Trends in taxonomic and functional diversity over succession in tropical secondary forests

Haley Arnold

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Abstract

Biodiverse tropical forests are declining rapidly, due in part to the appropriation of natural land for human use. There is an urgent need to better understand how biodiversity changes in response to this landscape transformation, and to find conservation solutions that support both people and nature. Cacao farming, a valuable source of agricultural revenue in many tropical countries, can lead to a mosaic of both active and abandoned agroforests. These abandoned agroforests undergo secondary succession and have the potential to be important reservoirs of biodiversity. To evaluate this potential, I assessed the biodiversity of active cacao agroforests, abandoned agroforests, and primary forest on the tropical island of Trinidad. I surveyed tree, ground vegetation, epiphyte, and bird assemblages, and computed taxonomic and functional diversity. I further asked whether there are generalisable patterns of biodiversity change over succession across taxa, and how my results fit within the wider narrative of ecological succession theory and research. I found that taxonomic and functional alpha-diversity in all assemblages were mostly either maintained throughout succession, or recovered quickly across taxa. There were, however, substantial changes in taxonomic and functional composition (beta-diversity) over succession, with patterns of biodiversity change largely uncorrelated across taxa. Overall, there was little congruence between expectations based on theory and existing empirical research, and the results of my study. This outcome emphasises the need to deepen our understanding of successional processes across biomes, starting points of succession, and taxa. My research also highlights that, while primary forests contain more specialist species, actively cultivated cacao agroforests and young secondary forests in Trinidad are remarkably biodiverse and jointly contribute to supporting regional gamma diversity. These results place cacao agroforests within a people and nature framework, and demonstrate that human-altered habitats can be important reservoirs of tropical biodiversity.

Acknowledgements

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Many thanks to those at the University of the West Indies and the National Herbarium of Trinidad and Tobago including Dr Yasmin Baksh-Comeau, Shane Ballah, Sarah Barath, Roma Wong Sang, Matthew Escalante, Carl Fitzjames, and Andrea Scoby for your help in my research and plant identifications. I would also like to extend special thanks to Dr Mark Hulme, Dr Alex Sansom and Dr Aidan Farrell as well for your support and guidance through my time in Trinidad and beyond.

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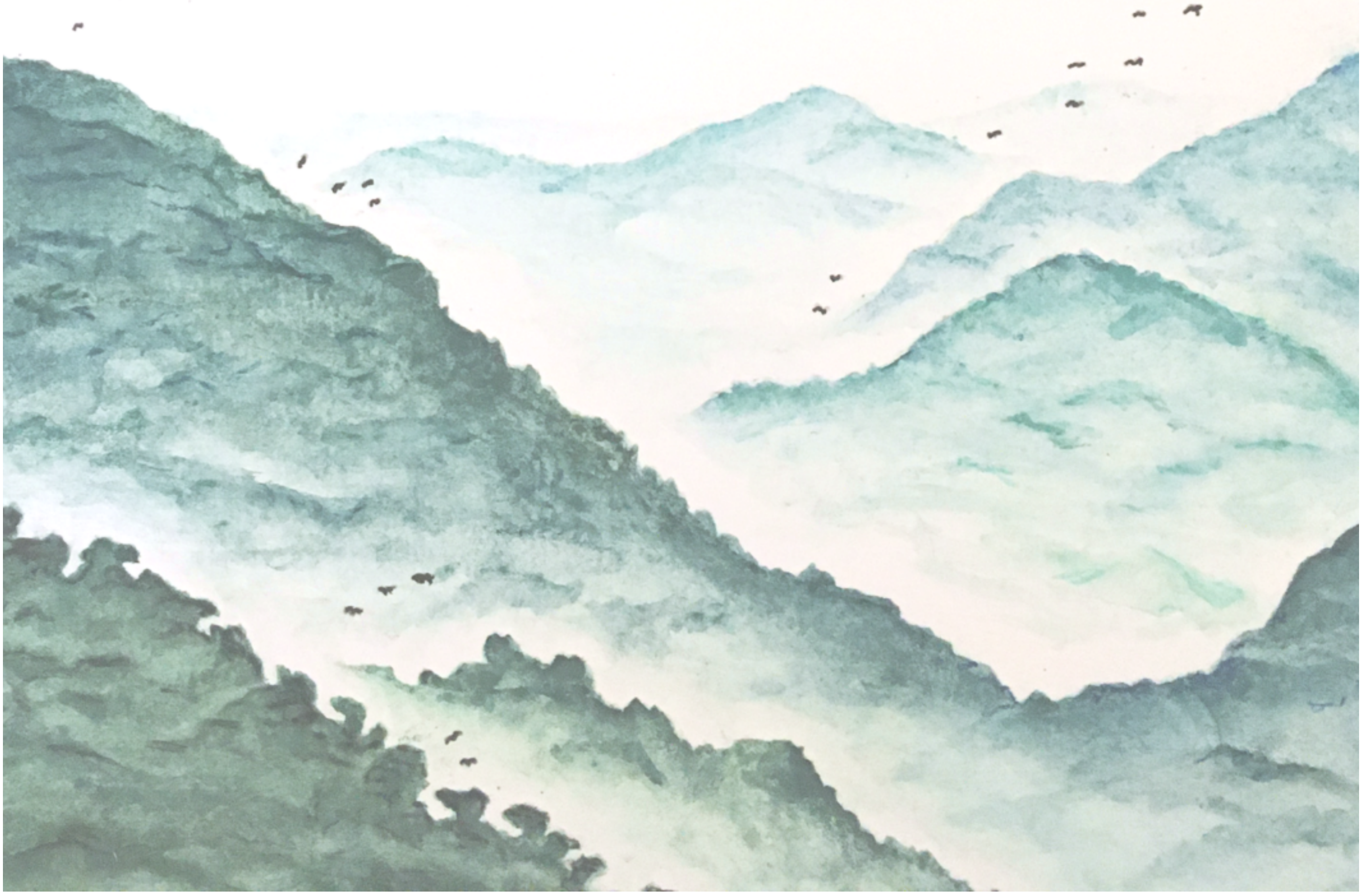
Chapter 1

