in plant functional traits across successional gradients

# The example provided is for specific leaf area (SLA) #

require(randomizr)
require (BSDA)
require(radiant.data)

library(randomizr)

# Create a vector of 1000 elements
sims <- 1000 #specify number of simulations to run

# Read in the traits table, i.e., total observed frequency in which trait is recorded per trait trend within studies
Traits <- read.csv("C:\\Randomisation example - Trait table.csv", header =T, sep = ";")
#Traits <- read.csv("C:\\Users\\samantha\\OneDrive - SAS Environmental\\Documents\\Sam\\PhD\\Chapter 3\\Randomisations - example codes and files\\Randomisation example - Trait table.csv", header =T, sep = ";")
head(Traits)

No <- apply(Traits[,2:5],1,sum) #sum the number of times each trait

#Create an empty table into which values indicating which trait trends are significantly different from random will be pasted
SignifTable <- matrix(nrow=nrow(Traits), ncol = 4) # four columns for each trait trend (incr, decr, valley and peak)
row.names(SignifTable) <- Traits[,1] # name rows as per the Traits.csv
colnames(SignifTable) <- c("Increase", "Decrease", "Valley", "Peak") # name the columns as per trait trend
head(SignifTable)

# Generate randomisations
for (j in 1:nrow(Traits))
{
  # Set up empty matrix to collect results from randomisations
  MM <- matrix(nrow=1000, ncol=4)
  colnames(MM) <- c("Increase", "Decrease", "Valley", "Peak")
  head (MM)

  # Loop through simulation 1000 times
  for(i in 1:sims)
  {

    # Conduct random assignment
    Z_simple <- simple_ra(N = No[j], num_arms =4) #N = the number of studies which recorded traits with trends
    # Reveal observed potential outcomes
    z <- table(Z_simple)
    z

    # save to Table
    MM[i,] <- z

    #MM
    #print(i)
  }

  #Determine the 2.5 and 97.5% quantiles for "significance"
```

```
  LowerQuant <- apply(MM, 2, function(x) quantile(x,0.025))
  UpperQuant <- apply(MM, 2, function(x) quantile(x,0.975))

  #Check whether your values fall outside the 95% data and put a value in your table indicating this
  SignifTable[j,1] <- ifelse(Traits[j,2] < LowerQuant[1], "SignSmaller",
                        ifelse(Traits[j,2] > UpperQuant[1], "SignLarger", "NS"))
  SignifTable[j,2] <- ifelse(Traits[j,3] < LowerQuant[2], "SignSmaller",
                        ifelse(Traits[j,3] > UpperQuant[2], "SignLarger", "NS"))
  SignifTable[j,3] <- ifelse(Traits[j,4] < LowerQuant[3], "SignSmaller",
                        ifelse(Traits[j,4] > UpperQuant[3], "SignLarger", "NS"))
  SignifTable[j,4] <- ifelse(Traits[j,5] < LowerQuant[4], "SignSmaller",
                        ifelse(Traits[j,5] > UpperQuant[4], "SignLarger", "NS"))
}

head(SignifTable)

## Plot histogram of random assemblages vs the observed value for each trait (e.g., SLA) per trend (incr, decr,
valley, peak) ##
# Example provided is for SLA

MM<-data.frame(MM) # make datframe

windows(8.8)
par(mfrow=c(2,2))
par(mar=c(4,4,4,4))

# INCREASE Patterns
hist(MM$Increase, xlim=c(0,15), ylim=c(0, 200), xlab = "Randomisation value", ylab = "Frequency", main =
"Increase")
points(x = 12, y = 0 ,col="red", pch=19) #SLA
mtext("a)", side=3, line=1, adj=0)
legend(15,300, legend=c("Observed SLA Value"),col=c("red"), pch=19, cex=0.7, box.lty = 0)

# Decrease Patterns
hist(MM$Decrease, xlim=c(0,40), ylim=c(0, 200), xlab = "Randomisation value", ylab = "Frequency", main =
"Decrease")
points(x = 36, y = 0 ,col="red", pch=19) #SLA
mtext("b)", side=3, line=1, adj=0)
legend(22,300, legend=c("Observed SLA Value"),col=c("red"), pch=19, cex=0.7, box.lty = 0)

# Valley Patterns
hist(MM$Valley, xlim=c(0,15), ylim=c(0, 200), xlab = "Randomisation value", ylab = "Frequency", main =
"Valley")
points(x = 3, y = 0 ,col="red", pch=19) #SLA
mtext("c)", side=3, line=1, adj=0)
legend(12,300, legend=c("Observed SLA Value"),col=c("red"), pch=19, cex=0.7, box.lty = 0)