Biodiversity and forest cover change



1.1 Introduction

Growing anthropogenic pressure on ecosystems are driving rapid changes in biodiversity and forest cover (Brown *et al*., 2001; Sax, 2002; Magurran and Dornelas, 2010; Magurran *et al*., 2010; Ellis, Antill and Kreft, 2012; Dornelas *et al*., 2014; Pandolfi and Lovelock, 2014; Isbell *et al*., 2017; Pecl *et al*., 2017; Blowes *et al*., 2019; FAO and UNEP, 2020; Global Forest Watch, 2020). This raises important questions such as: What do these changes mean for the future of forest and biodiversity conservation? How do forests recover following disturbance? Are patterns of biodiversity change over forest regeneration generalisable and do they translate across taxa? How can we improve land management and develop conservation solutions that support both people and nature? These themes (highlighted in bold print in the following chapter) are considered throughout this thesis.

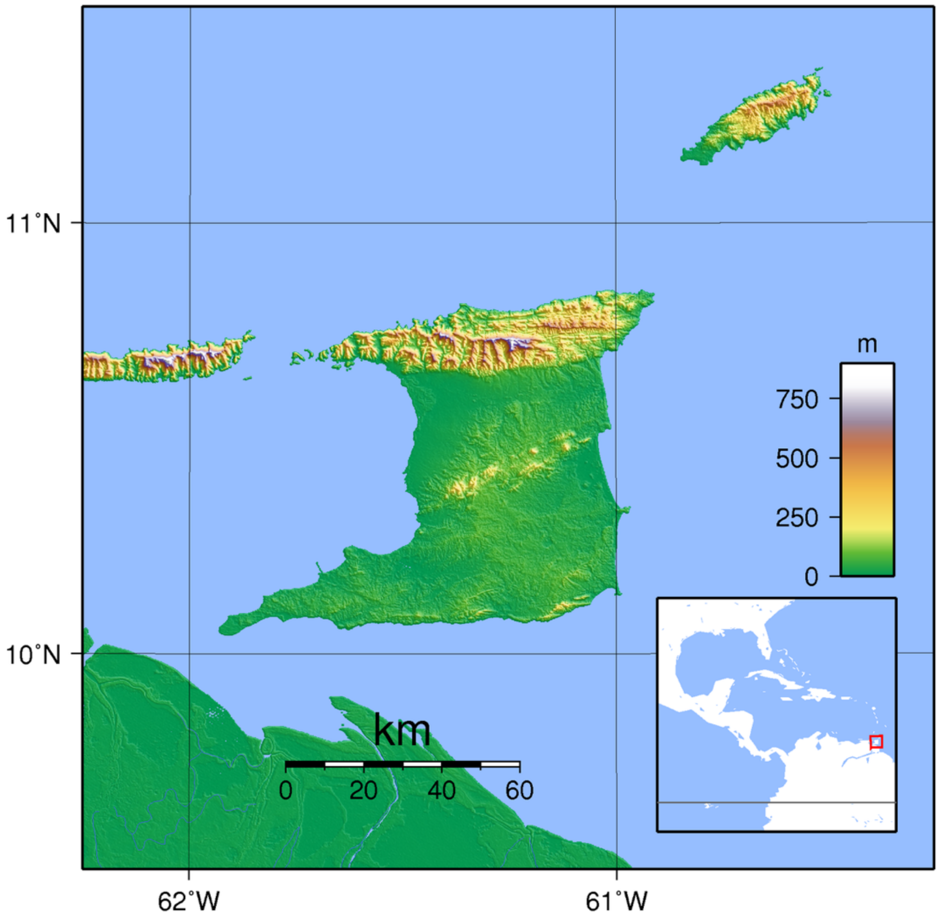


Figure 1.1 Topographic map of Trinidad and Tobago (Sadalmelik, 2007). Trinidad is the larger of the two islands, with the Northern Range mountains spanning the northern edge of the island.

My thesis focuses on cacao farming in Trinidad as a case study. Trinidad and Tobago is a twin-island nation in the Caribbean, located within a prominent biodiversity hotspot (Maunder *et al*., 2008; Hosein *et al*., 2017). Trinidad's Northern Range mountains are a mosaic of primary forests, agroforests, and secondary forest at different stages of regeneration following agricultural abandonment and other disturbances (Helmer *et al*., 2012). Tropical forests cover the Northern Range and there are many gaps in our knowledge of the biodiversity of this area.

This first chapter examines the history of Trinidad's cacao industry in the context of global biodiversity and forest cover change. Section 1.2 explores ongoing shifts in biodiversity and forest cover around the world. Section 1.3 provides further information on how these changes are reflected in the history of cacao farming in Trinidad. Lastly, section 1.4 outlines the aims of the following chapters.

1.2 Global biodiversity and forest cover change

Biodiversity

Biodiversity (Box 1.1) is under immense pressure due to increasing anthropogenic stresses on the environment (Magurran and Dornelas, 2010; Isbell *et al*., 2017; Blowes *et al*., 2019). Habitat loss and degradation, invasive species, the over-exploitation of species and natural resources, climate change, and the breakdown of ecological networks all contribute to the ongoing biodiversity crisis (Diamond, 1984; Daba and Dejene, 2018).

Biodiversity is fundamental to human wellbeing. Alongside the aesthetic value of biodiversity and the intrinsic right of species to exist, it underpins many important services that we rely on (Ehrlich and Ehrlich, 1997; Alho, 2008). For example, biodiversity is central to capturing carbon, pollination, the provision of food and industrial resources, climate regulation, and soil formation (Díaz, Hector and Wardle, 2009; Winfree, 2013; Oliver *et al*., 2015; Daba and Dejene, 2018). Furthermore, we depend on genetic diversity (diversity within species populations), for example, to create pest-resistant crop varieties and new medicines (Alho, 2008; McCouch *et al*., 2020).

The importance of biodiversity is increasingly being recognised and was brought to the forefront of global attention with the UN Decade on Biodiversity and the adoption of the 2011-2020 Strategic Plan for Biodiversity by the international community. While conservation efforts increased over this decade, most of the Aichi Targets which aimed to tackle the ongoing biodiversity crisis were not met by the 2020 deadline and the plan is widely believed to have failed (Hirsch, Mooney and Cooper, 2020). This highlights the pressing need for more ambitious conservation policies and actions to monitor and protect biodiversity. These shortcomings also emphasise the need for further research to **deepen our understanding of how biodiversity changes over time and space, and in response to human activity**, as many knowledge gaps remain (Magurran *et al.*, 2010; McGill *et al.*, 2015).

While studies have shown that patterns of biodiversity change over time and space are complex (Vellend *et al.*, 2013; Dornelas *et al.*, 2014; Supp and Ernest, 2014; McGill *et al.*, 2015; Newbold *et al.*, 2015), it is clear that anthropogenic activity has profoundly affected the environment, and biodiversity is being impacted. According to the Living Planet Index, vertebrate species' populations shrunk by 68% between 1970 and 2016 (McLellan *et al.*, 2014; Hirsch, Mooney and Cooper, 2020). In addition, the IUCN reported that overall, 27% of the species they assessed are threatened, and that the risk of extinction is growing rapidly for many species (especially cycads, amphibians, and corals; Hirsch, Mooney and Cooper, 2020). Global assessments estimate that 25.4% of mammals, 40.7% of amphibians, 21.1% of reptiles, and 13.6% of birds are at risk of extinction (IUCN, 2020; Cox *et al.*, 2022).

At a global scale, there is evidence that the rate of species extinctions has risen to become many magnitudes greater in the Anthropocene than average background rates over past millennia (Barnosky *et al.*, 2011; Pimm *et al.*, 2014; McGill *et al.*, 2015; Benton *et al.*, 2021). While it is challenging to contextualise these findings without a clear understanding of whether or how speciation rates have changed over the same geological timeframe, it is likely that species richness is declining at global scales (McGill *et al.*, 2015). It is also widely assumed that ecological assemblages are becoming more homogeneous globally, as non-native and invasive species which are often globally common (eg. feral pigeons *Columba livia*) colonise more areas around the world ("biotic homogenisation"; McKinney and Lockwood, 1999).