# Peak Patterns
hist(MM$Peak, xlim=c(0,15), ylim=c(0, 200), xlab = "Randomisation value", ylab = "Frequency", main = "Peak")
points(x = 0, y = 0 ,col="red", pch=19) #SLA
mtext("d)", side=3, line=1, adj=0)
legend(12,300, legend=c("Observed SLA Value"),col=c("red"), pch=19, cex=0.7, box.lty = 0)
```

CHAPTER 5: GENERAL CONCLUSION

Global change drivers are responsible for the creation of new environmental conditions and selective pressures which ultimately impact on species and communities in a variety of ways (Walther et al., 2002, Matesanz & Gianoli, 2014). Phenomena resulting as a consequence of global change include climate-related species distributional shifts pole-wards and towards higher elevations, increased incidences of woody encroachment within grassy ecosystems, changes in community composition and structure, and changing phenological patterns and relationships amongst others (Walther et al., 2002). Although such global change related phenomena have been well documented, the underlying drivers of global change and how these factors work simultaneously to influence biological communities are not always apparent. To achieve a better understanding of how global change drivers affect ecosystems, research from a multitude of scientific disciplines should be used to infer on the associated consequences that face biological communities. The focus of this thesis was thus to provide clarity on how global change drivers may impact vegetation dynamics (which manifest through changes in altered phenology patterns, increased woody encroachment, and altered functional trait patterns assembly patterns). Using a combination of experimental and observational data, this thesis revealed several key findings related to vegetation dynamics in the face of global change.

Although the major research themes and questions of each of the research chapters are variable, each chapter lent itself to the next to illustrate the broad implications that global change drivers can have on vegetation communities and associated assembly patterns (Figure 5.1).

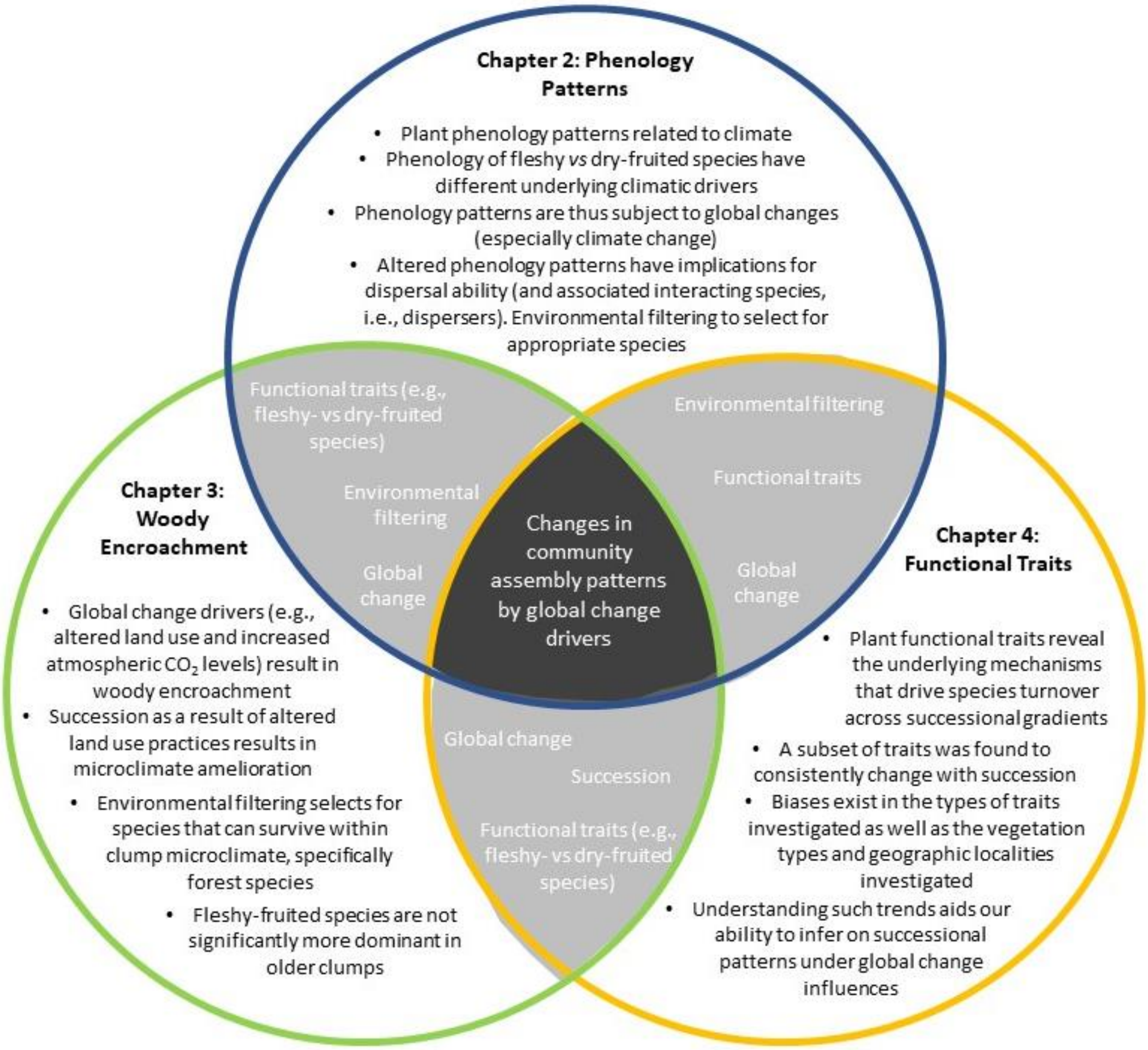


FIGURE 5.1 Schematic diagram illustrating new knowledge gained through this thesis, in the context of how the major themes of the thesis are connected. Blue, green, and yellow circles represent the different research chapters (chapters, 2, 3 and 4 respectively). Unshaded areas provide an indication of the main findings of each chapter. The light grey shaded areas of the Venn diagram illustrate the overlapping themes shared across the chapters (e.g., functional traits in various aspects, environmental filtering processes, global change impacts, and succession). The overarching theme, changes in community assembly patterns because of global change drivers (indicated in the dark grey shaded centre), is applicable to all three research chapters.

Provided below is a general indication of the findings of this thesis:

How climatic factors influence fruiting phenology across South Africa

In Chapter 2, I used herbarium records, to test which climatic factors influence the fruiting phenology of 58 South African fleshy- and dry-fruited tree species. Understanding which climatic variables influence phenology, particularly phenology patterns within the Southern Hemisphere, is important as the need to predict the associated climate change impacts on plants has become imperative in our ever-changing world. Climate is an important driver of plant phenology; thus, it could be expected that fleshy- and dry-fruited species would have different requirements for fruit production, especially as energy investments vary considerably between fruit type and because fruit maturation is thought to correspond with suitable conditions for effective seed dispersal. Indeed, the results from this thesis indicated that across 58 South African fleshy- and dry-fruited species, the mode fruiting day differed significantly between fleshy-fruited and dry-fruited species. Furthermore, it was evident that climatic variables and solar radiation should be considered important drivers that influence the fruiting phenology of tree species across South Africa.

The locality maps generated in Chapter 2 (The drivers of fruiting phenology) that illustrate the distribution of fleshy- and dry-fruited species warrants further investigation. From the maps it is clear that different patterns emerge for fleshy- and dry-fruited species; dry-fruited species were recorded less in the Grassland (Highveld) and Nama-karoo biomes, whereas fleshy-fruited species were more readily recorded within these areas, as well as along the eastern and southern coast lines. The underlying drivers of these patterns could be investigated further (across a larger subset of species) to establish if the different patterns are related to ecological advantages of fleshy- *vs* dry-fruited species within different biomes.

Understanding which climatic variables influence factors such as phenology, aid in our understanding of the associated impacts on plants especially as increasing human pressure and global change, continue to promote the emergence of novel ecosystems (Gravel et al., 2013). In particular, global change drivers are expected to have severe negative effects on the distribution and diversity of species because of altered abiotic conditions and the disruption of species interactions and dispersal dynamics (Thuiller et al., 2008, Tylianakis et al., 2008, Blois et al., 2013, Wisz et al., 2013). As these drivers affect species turnover rates, and can affect community dynamics, the ability to predict which interactions will occur in emerging communities as a response to global changes is of vital importance (Gravel et al., 2013). Such an understanding has important consequences for predicting which interactions will occur under pressure from global change. For example, future studies could investigate the impacts of global change drivers on ecological networks, i.e., representations of which frugivores interact with which fruit-bearing trees, and the modularity of such interactions (Ings et al., 2009). Indeed, I initially attempted to assess networks in the bush clump system I describe in Chapter 2 but had to abandon this chapter due to logistical challenges. The use of ecological networks will allow ecologists to predict community level effects on phenology changes. For example, resource availability (e.g., fruit availability) may vary seasonally because of changes in plant phenology (Bender et al., 2017). Consequently, consumer species need to respond to variable resource availability and often achieve this by switching to different resources between seasons or by switching to different species that that provide a similar resource type (Carnicer, Jordano & Melián, 2009). This switch in resource use can consequently alter the interactions present and thus cause a variation in network properties over short time scales (Carnicer, Jordano & Melián, 2009). Understanding the implications of how networks stabilize in the face of global change thus warrants further investigation.

How succession within an African savanna culminates in forest

As approximately 25% of the Earth's land surface comprises of savanna biomes, a better understanding of how woody encroachment proceeds is of global importance (Wigley, Bond & Hoffman, 2010, Chapin, Sala & Huber-Sannwald, 2013, Stevens et al., 2017). Woody encroachment alters the species composition and therefore significantly contributes to biodiversity degradation in savanna ecosystems. In Chapter 3, I investigated the underlying determinants of bush clump formation (a form of woody encroachment) in a South African savanna and explored whether bush clump succession is driven by deterministic (i.e., predictable changes in species composition) or stochastic (i.e., random) processes. Specifically, I tested (1) whether the similarity in species composition of saplings and trees differs among small and large clumps, (2) which environmental factors are driving succession, and (3) if forest specialization of tree and sapling species within bush clumps increases with the successional gradient. Similarity in species composition between saplings in small clumps and trees in large clumps was higher than similarity between trees in small clumps and trees in large clumps. Furthermore, temperature, soil moisture, relative humidity and light intensity were related to changes in species composition along the successional gradient. As expected, forest specialization of trees increased with increasing clump area indicating that late-successional bush clumps have more forest-type species. The directional changes of species found along the successional gradient suggest a deterministic process of succession driven by changes in local environmental conditions during clump formation.

Clump formation has received the least amount of research attention (O'Connor & Chamane, 2012) of the three main types of woody encroachment, i.e., densification (i.e., a significant increase in the establishment of more woody species) which results in the progression of somewhat open habitats to that of more closed habitats (Dean, Milton & Jeltsch, 1999)), forest expansion (i.e., the suppression of natural disturbances (e.g., fire or frost) that would otherwise prevent the establishment of forest trees (Swaine, 1992, Coetsee & Wigley, 2013)), and nucleation events (i.e., this form of encroachment often starts with the formation of small dense clumps of woody species, commonly referred to as bush clumps which subsequently expand in size (Gower et al., 1992, O'Connor & Chamane, 2012)). A point of contention in the context of these encroachment types is the apparent social and economic value of forests to society. Given the perception that forests are climax communities and that the establishment of trees within the ecosystems is ‘good’ (especially in the current reality that is climate change), encroachment through forest expansion may not always be perceived in a negative light, as opposed to encroachment through densification which is regarded as a threat to ecosystem integrity. Research aimed at illustrating the impacts of the different encroachment types is thus warranted.

Furthermore, grassy ecosystems have evolved in the presence of disturbance (e.g., fire and herbivory) and require such disturbance agents to maintain their ecological integrity (Wigley et al., 2020). In response to disturbance, plants within grassy ecosystems have thus evolved a variety of functional traits that aid in the plants’ ability to resist and/or survive disturbance events (Bond, Woodward & Midgley, 2005). An understanding of these functional traits within grassy ecosystems provides a valuable tool that will aid in our understanding of the ecological processes that shape plant communities within grassy ecosystems as well as aid in our ability to predict species specific responses in the face of disturbance. Future studies on bush clump formation could consider adopting a functional trait approach to assess which traits change with succession; such an approach will assist in our understanding of the heterogeneity and/or homogeneity in plant responses across global grassy ecosystems (i.e., how functionally analogous trait responses are among continents). Such an understanding will improve our ability to both forecast and manage grassy ecosystems in an ever-changing world (Wigley et al., 2020).