At local scales, compositional change (beta-diversity in Box 1.1) in ecological communities has accelerated globally, even when there is no change in the number of species (alpha-diversity; Brown *et al.*, 2001; Sax, 2002; Magurran *et al.*, 2010; Ellis, Antill and Kreft, 2012; Dornelas *et al.*, 2014; Pandolfi and Lovelock, 2014; Pecl *et al.*, 2017). This elevated temporal turnover likely results from anthropogenic changes to the environment and landscape. For example, turnover occurs when species shift their distribution as environmental conditions change, and when species are introduced to new areas or become locally extinct (McKinney, 2006; Hobbs, Higgs and Harris, 2009; Dornelas *et al.*, 2014; Magurran, 2016). **The effects of species compositional change on ecological interactions and processes remains a key knowledge gap**. Rapid changes in biodiversity (Dornelas *et al.*, 2014; McGill *et al.*, 2015; Newbold *et al.*, 2015) could endanger ecosystem functioning and the vital services we rely on (Cardinale *et al.*, 2012).

Forest cover

Forests are key habitats which support much of the world's terrestrial biodiversity and provide numerous services, including carbon sequestration, soil creation and stabilisation, and water regulation (Hansen *et al.*, 2013; Cox *et al.*, 2022). While it is challenging to accurately quantify the importance of forests in sustaining global biodiversity, it is estimated that around 80% of terrestrial plants and animals are found within forests despite these forests only accounting for about 31% of Earth's total land area (FAO and UNEP, 2020)

However, around 25.8 million hectares (Mha) of forest were lost in 2020 alone (Hansen et al., 2013; Global Forest Watch, 2020). Most of this deforestation is attributable to agriculture which accounted for over 70% of forest loss and degradation between 2000 and 2010, as well as forestry operations, natural and anthropogenic wildfires, mining, and urban expansion (FAO and UNEP, 2020; Global Forest Watch, 2020).

Box 1.1 Facets and aspects of biodiversity

Biological diversity (biodiversity) was defined by the UN Convention on Biological Diversity (1992) as “the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems” (UNEP, 1992).

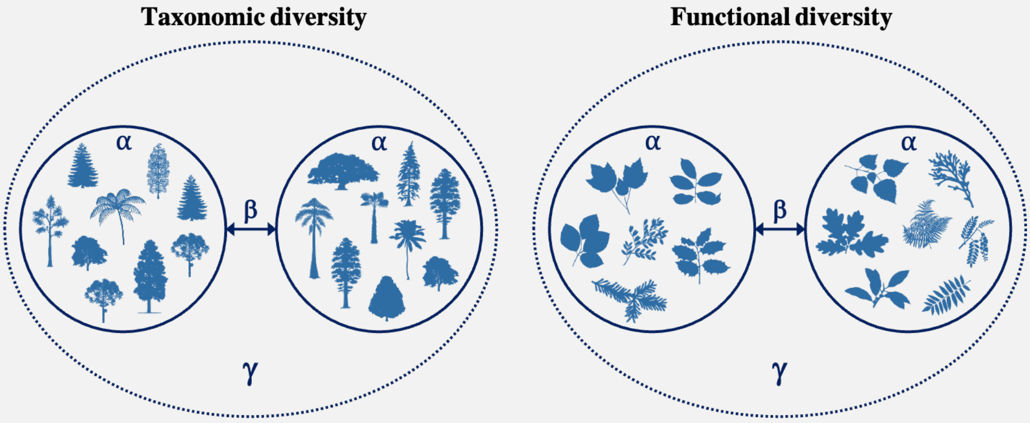


Figure 1.2. Schematic showing the facets and aspects of biodiversity measured in this study. Taxonomic diversity is related to the number and relative abundance of taxa (α), and the change in taxonomic composition (β) within and between assemblages. Functional diversity assesses the diversity and relative frequency (α), and the change (β) in certain phenotypic and behavioural traits expressed within and between assemblages.

Multiple facets and aspects of biodiversity were assessed throughout this thesis (Figure 1.2; Chapter 3.4). The facets of biodiversity explored were taxonomic diversity and functional diversity, and the alpha, beta, and gamma aspects of biodiversity were considered. Taxonomic alpha-diversity assesses the number and relative abundances of species in an assemblage (represented by the solid circles), while beta-diversity assess the change in species composition between assemblages. Functional alpha-diversity measures the range and prevalence of functional traits expressed by the species in an assemblage, while functional beta-diversity assesses changes in the functional traits expressed between

Continued

Box 1.1 Facets and aspects of biodiversity (continued)

assemblages. Gamma-diversity (dotted circle) signifies the overall landscape-level taxonomic or functional trait diversity.

While most studies focus on measures of taxonomic alpha-diversity such as species richness (the number of species in an assemblage), interest has been growing in the effects of species turnover on ecosystem processes (Díaz and Cabido, 2001). Turnover (species compositional change) in ecological communities has accelerated globally, even when there is no change in species richness (Brown et al., 2001; Sax, 2002; Magurran et al., 2010; Ellis, Antill and Kreft, 2012; Dornelas et al., 2014; Pandolfi and Lovelock, 2014; Pecl et al., 2017). This elevated temporal turnover likely results from anthropogenic changes to the environment.