As bush clumps provide shade and a potential source of food for a number of different animals they are often considered important for animal activity (Dean et al., 1999). That is, these bush clumps or ‘fertile islands’ (Dean et al., 1999) of trees provide attractive perching sites for birds as well as potential sources of food for many avian frugivores. Additionally, these bush clumps may prove attractive to mammals that seek a refuge from the surrounding environment as well as a possible region to locate food (Dean et al., 1999). Such animal activity may account for the enriched soil located in the sub-canopy of the bush clumps, indicating that, soils can be directly enriched by falling nest material from trees, bird droppings and mammal droppings among other factors (Dean et al., 1999). These conditions are thought to favour the establishment of trees, especially fleshy-fruited plant species that are thought to have a greater potential for seedling establishment with increased soil nutrient and shade availability (Manders & Richardson, 1992; Dean et al., 1999). Moreover, other studies have found a correlation between the distribution of fleshy-fruited plants and the level of soil fertility; in particular, both potassium and nitrogen seem to be important nutrients influencing the correlation between fleshy fruited plants and their spatial distributions (Milewski, 1982; Hughes et al., 1993). Thus, frugivore-dispersed plants are considered likely colonisers of bush clump sub-canopy sites. However, this warrants further investigation.

Identifying biases in trait-based successional studies can improve the use of functional traits in community dynamic science

The use of traits to answer questions related to ecosystem change and assembly patterns has become apparent (Navas et al., 2010, Chen et al., 2021). The growing evidence that differences in plant traits can be used to infer ecosystem processes such as succession has resulted in the need for 1) the use of consistent traits being measured across research fields, and 2) standardised ways in which to measure plant functional traits. In Chapter 4, I outlined the significance of functional traits and their associated use in understanding community dynamics and organisation. Six traits were identified as being frequently reported in the succession literature. Null model approaches were used to assess whether the direction of trait change with the successional gradient (i.e., increase, decrease, hump-shape or valley-shape) was consistent across studies, and whether biases in growth forms, geography and vegetation types were evident across the investigated studies. Across successional gradients SLA, LNC, and photosynthetic rate / capacity decreased, whereas plant height, seed mass, and plant life span increased. Clear biases in trait studies across successional gradients were observed: woody communities were studied more often than herbaceous and the combined woody and herbaceous communities; studies were biased towards Europe; and most studies were conducted in forest systems. If comparisons are to be drawn to make generalisations on community assembly during succession, the need to standardise trait types and measurements across studies is of vital importance.

Several global trait databases exist (e.g., Wright et al., 2004, Díaz et al., 2007, Stahl et al., 2013, Jeliazkov et al., 2020, Kattge et al., 2020, Wigley et al., 2020). Within these, a myriad of different trait values has been recorded. A major goal within trait-based studies has been a drive to find convergence in traits which ultimately infer of trait syndromes that can be used to infer on ecological processes across ecosystems (Wigley et al., 2020); indeed, a multitude of standardised functional trait measurement methods have been developed (Cornelissen et al., 2003, Perez-Harguindeguy et al., 2016, Wigley et al., 2020). The advantage of using standardised methods is that they allow for comparable data to address questions relating to ecosystem function and process at different scales and across different ecosystems. Although trait handbooks provide standardised methods for an array of functional traits, which traits are best to measure will always depend on the aims and types of questions investigated, as well as funding issues, and logistical and practical constraints (Trimble & van Aarde, 2012, Perez-Harguindeguy et al., 2016, Wigley et al., 2020). Although the use of standardised methods of trait measurement is advantageous, their use across ecosystems is not always apparent. For example, it has recently been reported that open *vs* closed ecosystems have different trait indicators that are applicable to each (Wigley et al., 2020), i.e., traits that may be important in closed systems (e.g., forests) may not be applicable within open systems (e.g., temperate savannas). For example, in fire-driven savanna systems, it is advantageous for seedlings to quickly establish below-ground resources which aid in their survival, particularly in ensuring their survival in the presence of fire (Abbadie et al., 2006). Having a high seedling leaf to shoot biomass ratio (SLS) is beneficial in such systems as rather than investing in aboveground space for light (which is more limited in forests than savannas), quick storage of belowground reserves aids in survival within this disturbance driven system (Gignoux et al., 2009). In contrast, forest species, which do not experience fire, invest less in leaves as they do not need underground storage reserves to survive disturbance. Instead, they invest more in growing taller to compete for light.

Despite this, the use of handbooks has proved useful in aiding the selection of appropriate traits and guiding the use of standardised methods in which to measure traits so that they are easily comparable with other such trait values from studies from a variety of vegetation types. Future research should focus on improving our overall understanding of successional-based trait change and to incorporate traits that represent different axes of plant function. Furthermore, additional focus should be placed on underrepresented geographic regions (i.e., Africa) and, perhaps more importantly, on under-researched vegetation types (e.g., grasslands).

Geographic biases in research

This thesis highlighted that a geographic skew in research effort exists across ecological research fields. For example, within the Northern hemisphere, long-term phenological time series are available (Parmesan & Yohe, 2003) which are often lacking for the Southern Hemisphere (Magurran et al., 2010), particularly in Africa. The availability of such databases has likely aided in the observed geographic skew towards the Northern hemisphere, especially in the context of phenological studies (Chambers et al., 2013). Similarly, I found evidence to suggest that a bias towards European countries and forests exists within trait-based successional studies; such biases may promote the impression that observed plant trait syndromes may be consistent across different ecosystems when in reality, different trait suites may be responsible for plant assembly patterns across spatial scales. Although Northern hemisphere countries tend to receive disproportionate amounts of research attention (an observation that has been well documented across several ecological fields (e.g., climate change biology, invasive species research and conservation) (Pyšek et al., 2008, Trimble & van Aarde, 2012)**)**, there is a drive across research fields aimed at filling our knowledge gaps and to include under-researched geographic areas and vegetation types in future research.

Conclusion

This thesis highlights the impacts that global change drivers may have on ecosystems. Here I provide clarity on how global change drivers may impact vegetation dynamics (which manifest through changes in, for example, altered phenology patterns, increased woody encroachment, and altered functional trait patterns assembly patterns). By influencing and changing climate patterns, altering, and increasing land use practices, polluting, and overharvesting resources (Gibert, Debat & Ghalambor, 2019), anthropogenic activities will ultimately result in negative impacts for ecosystems, species, as well as human health (Kerr, Kharouba & Currie, 2007, Gibert, Debat & Ghalambor, 2019).

References

ABBADIE, L., J. GIGNOUX, X. ROUX, AND M. LEPAGE. 2006. Lamto: structure, functioning, and dynamics of a savanna ecosystem. Springer Science & Business Media.

ABERNETHY, K., BUSH, E. R., FORGET, P. M., MENDOZA, I., MORELLATO, L. P., C. 2018. Current issues in tropical phenology: A synthesis. Biotropica, 50: 477–482.

ADOLE, T., DASH, J., RODRIGUEZ-GALIANO, V. AND ATKINSON, P.M., 2019. Photoperiod controls vegetation phenology across Africa. Communications biology, 2: 391.

AIZEN, M.A., 2003. Influences of animal pollination and seed dispersal on winter flowering in a temperate mistletoe. Ecology, 84: 2613-2627.

ALLAN, R. P., E. HAWKINS, N. BELLOUIN, AND B. COLLINS. 2021. IPCC, 2021: Summary for Policymakers. Cambridge University Press, Cambridge.

ALTIERI, A. H., S. B. HARRISON, J. SEEMANN, R. COLLIN, R. J. DIAZ, AND N. KNOWLTON. 2017. Tropical dead zones and mass mortalities on coral reefs. Proceedings of the National Academy of Sciences 114: 3660-3665.

ANTOS, J. A., H. J. GUEST, AND R. PARISH. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. Journal of Ecology 93: 536-543.

ARCHER, S. 1990. Development and Stability of Grass/Woody Mosaics in a Subtropical Savanna Parkland, Texas, U. S. A. Journal of Biogeography 17: 453-462.

ARCHER, S. 1995. Tree-grass dynamics in a Prosopis-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2: 83-99.

ARCHER, S., C. SCIFRES, C. BASSHAM, AND R. MAGGIO. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological monographs 58: 111-127.

ARCHER, S. R., E. M. ANDERSEN, K. I. PREDICK, S. SCHWINNING, R. J. STEIDL, AND S. R. WOODS. 2017a. Woody Plant Encroachment: Causes and Consequences. *In* D. D. Briske (Ed.). Rangeland Systems: Processes, Management and Challenges, pp. 25-84. Springer International Publishing, Cham.

ARCHER, S. R., E. M. ANDERSEN, K. I. PREDICK, S. SCHWINNING, R. J. STEIDL, AND S. R. WOODS. 2017b. Woody plant encroachment: causes and consequences. Rangeland systems, pp. 25-84. Springer.

ARCHIBALD, S., A. NICKLESS, N. GOVENDER, R. SCHOLES, AND V. LEHSTEN. 2010. Climate and the inter-annual variability of fire in southern Africa: a meta-analysis using long-term field data and satellite-derived burnt area data. Global Ecology and Biogeography 19: 794-809.

ARNHOLT, A. T., AND B. EVANS. 2017. Package 'BSDA'.

ASNER, G. P., A. J. ELMORE, L. P. OLANDER, R. E. MARTIN, AND T. A. HARRIS. 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources 29 261-299.

ÁVILA-LOVERA, E., G. R. GOLDSMITH, K. M. KAY, AND J. L. FUNK. 2022. Above-and below-ground functional trait coordination in the Neotropical understory genus *Costus*. AoB Plants 14: plab073.

BARNAGAUD, J.-Y., V. DEVICTOR, F. JIGUET, M. BARBET-MASSIN, I. LE VIOL, AND F. ARCHAUX. 2012. Relating habitat and climatic niches in birds. PLoS One 7: e32819.

BARNES, P. W., AND S. ARCHER. 1996. Influence of an overstorey tree (Prosopis glandulosa) on associated shrubs in a savanna parkland: implications for patch dynamics. Oecologia 105: 493-500.

BAUM, J. K., R. A. MYERS, D. G. KEHLER, B. WORM, S. J. HARLEY, AND P. A. DOHERTY. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science 299: 389-392.

BAZZAZ, F. 1979. The physiological ecology of plant succession. Annual review of Ecology and Systematics 10: 351-371.

BAZZAZ, F., AND S. PICKETT. 1980. Physiological ecology of tropical succession: a comparative review. Annual review of ecology and systematics 11: 287-310.

BELAYNEH, A., AND Z. K. TESSEMA. 2017. Mechanisms of bush encroachment and its inter-connection with rangeland degradation in semi-arid African ecosystems: a review. Journal of Arid Land 9: 299-312.

BELLUAU, M., AND B. SHIPLEY. 2018. Linking hard and soft traits: Physiology, morphology and anatomy interact to determine habitat affinities to soil water availability in herbaceous dicots. Plos one 13: e0193130.