For example, turnover occurs when species shift their distribution as environmental conditions change, and when species are introduced to new areas or become locally extinct (McKinney, 2006; Hobbs, Higgs and Harris, 2009; Dornelas et al., 2014; Magurran, 2016). In forests, species composition is changing with the conversion of old-growth to secondary forests. It is unclear what effect changes in species composition are having on ecosystem functioning.

Incorporating community composition when investigating the link between biodiversity and ecosystem functioning is important since not all species are functionally equivalent or perform the same ecological roles. Species have different phenotypic and behavioural traits (functional traits) which shape their interactions with other organisms and their environment (Díaz and Cabido, 2001; Weiher, 2011; Cadotte, 2017).

Species can have the same overlapping traits or different complementary traits. While more closely related individuals tend to be more similar, convergent and divergent evolution can cause distantly related individuals to have similar traits and vise-versa (Weiher, 2011; Schweiger *et al*., 2018). It is thought that trait overlap can increase functional stability,

Continued

Box 1.1 Facets and aspects of biodiversity (continued)

while greater trait complementarity can increase the functional capacity of an ecosystem. For example, if one species becomes locally extinct, a functionally redundant species could fill the same ecological role and so help maintain functional stability within the ecosystem (Bai *et al.*, 2004; Tilman, Reich and Knops, 2006; Griffin *et al.*, 2009; Hautier *et al.*, 2015; Isbell *et al.*, 2015). Greater trait complementarity on the other hand enables organisms to exploit different niches and capture more resources, such as different plants in a community capturing different wavelengths of light (Fargione *et al.*, 2007; Cardinale *et al.*, 2012; Zuppinger-Dingley *et al.*, 2014; Williams *et al.*, 2017).

The composition and diversity of traits represented within a community affect the propensity and efficiency of certain ecosystem functions (Tilman *et al.*, 1997; Weiher, 2011; Schweiger *et al.*, 2018), and the most dominant traits within a community tend to affect ecosystem functioning the most. Furthermore, some species are more effective in their roles and so contribute disproportionately to ecosystem functioning (Fargione *et al.*, 2007; Cadotte, 2017). Thus, the species which make up an ecosystem and the traits they possess can greatly influence ecosystem functioning, and understanding changes in functional trait diversity and composition is more informative in assessing forest functioning than changes in species diversity alone.

While temperate forests were mainly exploited historically, tropical forests are most at risk from anthropogenic deforestation today (Gibson *et al.*, 2011; Mora *et al.*, 2015). Temperate forests experienced the greatest losses before 1950**,** when trees were cut to fuel the western industrial revolution (Millennium Ecosystem Assessment, 2005). Tropical forests are now bearing the brunt of human destruction due to disproportionately rapid population growth in tropical regions and socio-political factors including international markets and economic inequality (Lambin *et al.*, 2001; Geist and Lambin, 2002a; Norden *et al.*, 2015).

The rapid loss of tropical forests is concerning as they are among the most biodiverse ecosystems, supporting many endemic and threatened species (Myers, 1980; Myers *et al.*, 2000; Shvidenko, McCallum and Nilsson, 2005; Aerts and Honnay, 2011; Morales-Hidalgo, Oswalt and Somanathan, 2015; Betts *et al.*, 2017). It is estimated that tropical forests support over 50% of all species (Wilson and Frances, 1988; Laurance, 1999; Dirzo and Raven, 2003) and represent approximately 37% of global terrestrial carbon (Laurance, 1999; Bradshaw, Sodhi and Brook, 2009; Martin, Newton and Bullock, 2013), yet over 50% of tropical forests have already vanished globally (Malhi *et al.*, 2014; Lewis, Edwards and Galbraith, 2015; Brancalion *et al.*, 2019).

Equally concerning is that much of the tropical forest being lost is also primary forest. Primary forests are centuries old, comprised of native species, and show no indication of recent severe disturbance or human activity. They are also exceptionally biodiverse, and support many sensitive and specialist species. Approximately 1.3 giga hectares (Gha) of the 4Gha total forest cover is primary forest (FAO, 2015), but primary forest cover is rapidly declining. In 2020, a further 12.2Mha of tropical land was deforested, 4.2Mha of which was humid tropical primary forest (Global Forest Watch, 2020).

Alongside these heavy and concerning losses, approximately 7.3Mha of forest is gained globally each year, largely from naturally-regenerating secondary forests and planted forests (estimate based on forest gains of 80.6Mha between 2001 and 2012; Hansen *et al.*, 2013; Global Forest Watch, 2020). The rate of net forest loss has been declining since 1990; this is mostly due to gains in temperate and boreal forest cover (FAO and UNEP, 2020). With current patterns of deforestation and afforestation, the area coverage of secondary forest is rapidly increasing relative to primary forest (Ellis, Antill and Kreft, 2012; Martin, Newton and Bullock, 2013). While the decrease in net forest loss is promising, **rapid shifts in the type of forest cover have important implications for ecological interactions, the maintenance of ecosystem functions and services, and biodiversity conservation**.

Secondary forests account for approximately 64% of all earth's forests (MacDicken et al., 2016). As the proportion of secondary and planted forests continues to rise, it is becoming increasingly important that we understand **how these human-altered ecosystems change and recover over time, and their potential to act biodiversity reservoirs**. While conservation initiatives and research have traditionally concentrated on old-growth forests, the contributions secondary forests can make to conservation is gaining recognition (Jos Barlow *et al.*, 2007; Gardner *et al.*, 2009; Tabarelli *et al.*, 2012; Barnosky *et al.*, 2017).

Research on secondary forests demonstrate their ability to sustain biodiverse communities and some of the same functions as their old-growth counterparts (Chapter 2; Guariguata *et al.*, 1997). For example, studies following secondary forest processes over succession indicate that secondary forests can recover species richness and some basic functions, including structural characteristics and aboveground biomass, quickly (within 50 years; Schoonmaker and McKee, 1988; Finegan, 1996; Guariguata *et al.*, 1997; Kennard, 2002; Chazdon, 2003; Lebrija-Trejos *et al.*, 2008; Martin, Newton and Bullock, 2013; Derroire *et al.*, 2016). More complex functions such as soil properties and nutrient cycling (Álvarez-Yépiz *et al.*, 2008; Derroire *et al.*, 2016) and tree species composition often remain different from that of primary forests for centuries (Chapter 2; Riswan, Kenworthy and Kartawinata, 1985; García-Montiel and Scatena, 1994; Finegan, 1996; Derroire *et al.*, 2016). While the protection of primary forests remains important, forest conservation could benefit from expanding its focus to further recognise the potential value of secondary and managed forests. **Though they are often overlooked, secondary and managed forests could prove to be vital reservoirs of biodiversity in the future**. Understanding tropical secondary forest dynamics can help identify which areas to conserve, improve land management, and support restoration programs.

1.3 People and nature

The importance of forests was acknowledged by 141 world leaders at the COP26 UN climate change summit in their commitments to halt and reverse deforestation by 2030 (COP26, 2021a, 2021c, 2021b). This pledge includes approximately $19.2 billion USD of public and private funds for forest conservation. The pledge also covers approximately 91% of the world’s forests, including the Brazilian Amazon, and asserts that countries should conserve and restore forests, recognise Indigenous Peoples’ rights, engage with local communities, and manage land sustainably overall. Twenty-eight of the signatories further committed to ensuring that globally important industries such as soy, palm oil, and cacao do not contribute to deforestation (COP26, 2021a, 2021c, 2021b). While this is an important step forward, previous deforestation initiatives have failed to meet their targets such as the 2006 UN forum on forests (UN, 2007) and the 2014 New York Declaration on forests (UNFCCC, 2015). Slowing deforestation has proved challenging and, as with the Aichi targets, past failures underscore the need for a better understanding of forest biodiversity as well as the need to expand on our approaches to conservation.

One key conservation challenge is to find solutions that support both people and nature (Mace, 2014). As the human population and our demand for earth's limited resources continues to rise, more and more land is being transformed for human use (Ehrlich and Pringle, 2008; Semper-Pascual *et al.*, 2019). While this poses a major threat to biodiversity, there is potential for human-managed land, such as agroforestry systems, to provide income and resources to humans while also benefitting wildlife (Calvo and Blake, 1998; Rice and Greenberg, 2000; Tscharntke *et al.*, 2012; Buechley *et al.*, 2015; Arroyo-Rodríguez *et al.*, 2017). Developing systems which are mutually beneficial for people and nature would allow us to expand on and improve current approaches to conservation, and better meet environmental targets for sustaining biodiversity. **Consequently, there is a pressing need to understand how biodiversity conservation can be supported, not as an alternative to human use of the environment, but as part of it**.

Developing agricultural systems that better support local biodiversity is a crucial step towards improving our capacity to coexist with nature (Grau, Kuemmerle and Macchi, 2013). Demands on the agricultural industry are increasing as a consequence of population growth. Agricultural expansion and intensification are of particular concern in biodiverse tropical regions where they are major drivers of deforestation and environmental degradation (FAO and UNEP, 2020).