BENDER, I., W. D. KISSLING, K. BÖHNING-GAESE, I. HENSEN, I. KÜHN, T. WIEGAND, D. M. DEHLING, AND M. SCHLEUNING. 2017. Functionally specialised birds respond flexibly to seasonal changes in fruit availability. Journal of Animal Ecology.

BERTIN, R. I. 2015. Climate change and flowering phenology in Worcester County, Massachusetts. International Journal of Plant Sciences 176: 107-119.

BEWS, J. W. 1917. The plant succession in the thorn veld. éditeur non identifié.

BLEHER, B., POTGIETER, C.J., JOHNSON, D.N. AND BÖHNING-GAESE, K., 2003. The importance of figs for frugivores in a South African coastal forest. Journal of Tropical Ecology, 19: 375-386.

BLOIS, J. L., P. L. ZARNETSKE, M. C. FITZPATRICK, AND S. FINNEGAN. 2013. Climate change and the past, present, and future of biotic interactions. Science 341: 499-504.

BOLMGREN, K., AND O. ERIKSSON. 2010. Seed mass and the evolution of fleshy fruits in angiosperms. Oikos 119: 707-718.

BOND, W., G. MIDGLEY, AND F. WOODWARD. 2003. What controls South African vegetation-climate or fire? South African Journal of Botany 69: 79-91.

BOND, W. J. 2008. What Limits Trees in C_4 Grasslands and Savannas? Annual Review of Ecology, Evolution, and Systematics 39: 641-659.

BOND, W. J., AND G. F. MIDGLEY. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology 6: 865-869.

BOND, W. J., AND C. L. PARR. 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. Biological Conservation 143: 2395-2404.

BOND, W. J., AND B. W. VAN WILGEN. 2012. Fire and plants. Springer Science & Business Media, Hong Kong.

BOND, W. J., F. I. WOODWARD, AND G. F. MIDGLEY. 2005. The global distribution of ecosystems in a world without fire. New phytologist 165: 525-538.

BOUKILI, V. K., AND R. L. CHAZDON. 2017. Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. Perspectives in Plant Ecology, Evolution and Systematics 24: 37-47.

BOULTER, S. L., C. L. LAMBKIN, AND N. T. STARICK. 2011. Assessing the abundance of seven major arthropod groups along an altitudinal gradient and across seasons in subtropical rainforest. Memoirs of the Queensland Museum 55: 303-313.

BRIGGS, J. M., A. K. KNAPP, J. M. BLAIR, J. L. HEISLER, G. A. HOCH, M. S. LETT, AND J. K. MCCARRON. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55: 243-254.

BRITTON, D., C. N. MUNDY, C. M. MCGRAW, A. T. REVILL, AND C. L. HURD. 2019. Responses of seaweeds that use CO_2 as their sole inorganic carbon source to ocean acidification: differential effects of fluctuating pH but little benefit of CO_2 enrichment. ICES Journal of Marine Science 76: 1860-1870.

BRITZ, M., AND D. WARD. 2007. Dynamics of woody vegetation in a semi-arid savanna, with a focus on bush encroachment. African Journal of Range and Forage Science 24: 131-140.

BROWN, J. R., AND S. ARCHER. 1989a. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. Oecologia 80: 19.

BROWN, J. R., AND S. ARCHER. 1989b. Woody plant invasion of grasslands: establishment of honey mesquite *(Prosopis glandulosa* var.*glandulosa*) on sites differing in herbaceous biomass and grazing history. Oecologia 80: 19-26.

BUFFELSKLOOF NATURE RESERVE. 2020. Buffelskloof Private Nature Reserve.

BURKE, J., J. MAHAN, AND J. HATFIELD. 1988. Crop-specific thermal kinetic windows in relation to wheat and cotton biomass production. Agronomy Journal 80: 553-556.

BURKE, M., L. GUSTA, H. QUAMME, C. WEISER, AND P. LI. 1976. Freezing and injury in plants. Annual Review of plant physiology 27: 507-528.

BURROWS, J. E., AND S. BURROWS. 2003. Buffelskloof Nature Reserve, Trails map. Creda, Johannesburg.

BUSH, E.R., BUNNEFELD, N., DIMOTO, E., DIKANGADISSI, J.T., JEFFERY, K., TUTIN, C., WHITE, L. AND ABERNETHY, K.A. 2018. Towards effective monitoring of tropical phenology: maximizing returns and reducing uncertainty in long-term studies. Biotropica, 50: 455-464.

CABAL, C., H. DE DEURWAERDER, AND S. MATESANZ. 2021. Field methods to study the spatial root density distribution of individual plants. Plant and Soil 462: 25-43.

CARNICER, J., P. JORDANO, AND C. J. MELIÁN. 2009. The temporal dynamics of resource use by frugivorous birds: a network approach. Ecology 90: 1958-1970.

CHAI, Y., M. YUE, M. WANG, J. XU, X. LIU, R. ZHANG, AND P. WAN. 2016. Plant functional traits suggest a change in novel ecological strategies for dominant species in the stages of forest succession. Oecologia 180: 771-783.

CHAMBERS, L. E., R. ALTWEGG, C. BARBRAUD, P. BARNARD, L. J. BEAUMONT, R. J. CRAWFORD, J. M. DURANT, L. HUGHES, M. R. KEATLEY, AND M. LOW. 2013. Phenological changes in the southern hemisphere. PloS one 8: e75514.

CHANG, C. C., AND B. L. TURNER. 2019. Ecological succession in a changing world. Journal of Ecology 107: 503-509.

CHAPIN, F. S., O. E. SALA, AND E. HUBER-SANNWALD. 2013. Global biodiversity in a changing environment: scenarios for the 21st century. Springer Science & Business Media.

CHAPMAN, C. A., L. J. CHAPMAN, A. E. ZANNE, J. R. POULSEN, AND C. J. CLARK. 2005. A 12-year phenological record of fruiting: implications for frugivore populations and indicators of climate change. Tropical fruits and frugivores, pp. 75-92. Springer.

CHAPMAN, C. A., K. VALENTA, T. R. BONNELL, K. A. BROWN, AND L. J. CHAPMAN. 2018. Solar radiation and ENSO predict fruiting phenology patterns in a 15-year record from Kibale National Park, Uganda. Biotropica 50: 384-395.

CHARLES-DOMINIQUE T, MIDGLEY GF, TOMLINSON KW, BOND WJ. 2018. Steal the light: shade vs fire adapted vegetation in forest–savanna mosaics. New Phytologist 218: 1419–1429

CHASE, J. M., AND J. A. MYERS. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society of London B: Biological Sciences 366: 2351-2363.

CHEN, G., K. YANG, J. ZHANG, M. WANG, L. WANG, AND J. XIAN. 2021. Effects of succession stages and altitudinal gradient on leaf surface area and biomass allocation of typical plants in the subalpine of Eastern Tibetan Plateau. Global Ecology and Conservation 27: e01590.

CHEN, S.-C., W. K. CORNWELL, H.-X. ZHANG, AND A. T. MOLES. 2016. Plants show more flesh in the tropics: variation in fruit type along latitudinal and climatic gradients. Ecography 40: 531-538.

CHEN, X., AND H. ISHWARAN. 2012. Random forests for genomic data analysis. Genomics 99: 323-329.

CHEN, X., J. SUN, M. WANG, M. LYU, K. J. NIKLAS, S. T. MICHALETZ, Q. ZHONG, AND D. CHENG. 2020. The leaf economics spectrum constrains phenotypic plasticity across a light gradient. Frontiers in Plant Science 11: 735.

CHMIELEWSKI, F.-M., AND T. RÖTZER. 2001. Response of tree phenology to climate change across Europe. Agricultural and Forest Meteorology 108: 101-112.

CHRISTENSEN, N. L., AND R. K. PEET. 1984. Convergence during secondary forest succession. The Journal of Ecology: 25-36.

CHRISTIE, A. P., T. AMANO, P. A. MARTIN, G. E. SHACKELFORD, B. I. SIMMONS, AND W. J. SUTHERLAND. 2019. Simple study designs in ecology produce inaccurate estimates of biodiversity responses. Journal of Applied Ecology 56: 2742-2754.

CLARK, D. A., AND D. B. CLARK. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. The American Naturalist 124: 769-788.

CLELAND, E. E., I. CHUINE, A. MENZEL, H. A. MOONEY, AND M. D. SCHWARTZ. 2007. Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22: 357-365.

CLIMATE-DATA.ORG. 2019. Climate Nakuru: Temperature, Climate graph, Climate table for Lydenburg.

COATES PALGRAVE, K. 2002. Trees of southern Africa. Struik, Cape Town.

COETSEE, C., AND B. J. WIGLEY. 2013. Virgilia divaricate may facilitate forest expansion in the afrotemperate forests of the southern Cape, South Africa. Koedoe: African Protected Area Conservation and Science 55: 1-8.

CONNELL, J. H., AND R. O. SLATYER. 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. The American Naturalist 111: 1119-1144.

COOMBE, B. 1976. The development of fleshy fruits. Annual Review of Plant Physiology 27: 207-228.

CORNELISSEN, J., S. LAVOREL, E. GARNIER, S. DÍAZ, N. BUCHMANN, D. GURVICH, P. REICH, H. TER STEEGE, H. MORGAN, AND M. VAN DER HEIJDEN. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51: 335-380.

CORNWELL, W. K., AND D. D. ACKERLY. 2010. A link between plant traits and abundance: evidence from coastal California woody plants. Journal of Ecology 98: 814-821.

CRAINE, J. M. 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of ecology 93: 1041-1052.

CRAMER, V. A. 2007. Old fields as complex systems: new concepts for describing the dynamics of abandoned farmland. Old fields: Dynamics and restoration of abandoned farmland: 334.

DARU, B. H., M. VAN DER BANK, AND T. J. DAVIES. 2018. Unravelling the evolutionary origins of biogeographic assemblages. Diversity and Distributions 24: 313-324.

DAVIS, M. B., AND R. G. SHAW. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292: 673-679.

DE SOUZA, A. C., AND J. A. PREVEDELLO. 2019. Geographic distribution of the threatened palm *Euterpe edulis* mart. in the atlantic forest: Implications for conservation. Oecologia Australis 23: 636-643.

DEAN, W. R. J., S. J. MILTON, AND F. JELTSCH. 1999. Large trees, fertile islands, and birds in arid savanna. Journal of Arid Environments 41: 61-78.

DENT, D. H., S. J. DEWALT, AND J. S. DENSLOW. 2013. Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. Journal of Vegetation Science 24: 530-542.

DERROIRE, G., P. BALVANERA, C. CASTELLANOS-CASTRO, G. DECOCQ, D. K. KENNARD, E. LEBRIJA-TREJOS, J. A. LEIVA, P. C. ODÉN, J. S. POWERS, AND V. RICO-GRAY. 2016. Resilience of tropical dry forests–a meta-analysis of changes in species diversity and composition during secondary succession. Oikos 125: 1386-1397.

DEZEURE, R., P. BÜHLMANN, L. MEIER, AND N. MEINSHAUSEN. 2015. High-dimensional inference: Confidence intervals, $ p $-values and R-software hdi. Statistical science 30: 533-558.

DÍAZ, S., J. KATTGE, J. H. CORNELISSEN, I. J. WRIGHT, S. LAVOREL, S. DRAY, B. REU, M. KLEYER, C. WIRTH, AND I. C. PRENTICE. 2016. The global spectrum of plant form and function. Nature 529: 167-171.

DÍAZ, S., S. LAVOREL, F. DE BELLO, F. QUÉTIER, K. GRIGULIS, AND T. M. ROBSON. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences 104: 20684-20689.

DÍAZ, S., I. NOY-MEIR, AND M. CABIDO. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? Journal of Applied Ecology 38: 497-508.

DÍAZ, S., A. PURVIS, J. H. CORNELISSEN, G. M. MACE, M. J. DONOGHUE, R. M. EWERS, P. JORDANO, AND W. D. PEARSE. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecology and evolution 3: 2958-2975.

DINI-ANDREOTE, F., J. C. STEGEN, J. D. VAN ELSAS, AND J. F. SALLES. 2015. Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. Proceedings of the National Academy of Sciences: 201414261.

DISKIN, E., H. PROCTOR, M. JEBB, T. SPARKS, AND A. DONNELLY. 2012. The phenology of *Rubus fruticosus* in Ireland: herbarium specimens provide evidence for the response of phenophases to temperature, with implications for climate warming. International Journal of Biometeorology 56: 1103-1111.

DIXON, D.J., CALLOW, J.N., DUNCAN, J.M., SETTERFIELD, S.A. AND PAULI, N., 2021. Satellite prediction of forest flowering phenology. Remote Sensing of Environment, 25: 112197.

DOI, H., AND M. TAKAHASHI. 2008. Latitudinal patterns in the phenological responses of leaf colouring and leaf fall to climate change in Japan. Global Ecology and Biogeography 17: 556-561.

DOLÉDEC, S., D. CHESSEL, AND C. GIMARET-CARPENTIER. 2000. Niche separation in community analysis: a new method. Ecology 81: 2914-2927.

DOUMA, J. C., M. W. DE HAAN, R. AERTS, J. P. M. WITTE, AND P. M. VAN BODEGOM. 2012a. Succession-induced trait shifts across a wide range of NW European ecosystems are driven by light and modulated by initial abiotic conditions. Journal of Ecology 100: 366-380.

DOUMA, J. C., M. W. A. DE HAAN, R. AERTS, J.-P. M. WITTE, AND P. M. VAN BODEGOM. 2012b. Succession-induced trait shifts across a wide range of NW European ecosystems are driven by light and modulated by initial abiotic conditions. Journal of Ecology 100: 366-380.