Cacao is one example of a globally important crop that is transforming tropical landscapes. The annual global market value of chocolate is worth over $100bn USD, and both demand for cacao products and the industry's market value have continued to rise dramatically throughout the past two decades (Vaast and Somarriba, 2014; Borda *et al.*, 2021). The rising demand and growing market for cacao has driven increases in the number and size of cacao farms in tropical regions around the world. The spread of cacao has also driven farmers to use more intensive farming practices with the aim of producing greater yields. Cacao farming is already a major driver of tropical deforestation, and the environmental impact of cacao cultivation is projected to worsen as the industry continues to grow (Vaast and Somarriba, 2014; Borda *et al.*, 2021).

It is estimated that over 80% of cacao is produced on small family-run farms globally (Vaast and Somarriba, 2014). Despite the booming global chocolate market, many of these small cacao farmers only receive around 4-6% of the final value of the chocolate and earn less than $1 USD a day on average (Yeung, 2019; Borda *et al.*, 2021). Demand for ethical and environmentally responsible cacao products such as fair trade and organic chocolate is growing, however (Poelmans and Rousseau, 2016; ICCO, 2021). While certification schemes require more effort and investment initially, they offer greater equality and transparency, and can generate greater income for farmers. Ethical cacao farmers can sell their cacao for higher prices and can receive a greater share of the final value of cacao products (ICCO, 2021). Ethical and sustainable farmers who grow a variety of different agricultural and shade trees can have a more diverse and stable income, and create more ecologically resilient farming systems (Chapter 7; Vaast and Somarriba, 2014).

Ethically and sustainably produced cacao, along with other agroforestry systems such as coffee and vanilla, show promise in being able to support wildlife as well as livelihoods in the tropics (Calvo and Blake, 1998; Buechley *et al.*, 2015; Arroyo-Rodríguez *et al.*, 2017). **The extent to which these agricultural systems can support biodiversity, however, is not well understood**. Deepening our understanding of agroforestry and the contributions it makes to biodiversity conservation would allow us to develop land management strategies which better support wildlife, and which maximise ecosystem services and agricultural yields.

1.4 Cacao farming in Trinidad & Tobago

The global patterns in biodiversity and forest cover change explored in the previous section are reflected at a local scale in Trinidad and Tobago. While the change in forest cover was small overall, analyses using data from Hansen et al. (2013) in Google Earth Engine illustrated that there was net forest loss between 2001 and 2012 in Trinidad’s Northern Range

(Figure 1.3; Hansen *et al*., 2013; Gorelick *et al*., 2017). An estimated 15.2Kha of forest was lost, and while 1.6Kha was gained over the same time period in Trinidad and Tobago overall (Global Forest Watch, 2022). The conversion of land for cacao farming has been a major driver of land cover change in the Northern Range for over a century.

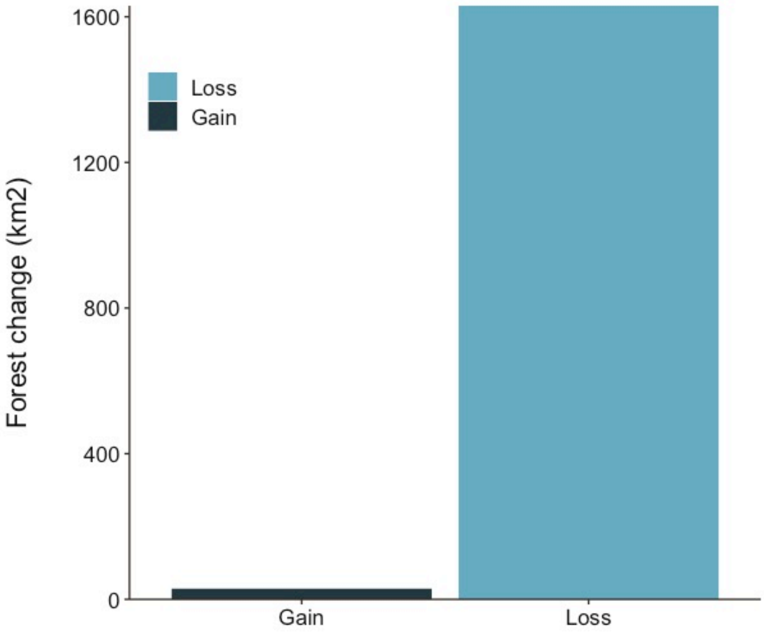
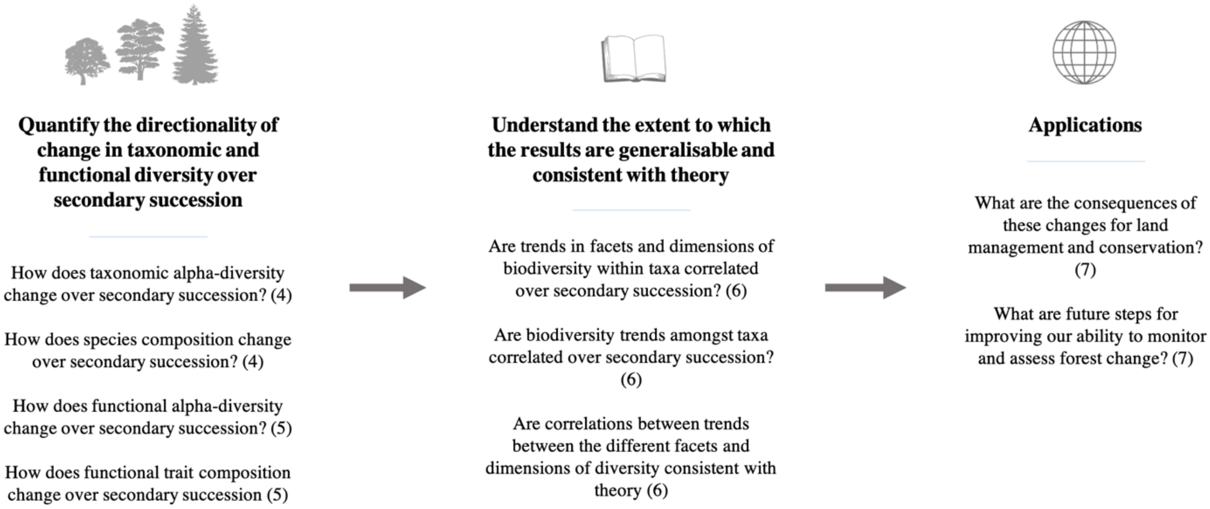