DOWNS, C. T. 2011. 14 th Annual Parrot Count-Report on the 2011 Cape Parrot Big Birding Day. Unpublished report. Pietermaritzburg: University of KwaZulu-Natal.

DOWNS, C. T., M. PFEIFFER, AND L. A. HART. 2014. Fifteen years of annual Cape Parrot *Poicephalus robustus* censuses: current population trends and conservation contributions. Ostrich 85: 273-280.

DUNN, R. R., D. AGOSTI, A. N. ANDERSEN, X. ARNAN, C. A. BRUHL, X. CERDÁ, A. M. ELLISON, B. L. FISHER, M. C. FITZPATRICK, AND H. GIBB. 2009. Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. Ecology Letters 12: 324-333.

ELDRIDGE, D. J., M. A. BOWKER, F. T. MAESTRE, E. ROGER, J. F. REYNOLDS, AND W. G. WHITFORD. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters 14: 709-722.

ERASMUS, B, VAN JAARSVELD, A., S, CHOWN, S. L., KSHATRIYA, M., AND WESSELS, K., J. 2002. Vulnerability of South African animal taxa to climate change. Global Change Biology, 8: 679-693.

ESRI. 2011. ArcGIS Desktop: Realease 10. Relands, CA: Environmental Systems Research Institute.

ESTES, J. A., J. TERBORGH, J. S. BRASHARES, M. E. POWER, J. BERGER, W. J. BOND, S. R. CARPENTER, T. E. ESSINGTON, R. D. HOLT, AND J. B. JACKSON. 2011. Trophic downgrading of planet Earth. Science 333: 301-306.

EVANS, J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C 3 plants. Oecologia 78: 9-19.

EVERINGHAM, S. E., R. A. BLICK, M. E. SABOT, E. SLAVICH, AND A. T. MOLES. 2021. Southern hemisphere plants show more delays than advances in flowering phenology. Journal of ecology 1: 1-11.

FELTON, A., J. FISCHER, D. B. LINDENMAYER, R. MONTAGUE-DRAKE, A. R. LOWE, D. SAUNDERS, A. M. FELTON, W. STEFFEN, N. T. MUNRO, AND K. YOUNGENTOB. 2009. Climate change, conservation and management: an assessment of the peer-reviewed scientific journal literature. Biodiversity and conservation 18: 2243-2253.

FICK, S. E., AND R. J. HIJMANS. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37: 4302-4315.

FILOTAS, E., L. PARROTT, P. J. BURTON, R. L. CHAZDON, K. D. COATES, L. COLL, S. HAEUSSLER, K. MARTIN, S. NOCENTINI, AND K. J. PUETTMANN. 2014. Viewing forests through the lens of complex systems science. Ecosphere 5: 1-23.

FLAKE, S.W., HONDA, E.A., PILON, N.A., HOFFMANN, W.A. AND DURIGAN, G., 2022. Not all trees can make a forest: Tree species composition and competition control forest encroachment in a tropical savanna. Journal of Ecology, 110: 301-312.

FODEN, W., G. F. MIDGLEY, G. HUGHES, W. J. BOND, W. THUILLER, M. T. HOFFMAN, P. KALEME, L. G. UNDERHILL, A. REBELO, AND L. HANNAH. 2007. A changing climate is eroding the geographical range of the Namib Desert tree Aloe through population declines and dispersal lags. Diversity and Distributions 13: 645-653.

FOLLAND, C. K., T. R. KARL, AND M. J. SALINGER. 2002. Observed climate variability and change. Weather 57: 269-278.

FORREST, J., AND A. J. MILLER-RUSHING. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. The Royal Society.

FORREST, J. R., AND J. D. THOMSON. 2011. An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. Ecological Monographs 81: 469-491.

FOX, J., S. WEISBERG, D. ADLER, D. BATES, G. BAUD-BOVY, S. ELLISON, D. FIRTH, M. FRIENDLY, G. GORJANC, AND S. GRAVES. 2012. Package 'car'. Vienna: R Foundation for Statistical Computing.

GALLAGHER, R., L. HUGHES, AND M. LEISHMAN. 2009. Phenological trends among Australian alpine species: using herbarium records to identify climate-change indicators. Australian Journal of Botany 57: 1-9.

GARNIER, E., J. CORTEZ, G. BILLÈS, M.-L. NAVAS, C. ROUMET, M. DEBUSSCHE, G. LAURENT, A. BLANCHARD, D. AUBRY, AND A. BELLMANN. 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85: 2630-2637.

GIAM, X. 2017. Global biodiversity loss from tropical deforestation. Proceedings of the National Academy of Sciences 114: 5775-5777.

GIBERT, P., V. DEBAT, AND C. K. GHALAMBOR. 2019. Phenotypic plasticity, global change, and the speed of adaptive evolution. Current Opinion in Insect Science 35: 34-40.

GIGNOUX, J., G. LAHOREAU, R. JULLIARD, AND S. BAROT. 2009. Establishment and early persistence of tree seedlings in an annually burned savanna. Journal of Ecology 97: 484-495.

GILLIAM, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57: 845-858.

GIORGI, F. 2006. Climate change hot-spots. Geophysical Research Letters 33: 8.

GORDO, O., AND J. J. SANZ. 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. Global Change Biology 16: 1082-1106.

GOTSCH, S. G., E. L. GEIGER, A. C. FRANCO, G. GOLDSTEIN, F. C. MEINZER, AND W. A. HOFFMANN. 2010. Allocation to leaf area and sapwood area affects water relations of co-occurring savanna and forest trees. Oecologia 163: 291-301.

GOVERDE, M., AND A. ERHARDT. 2003. Effects of elevated CO_2 on development and larval food-plant preference in the butterfly *Coenonympha pamphilus* (Lepidoptera, Satyridae). Global Change Biology 9: 74-83.

GOWER, C., G. STUART-HILL, P. ZACHARIAS, C. HURT, AND P. ZACHARIAS. 1992. Towards understanding the influence of termitaria on bush clump development in Natal Valley Bushveld. Proceedings of the first Natal Bushveld symposium. Grassland Society of southern Africa, Scottsville, pp. 40-42.

GRAHAM, E. A., S. S. MULKEY, K. KITAJIMA, N. G. PHILLIPS, AND S. J. WRIGHT. 2003. Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. Proceedings of the National Academy of Sciences 100: 572-576.

GRAVEL, D., T. POISOT, C. ALBOUY, L. VELEZ, AND D. MOUILLOT. 2013. Inferring food web structure from predator–prey body size relationships. Methods in Ecology and Evolution 4: 1083-1090.

GREINER, R., I. GORDON, AND C. COCKLIN. 2009. Ecosystem services from tropical savannas: economic opportunities through payments for environmental services. The Rangeland Journal 31: 51-59.

GREVE, M., K. J. GASTON, B. J. VAN RENSBURG, AND S. L. CHOWN. 2008. Environmental factors, regional body size distributions and spatial variation in body size of local avian assemblages. Global Ecology and Biogeography 17: 514-523.

GREVE, M., A. M. LYKKE, C. W. FAGG, R. E. GEREAU, G. P. LEWIS, R. MARCHANT, A. R. MARSHALL, J. NDAYISHIMIYE, J. BOGAERT, AND J.-C. SVENNING. 2016. Realising the potential of herbarium records for conservation biology. South African Journal of Botany 105: 317-323.

GRIME, J. 1979. Primary strategies in plants. Transactions of the Botanical Society of Edinburgh, pp. 151-160. Taylor & Francis.

GRIZ, L. M. S., AND I. C. S. MACHADO. 2001. Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. Journal of tropical Ecology 17: 303-321.

GUARIGUATA, M. R., AND R. OSTERTAG. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. For. Ecol. Manage. 148: 185-206.

HADDAD, W. A. 2011. Regeneration and expansion of Afromontane forest in Buffelskloof Private Nature Reserve, Mpumalanga. PhD Dissertation.

HALLIDAY, F. W., R. W. HECKMAN, P. A. WILFAHRT, AND C. E. MITCHELL. 2020. Eutrophication, biodiversity loss, and species invasions modify the relationship between host and parasite richness during host community assembly. Global Change Biology 26: 4854-4867.

HART, L. A., G. R. H. GRIEVE, AND C. T. DOWNS. 2013. Fruiting phenology and implications of fruit availability in the fragmented Ngele Forest Complex, KwaZulu-Natal, South Africa. South African Journal of Botany 88: 296-305.

HE, D., Y. CHEN, K. ZHAO, J. CORNELISSEN, AND C. CHU. 2018. Intra-and interspecific trait variations reveal functional relationships between specific leaf area and soil niche within a subtropical forest. Annals of Botany 121: 1173-1182.

HEMPSON, G. P., S. ARCHIBALD, AND W. J. BOND. 2017. The consequences of replacing wildlife with livestock in Africa. Scientific reports 7: 1-10.

HESTER, A. J., P. F. SCOGINGS, AND W. S. TROLLOPE. 2006. Long-term impacts of goat browsing on bush-clump dynamics in a semi-arid subtropical savanna. Plant Ecology 183: 277-290.

HEYWARD, J. 1931. Flowering periods of Victorian plants. Royal Society of Victoria.

HIGGINS, S. I., W. J. BOND, AND W. S. W. TROLLOPE. 2000. Fire, resprouting and variability: A recipe for grass-tree coexistence in savanna. J. Ecol 88: 213-229.

HOEKSTRA, J. M., T. M. BOUCHER, T. H. RICKETTS, AND C. ROBERTS. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8: 23-29.

HOFFMANN, W. A. 2000. Post-Establishment Seedling Success in the Brazilian Cerrado: A Comparison of Savanna and Forest Species 1. Biotropica 32: 62-69.

HOFFMANN, W. A., E. L. GEIGER, S. G. GOTSCH, D. R. ROSSATTO, L. C. SILVA, O. L. LAU, M. HARIDASAN, AND A. C. FRANCO. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecology letters 15: 759-768.

HOFFMANN, W. A., B. ORTHEN, AND A. C. FRANCO. 2004. Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. Oecologia 140: 252-260.

HOOPER, D. U., F. CHAPIN III, J. J. EWEL, A. HECTOR, P. INCHAUSTI, S. LAVOREL, J. H. LAWTON, D. LODGE, M. LOREAU, AND S. NAEEM. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological monographs 75: 3-35.

HORN, H. S. 1974. The ecology of secondary succession. Annual review of ecology and systematics 5: 25-37.

HOWE, H. F., AND J. SMALLWOOD. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201-228.

HUI, F. K. 2016. boral–Bayesian ordination and regression analysis of multivariate abundance data in R. Methods in Ecology and Evolution 7: 744-750.

HUSTON, M., AND T. SMITH. 1987. Plant succession: life history and competition. The American Naturalist 130: 168-198.

INGS, T. C., J. M. MONTOYA, J. BASCOMPTE, N. BLÜTHGEN, L. BROWN, C. F. DORMANN, F. EDWARDS, D. FIGUEROA, U. JACOB, J. I. JONES, R. B. LAURIDSEN, M. E. LEDGER, H. M. LEWIS, J. M. OLESEN, F. J. F. VAN VEEN, P. H. WARREN, AND G. WOODWARD. 2009. Review: Ecological networks – beyond food webs. Journal of Animal Ecology 78: 253-269.

JAMISON, S. L., B. H. DARU, W. D. KISSLING, A. E. VAN WYK, AND M. GREVE. 2017. Unlocking bird-tree relationships: exploring biogeographical patterns across southern Africa. PhD Dissertation. University of Pretoria.

JANSE-TEN KLOOSTER, S. H., E. J. THOMAS, AND F. J. STERCK. 2007. Explaining interspecific differences in sapling growth and shade tolerance in temperate forests. Journal of Ecology 95: 1250-1260.

JARVEL, L., AND T. O'CONNOR. 1999. Bushclump-grass interactions: influence of bushclumps on their local environment in a south-east African savanna. African Journal of Range and Forage Science 16: 32-43.

JELIAZKOV, A., D. MIJATOVIC, S. CHANTEPIE, N. ANDREW, R. ARLETTAZ, L. BARBARO, N. BARSOUM, A. BARTONOVA, E. BELSKAYA, AND N. BONADA. 2020. A global database for metacommunity ecology, integrating species, traits, environment and space. Scientific Data 7: 1-15.

JOËT, T., OURCIVAL, J.M. AND DUSSERT, S., 2013. Ecological significance of seed desiccation sensitivity in Quercus ilex. Annals of Botany, 111: 693-701.

JONES, C. A., AND C. C. DAEHLER. 2018. Herbarium specimens can reveal impacts of climate change on plant phenology; a review of methods and applications. PeerJ 6: e4576.

JOUBERT, D., G. SMIT, AND M. HOFFMAN. 2012. The role of fire in preventing transitions from a grass dominated state to a bush thickened state in arid savannas. Journal of Arid environments 87: 1-7.

KAHMEN, S., AND P. POSCHLOD. 2004. Plant functional trait responses to grassland succession over 25 years. Journal of Vegetation Science 15: 21-32.

KATTGE, J., G. BÖNISCH, S. DÍAZ, S. LAVOREL, I. C. PRENTICE, P. LEADLEY, S. TAUTENHAHN, G. D. WERNER, T. AAKALA, AND M. ABEDI. 2020. TRY plant trait database–enhanced coverage and open access. Global Change Biology 26: 119-188.

KEDDY, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of vegetation science 3: 157-164.

KERR, J. T., H. M. KHAROUBA, AND D. J. CURRIE. 2007. The macroecological contribution to global change solutions. Science 316: 1581-1584.

KHURANA, E., AND J. SINGH. 2004. Impact of elevated nitrogen inputs on seedling growth of five dry tropical tree species as affected by life-history traits. Canadian Journal of Botany 82: 158-167.

KOPPER, B. J., AND R. L. LINDROTH. 2003. Effects of elevated carbon dioxide and ozone on the phytochemistry of aspen and performance of an herbivore. Oecologia 134: 95-103.

KOSANIC, A., K. ANDERSON, S. HARRISON, T. TURKINGTON, AND J. BENNIE. 2018. Changes in the geographical distribution of plant species and climatic variables on the West Cornwall peninsula (South West UK). PLoS One 13: e0191021.

KRAAIJ, T., AND D. WARD. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. Plant Ecology 186: 235-246.

KRAFT, N., AND ACKERLY, D., D. 2014. Assembly of plant communities. Ecology and the Environment 8: 67-88.

KRAMER-WALTER, K. R., P. J. BELLINGHAM, T. R. MILLAR, R. D. SMISSEN, S. J. RICHARDSON, AND D. C. LAUGHLIN. 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. Journal of Ecology 104: 1299-1310.

KUHN, M. 2012. The caret package. R Foundation for Statistical Computing, Vienna, Austria. URL https://cran. r-project. org/package= caret.

KUMAR, D., PFEIFFER, M., GAILLARD, C., LANGAN, L., MARTENS, C. AND SCHEITER, S., 2020. Misinterpretation of Asian savannas as degraded forest can mislead management and conservation policy under climate change. Biological Conservation, 241: 108293.

LALIBERTÉ, E. 2017. Below-ground frontiers in trait-based plant ecology. New Phytologist 213: 1597-1603.

LANE, J.E., KRUUK, L.E., CHARMANTIER, A., MURIE, J.O. AND DOBSON, F.S., 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. Nature, 489: pp.554-557.

LAMOUREUX, C. H. 1973. Phenology and growth of Hawaiian plants, a preliminary report.

LATTANZI, F. A. 2010. C3/C4 grasslands and climate change. Grassland Science in Europe, pp. 3-13.

LAUGHLIN, D. C. 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. Journal of Ecology 102: 186-193.

LEHIKOINEN, E., T. H. SPARKS, AND M. ZALAKEVICIUS. 2004. Arrival and departure dates. Advances in Ecological Research 35: 1-31.

LEIMU, R., P. VERGEER, F. ANGELONI, AND N. J. OUBORG. 2010. Habitat fragmentation, climate change, and inbreeding in plants. Annals of the New York Academy of Sciences 1195: 84-98.

LEISHMAN, M. R. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. Oikos 93: 294-302.

LI, Q., CHEN, X., YUAN, W., LU, H., SHEN, R., WU, S., GONG, F., DAI, Y., LIU, L., SUN, Q. AND ZHANG, C., 2021. Remote sensing of seasonal climatic constraints on leaf phenology across pantropical evergreen forest biome. Earth's Future, 9: e2021EF002160.

LIAUTAUD, K., E. H. VAN NES, M. BARBIER, M. SCHEFFER, AND M. LOREAU. 2019. Superorganisms or loose collections of species? A unifying theory of community patterns along environmental gradients. Ecology Letters 22: 1243-1252.

LIAW, A., AND M. WIENER. 2015. randomForest: Breiman and Cutler's random forests for classification and regression. R package version 4: 6-10.

LIEBERMAN, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. The Journal of Ecology 70: 791-806.

LIMA, D. F., J. H. MELLO, I. T. LOPES, R. C. FORZZA, R. GOLDENBERG, AND L. FREITAS. 2021. Phenological responses to climate change based on a hundred years of herbarium collections of tropical Melastomataceae. PloS one 16: e0251360.

LINDSEY, R. 2018. Climate change: global sea level. Climate. gov. USA Government.

MACE, G. M., K. NORRIS, AND A. H. FITTER. 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology & Evolution 27: 19-26.

MAEGHT, J.-L., B. REWALD, AND A. PIERRET. 2013. How to study deep roots—and why it matters. Frontiers in plant science 4: 299.

MAGURRAN, A. E. 2013. Measuring biological diversity. John Wiley & Sons.

MAGURRAN, A. E., S. R. BAILLIE, S. T. BUCKLAND, J. M. DICK, D. A. ELSTON, E. M. SCOTT, R. I. SMITH, P. J. SOMERFIELD, AND A. D. WATT. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends in Ecology & Evolution 25: 574-582.

MAINKA, S. A., AND G. W. HOWARD. 2010. Climate change and invasive species: double jeopardy. Integrative Zoology 5: 102-111.

MANGANARIS, G.A., VICENTE, A.R. AND CRISOSTO, C.H., 2008. Effect of pre-harvest and post-harvest conditions and treatments on plum fruit quality. CABI Reviews, 10.

MÅREN, I. E., J. KAPFER, P. A. AARRESTAD, J. A. GRYTNES, AND V. VANDVIK. 2018. Changing contributions of stochastic and deterministic processes in community assembly over a successional gradient. Ecology 99: 148-157.

MARQUES, A., I. S. MARTINS, T. KASTNER, C. PLUTZAR, M. C. THEURL, N. EISENMENGER, M. A. HUIJBREGTS, R. WOOD, K. STADLER, AND M. BRUCKNER. 2019. Increasing impacts of land use on biodiversity and carbon sequestration driven by population and economic growth. Nature Ecology & Evolution 3: 628-637.

MATESANZ, S., AND E. GIANOLI. 2014. Global change and the evolution of phenotypic plasticity in plants.

MATTHEWS, M. A., AND K. A. SHACKEL. 2005. Growth and water transport in fleshy fruit. Vascular transport in plants, pp. 181-197. Elsevier.

MAZER, S. J., AND N. T. WHEELWRIGHT. 1993. Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. Evolutionary Ecology 7: 556-575.

MCCULLOH, K. A., F. C. MEINZER, J. S. SPERRY, B. LACHENBRUCH, S. L. VOELKER, D. R. WOODRUFF, AND J.-C. DOMEC. 2011. Comparative hydraulic architecture of tropical tree species representing a range of successional stages and wood density. Oecologia 167: 27-37.

MCGILL, B. J., B. J. ENQUIST, E. WEIHER, AND M. WESTOBY. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21: 178-185.

MEINERS, S. J., M. W. CADOTTE, J. D. FRIDLEY, S. T. PICKETT, AND L. R. WALKER. 2015. Is successional research nearing its climax? New approaches for understanding dynamic communities. Functional Ecology 29: 154-164.

MENON, S., R. G. PONTIUS JR, J. ROSE, M. KHAN, AND K. S. BAWA. 2001. Identifying conservation-priority areas in the tropics: a land-use change modeling approach. Conservation Biology 15: 501-512.

MENZEL, A. 2002. Phenology: its importance to the global change community. Climatic Change 54: 379.

MILLS, A. M. 2005. Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. Ibis 147: 259-269.

MOHER, D., A. LIBERATI, J. TETZLAFF, D. G. ALTMAN, AND P. GROUP*. 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. Annals of internal medicine 151: 264-269.

MOLES, A. T., AND M. WESTOBY. 2004. Seedling survival and seed size: a synthesis of the literature. Journal of Ecology 92: 372-383.

MONTGOMERY, R. A., AND R. L. CHAZDON. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82: 2707-2718.

MORDELET, P., L. ABBADIE, AND J.-C. MENAUT. 1993. Effects of tree clumps on soil characteristics in a humid savanna of West Africa (Lamto, Côte d'Ivoire). Plant and Soil 153: 103-111.

MORELLATO, L. P. C., M. G. G. CAMARGO, AND E. GRESSLER. 2013. A review of plant phenology in South and Central America. Phenology: an integrative environmental science, pp. 91-113. Springer.

MUCINA, L., AND M. C. RUTHERFORD. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute.

MULLER-LANDAU, H. C. 2010. The tolerance–fecundity trade-off and the maintenance of diversity in seed size. Proceedings of the National Academy of Sciences 107: 4242-4247.

MURALI, K.; SUKUMAR, R. 1993. Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. Oecologia 1993, 94: 114–119.

MYERS, R. A., AND B. WORM. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423: 280-283.

NAVARRO-CANO, J. A., B. KARLSSON, D. POSLEDOVICH, T. TOFTEGAARD, C. WIKLUND, J. EHRLÉN, AND K. GOTTHARD. 2015. Climate change, phenology, and butterfly host plant utilization. AMBIO 44: 78-88.

NAVAS, M.-L., C. ROUMET, A. BELLMANN, G. LAURENT, AND E. GARNIER. 2010. Suites of plant traits in species from different stages of a Mediterranean secondary succession. Plant Biology 12: 183-196.

NAVAS, M. L., B. DUCOUT, C. ROUMET, J. RICHARTE, J. GARNIER, AND E. GARNIER. 2003. Leaf life span, dynamics and construction cost of species from Mediterranean old-fields differing in successional status. New phytologist 159: 213-228.

NEIL, K., AND J. WU. 2006. Effects of urbanization on plant flowering phenology: A review. Urban Ecosystems 9: 243-257.

NIGAM, S. N., AND R. ARUNA. 2008. Stability of soil plant analytical development (SPAD) chlorophyll meter reading (SCMR) and specific leaf area (SLA) and their association across varying soil moisture stress conditions in groundnut (*Arachis hypogaea* L.). Euphytica 160: 111-117.

NOCK, C. A., R. J. VOGT, AND B. E. BEISNER. 2016. Functional traits. Encyclopedia of Life Sciences: 1-8.

NORDEN, N., H. A. ANGARITA, F. BONGERS, M. MARTÍNEZ-RAMOS, I. GRANZOW-DE LA CERDA, M. VAN BREUGEL, E. LEBRIJA-TREJOS, J. A. MEAVE, J. VANDERMEER, AND G. B. WILLIAMSON. 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. Proceedings of the National Academy of Sciences 112: 8013-8018.

NORDEN, N., R. L. CHAZDON, A. CHAO, Y.-H. JIANG, AND B. VÍLCHEZ-ALVARADO. 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. Ecology Letters 12: 385-394.

NORTHRUP, B., J. STUTH, S. ARCHER, D. MCKOWN, AND A. CRANE. 1995. Structure of shrub clusters in a subtropical savanna in South Texas. Rangelands in a sustainable biosphere. Proceedings of the Fifth International Range Congress.

NUÑEZ, N. H., R. L. CHAZDON, AND S. E. RUSSO. 2019. Determinism and stochasticity in seed dispersal-successional feedbacks. bioRxiv: 791988.

O'CONNOR, T., AND V. CROW. 1999. Rate and pattern of bush encroachment in Eastern Cape savanna and grassland. African Journal of Range and Forage Science 16: 26-31.

O'CONNOR, T. G., AND S. C. CHAMANE. 2012. Bush clump succession in grassland in the Kei Road region of the Eastern Cape, South Africa. African Journal of Range & Forage Science 29: 133-146.

O'CONNOR, T. G., J. R. PUTTICK, AND M. T. HOFFMAN. 2014. Bush encroachment in southern Africa: changes and causes. African Journal of Range & Forage Science 31: 67-88.

OKSANEN, J., R. KINDT, P. LEGENDRE, B. O'HARA, M. H. H. STEVENS, M. J. OKSANEN, AND M. SUGGESTS. 2007. The vegan package. R package version 1.0–7. Avaliable at http://CRAN.R-project.org/package=vegan.

PACALA, S. W., AND M. REES. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. The American Naturalist 152: 729-737.

PALMER, M. W., AND P. M. DIXON. 1990. Small-scale environmental heterogeneity and the analysis of species distributions along gradients. Journal of Vegetation Science 1: 57-65.

PARK, I. W., AND M. D. SCHWARTZ. 2015. Long-term herbarium records reveal temperature-dependent changes in flowering phenology in the southeastern USA. International Journal of Biometeorology 59: 347-355.

PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37.

PARR, C.L., GRAY, E.F. AND BOND, W.J., 2012. Cascading biodiversity and functional consequences of a global change–induced biome switch. Diversity and Distributions, 18: 493-503.

PASTOR, J., AND W. POST. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2: 3-27.

PAU, S.; WOLKOVICH, E.M.; COOK, B.I.; NYTCH, C.J.; REGETZ, J.; ZIMMERMAN, J.K.; WRIGHT, S.J. 2013. Clouds and temperature drive dynamic changes in tropical flower production. Nat. Clim. Chang., 3: 838.

PAUSAS, JULI G., AND WILLIAM J. BOND. 2019. Humboldt and the reinvention of nature. Journal of Ecology, 107: 1031-1037.

PEARSON, K. D., G. NELSON, M. F. ARONSON, P. BONNET, L. BRENSKELLE, C. C. DAVIS, E. G. DENNY, E. R. ELLWOOD, H. GOËAU, AND J. M. HEBERLING. 2020. Machine learning using digitized herbarium specimens to advance phenological research. BioScience 70: 610-620.

PENNEC, A., V. GOND, AND D. SABATIER. 2011. Tropical forest phenology in French Guiana from MODIS time series. Remote Sensing Letters 2: 337-345.

PEREZ-HARGUINDEGUY, N., S. DIAZ, E. GARNIER, S. LAVOREL, H. POORTER, P. JAUREGUIBERRY, M. S. BRET-HARTE, W. K. CORNWELL, J. M. CRAINE, AND D. E. GURVICH. 2016. Corrigendum to: new handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 64: 715-716.

PETERSON, C., AND W. CARSON. 2008. Processes constraining woody species succession on abandoned pastures in the tropics: on the relevance of temperate models of succession. Tropical forest community ecology. Oxford: Wiley-Blackwell: 367-383.

PILSON, D. 2000. Herbivory and natural selection on flowering phenology in wild sunflower, Helianthus annuus. Oecologia 122: 72-82.

PIMM, S. L., AND J. H. LAWTON. 1998. Planning for biodiversity. Science 279: 2068-2069.

PIQUERAY, J., L. FERRONI, L.-M. DELESCAILLE, M. SPERANZA, G. MAHY, AND P. POSCHLOD. 2015. Response of plant functional traits during the restoration of calcareous grasslands from forest stands. Ecological Indicators 48: 408-416.

POLLEY, H. W., V. L. JIN, AND P. A. FAY. 2012. Feedback from plant species change amplifies CO_2 enhancement of grassland productivity. Global Change Biology 18: 2813-2823.

POLLEY, H. W., H. B. JOHNSON, AND H. S. MAYEUX. 1994. Increasing CO_2: comparative responses of the C4 grass Schizachyrium and grassland invader *Prosopis*. Ecology 75: 976-988.

PRACH, K., AND L. R. WALKER. 2011. Four opportunities for studies of ecological succession. Trends in Ecology & Evolution 26: 119-123.

PRACH, K., AND L. R. WALKER. 2020. Comparative Plant Succession Among Terrestrial Biomes of the World. Cambridge University Press.

PURESWARAN, D. S., L. DE GRANDPRÉ, D. PARÉ, A. TAYLOR, M. BARRETTE, H. MORIN, J. RÉGNIÈRE, AND D. D. KNEESHAW. 2015. Climate-induced changes in host tree–insect phenology may drive ecological state-shift in boreal forests. Ecology 96: 1480-1491.

PURSCHKE, O., B. C. SCHMID, M. T. SYKES, P. POSCHLOD, S. G. MICHALSKI, W. DURKA, I. KÜHN, M. WINTER, AND H. C. PRENTICE. 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. Journal of Ecology 101: 857-866.

PYŠEK, P., D. M. RICHARDSON, J. PERGL, V. JAROŠÍK, Z. SIXTOVÁ, AND E. WEBER. 2008. Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution 23: 237-244.

QIAN, H., W. D. KISSLING, X. WANG, AND P. ANDREWS. 2009. Effects of woody plant species richness on mammal species richness in southern Africa. Journal of Biogeography 36: 1685-1697.

R DEVELOPMENT CORE TEAM. 2022a. The R Base Package.

R DEVELOPMENT CORE TEAM. 2022b. R: A language and environment for statistical computing. R Foundation for Statistical Computing. . R Core Team. Vienna, Austria.

RABALAIS, N. N., R. E. TURNER, R. J. DÍAZ, AND D. JUSTIĆ. 2009. Global change and eutrophication of coastal waters. ICES Journal of Marine Science 66: 1528-1537.

RAEVEL, V., C. VIOLLE, AND F. MUNOZ. 2012. Mechanisms of ecological succession: insights from plant functional strategies. Oikos 121: 1761-1770.

RAFFERTY, N. E., P. J. CARADONNA, AND J. L. BRONSTEIN. 2015. Phenological shifts and the fate of mutualisms. Oikos 124: 14-21.

RANDLE, M., N. STEVENS, AND G. MIDGLEY. 2018. Comparing the differential effects of canopy shading by Dichrostachys cinerea and Terminalia sericea on grass biomass. South African Journal of Botany 119: 271-277.

RAMOS, M., E, ANA ROBLES, B., AND CASTRO, J. 2006. Efficiency of endozoochorous seed dispersal in six dry-fruited species (Cistaceae): from seed ingestion to early seedling establishment. Plant Ecology 185: 97-106.

RATAJCZAK, Z., J. B. NIPPERT, AND S. L. COLLINS. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93: 697-703.

RATNAM, J., BOND, W.J., FENSHAM, R.J., HOFFMANN, W.A., ARCHIBALD, S., LEHMANN, C.E., ANDERSON, M.T., HIGGINS, S.I. AND SANKARAN, M., 2011. When is a 'forest'a savanna, and why does it matter?. Global Ecology and Biogeography, 20: 653-660.

RAWAL, D. S., S. KASEL, M. R. KEATLEY, AND C. R. NITSCHKE. 2015. Herbarium records identify sensitivity of flowering phenology of eucalypts to climate: implications for species response to climate change. Austral Ecology 40: 117-125.

READER, R. J. 1983. Using Heatsum Models to Account for Geographic Variation in the Floral Phenology of Two Ericaceous Shrubs. Journal of Biogeography 10: 47-64.

REED, M. S., A. J. DOUGILL, AND T. R. BAKER. 2008. Participatory indicator development: what can ecologists and local communities learn from each other. Ecological Applications 18: 1253-1269.

REED, M. S., L. C. STRINGER, A. J. DOUGILL, J. S. PERKINS, J. R. ATLHOPHENG, K. MULALE, AND N. FAVRETTO. 2015. Reorienting land degradation towards sustainable land management: Linking sustainable livelihoods with ecosystem services in rangeland systems. Journal of Environmental Management 151: 472-485.

REICH, P. B. 2014. The world-wide 'fast–slow'plant economics spectrum: a traits manifesto. Journal of Ecology 102: 275-301.

RICHARDSON, D. M., L. C. FOXCROFT, G. LATOMBE, D. C. LE MAITRE, M. ROUGET, AND J. R. WILSON. 2020. The biogeography of South African terrestrial plant invasions. Springer.

ROBBIRT, K. M., A. J. DAVY, M. J. HUTCHINGS, AND D. L. ROBERTS. 2011. Validation of biological collections as a source of phenological data for use in climate change studies: a case study with the orchid Ophrys sphegodes. Journal of Ecology 99: 235-241.

ROTTER, R.P., SCHEITER, S., HOFFMANN, M.P., PFEIFFER, M., NELSON, W.C., AYISI, K., TAYLOR, P.J., FEIL, J.H., BAKHSH, S.Y., ISSELSTEIN, J. AND LINDSTAEDTER, A., 2021. Modeling the multi-functionality of African savanna landscapes under global change.

RUMPFF, L., F. COATES, AND J. W. MORGAN. 2010. Biological indicators of climate change: evidence from long-term flowering records of plants along the Victorian coast, Australia. Australian Journal of Botany 58: 428-439.

RUSSELL, J. M., AND D. WARD. 2014. Remote sensing provides a progressive record of vegetation change in northern KwaZulu-Natal, South Africa, from 1944 to 2005. International Journal of Remote Sensing 35: 904-926.

RYSER, P., AND P. URBAS. 2000. Ecological significance of leaf life span among Central European grass species. Oikos 91: 41-50.

SACK, L., W. K. CORNWELL, L. S. SANTIAGO, M. M. BARBOUR, B. CHOAT, J. R. EVANS, R. MUNNS, AND A. NICOTRA. 2010. A unique web resource for physiology, ecology and the environmental sciences: PrometheusWiki. Functional Plant Biology 37: 687-693.

SAGE, R. F. 2020. Global change biology: A primer. Global Change Biology 26: 3-30.

Sala, O. E., F. Stuart Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, and A. Kinzig. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770-1774.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, and F. Ludwig. 2005. Determinants of woody cover in African savannas. Nature 438: 846-849.

Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. Global Ecology and Biogeography 17: 236-245.

Schleicher, A., C. Peppler-Lisbach, and M. Kleyer. 2011. Functional traits during succession: is plant community assembly trait-driven? Preslia 83: 347-370.

Schlesinger, W. H., J. Reynolds, G. L. Cunningham, L. Huenneke, W. Jarrell, R. Virginia, and W. Whitford. 1990. Biological feedbacks in global desertification. Science 247: 1043-1048.

Schmidt, E., M. Lotter, and W. McCleland. 2002. Trees and shrubs of Mpumalanga and Kruger national park. Jacana Media.

Schneider, J. V., D. Zipp, J. Gaviria, and G. Zizka. 2003. Successional and mature stands in an upper Andean rain forest transect of Venezuela: do leaf characteristics of woody species differ? Journal of Tropical Ecology 19: 251-259.

Schönbeck, L., M. Lohbeck, F. Bongers, M. Ramos, and F. Sterck. 2015. How do light and water acquisition strategies affect species selection during secondary succession in moist tropical forests? Forests 6: 2047-2065.

Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, P. Pyšek, M. van Kleunen, and M. Winter. 2018. Global rise in emerging alien species results from increased accessibility of new source pools. Proceedings of the National Academy of Sciences 115: E2264-E2273.

Seitzinger, S., C. Kroeze, A. Bouwman, N. Caraco, F. Dentener, and R. Styles. 2002. Global patterns of dissolved inorganic and particulate nitrogen inputs to coastal systems: Recent conditions and future projections. Estuaries 25: 640-655.

Shen, Y., G. S. Gilbert, W. Li, M. Fang, H. Lu, and S. Yu. 2019. Linking aboveground traits to root traits and local environment: implications of the plant economics spectrum. Frontiers in plant science 10: 1412.

Siebert, F., and N. Dreber. 2019. Forb ecology research in dry African savannas: Knowledge, gaps, and future perspectives. Ecology and Evolution 9: 7875-7891.

Silveira, E.M.D.O., Espírito-Santo, F.D.B., Acerbi-Júnior, F.W., Galvão, L.S., Withey, K.D., Blackburn, G.A., de Mello, J.M., Shimabukuro, Y.E., Domingues, T. and Scolforo, J.R.S., 2019. Reducing the effects of vegetation phenology on change detection in tropical seasonal biomes. GIScience & Remote Sensing, 56: 699-717.

Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biological journal of the Linnean Society 14: 235-250.

Sinnott-Armstrong, M. A., A. E. Downie, S. Federman, A. Valido, P. Jordano, and M. J. Donoghue. 2018. Global geographic patterns in the colours and sizes of animal-dispersed fruits. Global Ecology and Biogeography 27: 1339-1351.

Skowno, A. L., M. W. Thompson, J. Hiestermann, B. Ripley, A. G. West, and W. J. Bond. 2017. Woodland expansion in South African grassy biomes based on satellite observations (1990–2013): general patterns and potential drivers. Global Change Biology 23: 2358-2369.

Smit, A. L., A. G. Bengough, C. Engels, M. van Noordwijk, S. Pellerin, and S. C. van de Geijn. 2013. Root methods: a handbook. Springer Science & Business Media.

Smith, P., J. I. House, M. Bustamante, J. Sobocká, R. Harper, G. Pan, P. C. West, J. M. Clark, T. Adhya, and C. Rumpel. 2016. Global change pressures on soils from land use and management. Global change biology 22: 1008-1028.

Sparks, T., D. Roy, and R. Dennis. 2005. The influence of temperature on migration of Lepidoptera into Britain. Global Change Biology 11: 507-514.

Stafford, W., C. Birch, H. Etter, R. Blanchard, S. Mudavanhu, P. Angelstam, J. Blignaut, L. Ferreira, and C. Marais. 2017. The economics of landscape restoration: Benefits of controlling bush encroachment and invasive plant species in South Africa and Namibia. Ecosystem Services 27: 193-202.

STAGGEMEIER, V. G., M. G. G. CAMARGO, J. A. F. DINIZ-FILHO, R. FRECKLETON, L. JARDIM, AND L. P. C. MORELLATO. 2020. The circular nature of recurrent life cycle events: a test comparing tropical and temperate phenology. Journal of Ecology 108: 393-404.

STAHL, U., J. KATTGE, B. REU, W. VOIGT, K. OGLE, J. DICKIE, AND C. WIRTH. 2013. Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. Ecosphere 4: 1-28.

STANTON JR, R. A., W. W. BOONE IV, J. SOTO-SHOENDER, R. J. FLETCHER JR, N. BLAUM, AND R. A. MCCLEERY. 2018. Shrub encroachment and vertebrate diversity: A global meta-analysis. Global Ecology and Biogeography 27: 368-379.

STEVENS, C. J., T. I. DAVID, AND J. STORKEY. 2018. Atmospheric nitrogen deposition in terrestrial ecosystems: Its impact on plant communities and consequences across trophic levels. Functional Ecology 32: 1757-1769.

STEVENS, N., W. BOND, A. FEURDEAN, AND C. E. LEHMANN. 2022. Grassy Ecosystems in the Anthropocene. Annual Review of Environment and Resources 47: 261-289.

STEVENS, N., C. E. LEHMANN, B. P. MURPHY, AND G. DURIGAN. 2017. Savanna woody encroachment is widespread across three continents. Global change biology 23: 235-244.

STILING, P., AND T. CORNELISSEN. 2007. How does elevated carbon dioxide (CO_2) affect plant–herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. Global Change Biology 13: 1823-1842.

SWAINE, M. 1992. Characteristics of dry forest in West Africa and the influence of fire. Journal of Vegetation Science 3: 365-374.

TANG, J., C. KÖRNER, H. MURAOKA, S. PIAO, M. SHEN, S. J. THACKERAY, AND X. YANG. 2016. Emerging opportunities and challenges in phenology: a review. Ecosphere 7: e01436.

TAUB, D. 2010. Effects of rising atmospheric concentrations of carbon dioxide on plants. Nature Education Knowledge 1.

TEDDER, M., K. KIRKMAN, C. MORRIS, AND R. FYNN. 2014. Tree–grass competition along a catenal gradient in a mesic grassland, South Africa. Grassland Science 60: 1-8.

TESSEMA, Z. K., W. F. DE BOER, R. M. BAARS, AND H. H. PRINS. 2012. Influence of grazing on soil seed banks determines the restoration potential of aboveground vegetation in a semi-arid savanna of Ethiopia. Biotropica 44: 211-219.

TEWS, J., U. BROSE, V. GRIMM, K. TIELBÖRGER, M. WICHMANN, M. SCHWAGER, AND F. JELTSCH. 2004a. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31: 79-92.

TEWS, J., F. SCHURR, F. JELTSCH, AND C. SKARPE. 2004b. Seed dispersal by cattle may cause shrub encroachment of Grewia flava on southern Kalahari rangelands. Applied Vegetation Science 7: 89-102.

THOMPSON, J. N., AND M. F. WILLSON. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. Evolution 33: 973-982.

THUILLER, W., C. ALBERT, M. B. ARAÚJO, P. M. BERRY, M. CABEZA, A. GUISAN, T. HICKLER, G. F. MIDGLEY, J. PATERSON, F. M. SCHURR, M. T. SYKES, AND N. E. ZIMMERMANN. 2008. Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics 9: 137-152.

TING, S., S. HARTLEY, AND K. BURNS. 2008. Global patterns in fruiting seasons. Global Ecology and Biogeography 17: 648-657.

TRIMBLE, M. J., AND R. J. VAN AARDE. 2012. Geographical and taxonomic biases in research on biodiversity in human-modified landscapes. Ecosphere 3: 1-16.

TURETSKY, M. R., B. BENSCOTER, S. PAGE, G. REIN, G. R. VAN DER WERF, AND A. WATTS. 2015. Global vulnerability of peatlands to fire and carbon loss. Nature Geoscience 8: 11-14.

TYLIANAKIS, J. M., R. K. DIDHAM, J. BASCOMPTE, AND D. A. WARDLE. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11: 1351-1363.

TWEDDLE, J.C., DICKIE, J.B., BASKIN, C.C. AND BASKIN, J.M., 2003. Ecological aspects of seed desiccation sensitivity. Journal of ecology, 91: 294-304.

URIARTE, M., J. R. LASKY, V. K. BOUKILI, AND R. L. CHAZDON. 2016. A trait-mediated, neighbourhood approach to quantify climate impacts on successional dynamics of tropical rainforests. Functional Ecology 30: 157-167.

USCHNER, D., D. SCHINDLER, R.-D. HILGERS, AND N. HEUSSEN. 2018. randomizeR: an R package for the assessment and implementation of randomization in clinical trials. Journal of Statistical Software 85: 1-22.

VAN DER LINDEN, J., S. SIEBERT, F. SIEBERT, D. FERREIRA, AND G. BREDENKAMP. 2005. Vegetation of the Owen Sitole College of Agriculture in Zululand, KwaZulu-Natal. Koedoe 48: 33-56.

VAN DER PIJL, L. 1982. Principles of dispersal in higher plants. Springer, Berlin.

VAN SCHAIK, C. P., J. W. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annual Review of ecology and Systematics 24: 353-377.

VAN WYK, B., AND P. VAN WYK. 2013. Field guide to trees of southern Africa. Struik, Cape Town, South Africa.

VERMAAT, J. E., F. A. HELLMANN, A. J. VAN TEEFFELEN, J. VAN MINNEN, R. ALKEMADE, R. BILLETER, C. BEIERKUHNLEIN, L. BOITANI, M. CABEZA, AND C. K. FELD. 2017. Differentiating the effects of climate and land use change on European biodiversity: A scenario analysis. Ambio 46: 277-290.

VETTER, S. 2020. With power comes responsibility–a rangelands perspective on forest landscape restoration. Frontiers in Sustainable Food Systems 4: 549483.

VILE, D., B. SHIPLEY, AND E. GARNIER. 2006. A structural equation model to integrate changes in functional strategies during old-field succession. Ecology 87: 504-517.

VIOLLE, C., AND L. JIANG. 2009. Towards a trait-based quantification of species niche. Journal of Plant Ecology 2: 87-93.

VIOLLE, C., M.-L. NAVAS, D. VILE, E. KAZAKOU, C. FORTUNEL, I. HUMMEL, AND E. GARNIER. 2007. Let the concept of trait be functional! Oikos 116: 882-892.

VISSER, M. E., AND C. BOTH. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B: Biological Sciences 272: 2561-2569.

VISSER, M. E., C. BOTH, AND M. M. LAMBRECHTS. 2004. Global climate change leads to mistimed avian reproduction. Advances in Ecological Research 35: 89-110.

VITTOZ, P., N. DUSSEX, J. WASSEF, AND A. GUISAN. 2009. Diaspore traits discriminate good from weak colonisers on high-elevation summits. Basic and Applied Ecology 10: 508-515.

VOGT, R. J., B. E. BEISNER, AND Y. T. PRAIRIE. 2010. Functional diversity is positively associated with biomass for lake diatoms. Freshwater Biology 55: 1636-1646.

WAKELING, J. L., M. D. CRAMER, AND W. J. BOND. 2012. The savanna-grassland 'treeline': why don't savanna trees occur in upland grasslands? Journal of Ecology 100: 381-391.

WALKER, L., R, AND MORAL, R., D. 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge.

WALKER, J., C. THOMPSON, P. REDDELL, AND D. RAPPORT. 2001. The importance of landscape age in influencing landscape health. Ecosystem Health 7: 7-14.

WALKER, L. R., AND R. DEL MORAL. 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press.

WALKER, L. R., AND R. DEL MORAL. 2009. Transition dynamics in succession: implications for rates, trajectories and restoration. Island Press, USA.

WALKER, L. R., D. A. WARDLE, R. D. BARDGETT, AND B. D. CLARKSON. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98: 725-736.

WALSH, J. R., S. R. CARPENTER, AND M. J. VANDER ZANDEN. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences 113: 4081-4085.

WALTHER, G.-R., E. POST, P. CONVEY, A. MENZEL, C. PARMESAN, T. J. BEEBEE, J.-M. FROMENTIN, O. HOEGH-GULDBERG, AND F. BAIRLEIN. 2002. Ecological responses to recent climate change. Nature 416: 389-395.

WAN, X., X. CHEN, Z. HUANG, AND H. Y. CHEN. 2021. Global soil microbial biomass decreases with aridity and land-use intensification. Global Ecology and Biogeography 30: 1056-1069.

WANG, J., M, AND ZHANG, X., Y. 2017. Impacts of wildfires on interannual trends in land surface phenology: an investigation of the Hayman Fire Environ. Res. Lett. 12: 054008.

WARBURTON, M., R. SCHULZE, AND M. MAHARAJ. 2005. Is South Africa's temperature changing? An analysis of trends from daily records, 1950–2000. Water Resource Commission, RSA.

WARDLE, D. A., L. R. WALKER, AND R. D. BARDGETT. 2004. Ecosystem Properties and Forest Decline in Contrasting Long-Term Chronosequences. Science 305: 509-513.

WEI, T., V. SIMKO, M. LEVY, Y. XIE, Y. JIN, AND J. ZEMLA. 2017. Package 'corrplot'. Statistician 56: 316-324.

WELCH, B. L. 1947. The generalization ofstudent's' problem when several different population variances are involved. Biometrika 34: 28-35.

WHEELWRIGHT, N. T. 1985. Fruit-size, gape width, and the diets of fruit-eating birds. Ecology 66: 808-818.

WHEELWRIGHT, N. T., AND C. H. JANSON. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. The American Naturalist 126: 777-799.

WHITE, L. J. 1994. Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. Journal of Tropical Ecology 10: 289-312.

WHITECROSS, M., A, WITKOWSKI, E., T. AND ARCHIBALD, S. 2017. Assessing the frequency and drivers of early-greening in broad-leaved woodlands along a latitudinal gradient in southern Africa. Austral ecology, 42: 341-353.

WIECZORKOWSKI, J. D., AND C. E. LEHMANN. 2022. Encroachment diminishes herbaceous plant diversity in grassy ecosystems worldwide. Global Change Biology 28: 5532-5546.

WIGLEY, B. J., W. J. BOND, AND M. T. HOFFMAN. 2009. Bush encroachment under three contrasting land-use practices in a mesic South African savanna. African Journal of Ecology 47: 62-70.

WIGLEY, B. J., W. J. BOND, AND M. T. HOFFMAN. 2010. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? Global Change Biology 16: 964-976.

WIGLEY, B. J., T. CHARLES-DOMINIQUE, G. HEMPSON, N. STEVENS, M. TEBEEST, S. ARCHIBALD, W. BOND, K. BUNNEY, C. COETSEE, AND J. DONALDSON. 2020. A handbook for the standardised sampling of plant functional traits in disturbance-prone ecosystems, with a focus on open ecosystems. Australian Journal of Botany 68: 473-531.

WILFAHRT, P. A., B. COLLINS, AND P. S. WHITE. 2014. Shifts in functional traits among tree communities across succession in eastern deciduous forests. For. Ecol. Manage. 324: 179-185.

WILLIAMS, M. 1992. Americans and their forests: a historical geography. Cambridge University Press.

WILLMOTT, C. J., AND K. MATSUURA. 2001. Terrestrial water budget data archive: monthly time series (1950–1999). University of Delaware, USA.

WIRMINGHAUS, J., C. DOWNS, C. SYMES, AND M. PERRIN. 2001. Fruiting in two afromontane forests in KwaZulu-Natal, South Africa: the habitat type of the endangered Cape Parrot Poicephalus robustus. South African Journal of Botany 67: 325-332.

WISZ, M. S., J. POTTIER, W. D. KISSLING, L. PELLISSIER, J. LENOIR, C. F. DAMGAARD, C. F. DORMANN, M. C. FORCHHAMMER, J. A. GRYTNES, AND A. GUISAN. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews 88: 15-30.

WITTMANN, A. C., AND H.-O. PÖRTNER. 2013. Sensitivities of extant animal taxa to ocean acidification. Nature climate change 3: 995-1001.

WOLKOVICH, E. M., B. I. COOK, AND T. J. DAVIES. 2014. Progress towards an interdisciplinary science of plant phenology: building predictions across space, time and species diversity. New Phytologist 201: 1156-1162.

WOOD, S., AND M. S. WOOD. 2015. Package 'mgcv'. R package version 1: 29.

WOODFORD, D. J., P. IVEY, A. NOVOA, R. SHACKLETON, D. RICHARDSON, O. WEYL, B. VAN WILGEN, AND T. ZENGEYA. 2017. Managing conflict-generating invasive species in South Africa: Challenges and trade-offs. Bothalia-African Biodiversity & Conservation 47: 1-11.

WRIGHT, I. J., P. B. REICH, M. WESTOBY, D. D. ACKERLY, Z. BARUCH, F. BONGERS, J. CAVENDER-BARES, T. CHAPIN, J. H. CORNELISSEN, AND M. DIEMER. 2004. The worldwide leaf economics spectrum. Nature 428: 821-827.

WRIGHT, S. J., AND O. CALDERÓN. 2006. Seasonal, El Nino and longer term changes in flower and seed production in a moist tropical forest. Ecology letters 9: 35-44.

WU, J., L. P. ALBERT, A. P. LOPES, N. RESTREPO-COUPE, M. HAYEK, K. T. WIEDEMANN, K. GUAN, S. C. STARK, B. CHRISTOFFERSEN, N. PROHASKA, J. V. TAVARES, S. MAROSTICA, H. KOBAYASHI, M. L. FERREIRA, K. S. CAMPOS, R. DA SILVA, P. M. BRANDO, D. G. DYE, T. E. HUXMAN, A. R. HUETE, B. W. NELSON, AND S. R. SALESKA. 2016. Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests. Science 351: 972-976.

YANG, Y., XU, W., HOU, P., LIU, G., LIU, W., WANG, Y., ZHAO, R., MING, B., XIE, R., WANG, K. AND LI, S., 2019. Improving maize grain yield by matching maize growth and solar radiation. Scientific reports, 9: 3635.

YARRANTON, G. A., AND R. G. MORRISON. 1974. Spatial Dynamics of a Primary Succession: Nucleation. Journal of Ecology 62: 417-428.

ZHANG, S., Y. ZHANG, K. XIONG, Y. YU, AND X. MIN. 2020. Changes of leaf functional traits in karst rocky desertification ecological environment and the driving factors. Global Ecology and Conservation 24: e01381.

ZHANG, X., L. LIU, AND G. M. HENEBRY. 2019. Impacts of land cover and land use change on long-term trend of land surface phenology: a case study in agricultural ecosystems. Environmental Research Letters 14: 044020.

ZHAO, Y.-T., A. ALI, AND E.-R. YAN. 2017. The plant economics spectrum is structured by leaf habits and growth forms across subtropical species. Tree Physiology 37: 173-185.

ZHONGMING, Z., AND L. WEI. 2022. Climate Change 2022: Impacts, Adaptation and Vulnerability-Summary for Policymakers released.

ZHOU, J., Y. DENG, P. ZHANG, K. XUE, Y. LIANG, J. D. VAN NOSTRAND, Y. YANG, Z. HE, L. WU, AND D. A. STAHL. 2014. Stochasticity, succession, and environmental perturbations in a fluidic ecosystem. Proceedings of the National Academy of Sciences 111: E836-E845.

ZHU, S.-D., J.-J. SONG, R. H. LI, AND Q. YE. 2013. Plant hydraulics and photosynthesis of 34 woody species from different successional stages of subtropical forests. Plant, Cell & Environment 36: 879-891.

ZOHNER, C. M., AND S. S. RENNER. 2014. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. Ecology letters 17: 1016-1025.

ZUUR, A., E. N. IENO, N. WALKER, A. A. SAVELIEV, AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media.

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