Figure 1.3 Forest gains and losses (km^2) in Trinidad's Northern Range mountains between 2000 and 2012. The change in forest cover were quantified using data from Hansen et al. (2013) in Google Earth Engine within a polygon covering the Northern Range mountains.

Cacao (*Theobroma cacao*) is a shade-tolerant tree species that naturally grows in the lower canopy layers of a forest (Tscharntke *et al*., 2012). While there are different methods of growing cacao, it is predominantly cultivated in polyculture, multi-strata agroforestry systems in Trinidad. This form of management involves growing cacao under taller trees which provide shade ("shade trees"; Seedial, 2009, 2013) and alongside other agricultural trees such as mango (*Mangifera indica*), coconut (*Cocos nucifera*), avocado (*Persea americana*), and oranges (*Citrus sinensis*). Mountain immortelle (*Erythrina poeppigiana*) are commonly planted as shade trees for cocoa in Trinidad. In recently established farms, tall herbaceous plants such as bananas and plantains (*Musa sp*.) are often used to provide shade until the shade trees mature. While cacao trees are naturally short, they are pruned in managed agroforests to ensure cacao pods can be harvested easily. The ground vegetation is sometimes masticated or suppressed using herbicides to make harvesting the cacao and regular management of the agroforest easier. Some farmers also use fertilisers to improve crop yields. Lastly, large epiphytes such as bromeliads and vines are often removed from cacao trees (Seedial, 2009, 2013). Cacao is cauliflorous (producing fruit from the tree trunk) and it is widely thought that epiphytes may supress the growth cacao pods among cacao farmers (Sporn, Bos and Gradstein, 2007).

Trinidad was the third largest cacao producer in the world by 1830, and the cacao industry dominated its economy from approximately 1866 to 1920 (Bekele, 2004). Though the cacao industry has declined in Trinidad and many old cacao estates have been abandoned, much of Trinidad’s land has been used for cacao production at some point and there are still many cacao farmers today (an estimated 3,500 farmers in 2004; Bekele, 2004; NATT, 2018). The cocoa industry has shaped parts of the Northern Range as many of the cacao farms were periodically abandoned and new farms formed over time, creating a natural chronosequence of forest regeneration (Bekele, 2004; NATT, 2018). This pattern of transformation provides an informative case study for **understanding how Trinidad’s history of cocoa farming has shaped patterns of biodiversity, and the potential contributions of actively managed and abandoned cocoa agroforests to biodiversity conservation**.

1.5 Aims of thesis



Quantify the directionality of change in taxonomic and functional diversity over secondary succession

How does taxonomic alpha-diversity change over secondary succession? (4)

How does species composition change over secondary succession? (4)

How does functional alpha-diversity change over secondary succession? (5)

How does functional trait composition change over secondary succession (5)

Understand the extent to which the results are generalisable and consistent with theory

Are trends in facets and dimensions of biodiversity within taxa correlated over secondary succession? (6)

Are biodiversity trends amongst taxa correlated over secondary succession? (6)

Are correlations between trends between the different facets and dimensions of diversity consistent with theory (6)

Applications

What are the consequences of these changes for land management and conservation? (7)

What are future steps for improving our ability to monitor and assess forest change? (7)

Figure 1.4 Schematic of questions being addressed in this thesis. The chapters in which these questions are addressed are indicated in brackets.

There is an urgent need to deepen our understanding of how ongoing changes in tropical landscapes affect the ability of forests to sustain biodiversity, to improve land management, and to find conservation solutions which can support both people and nature.

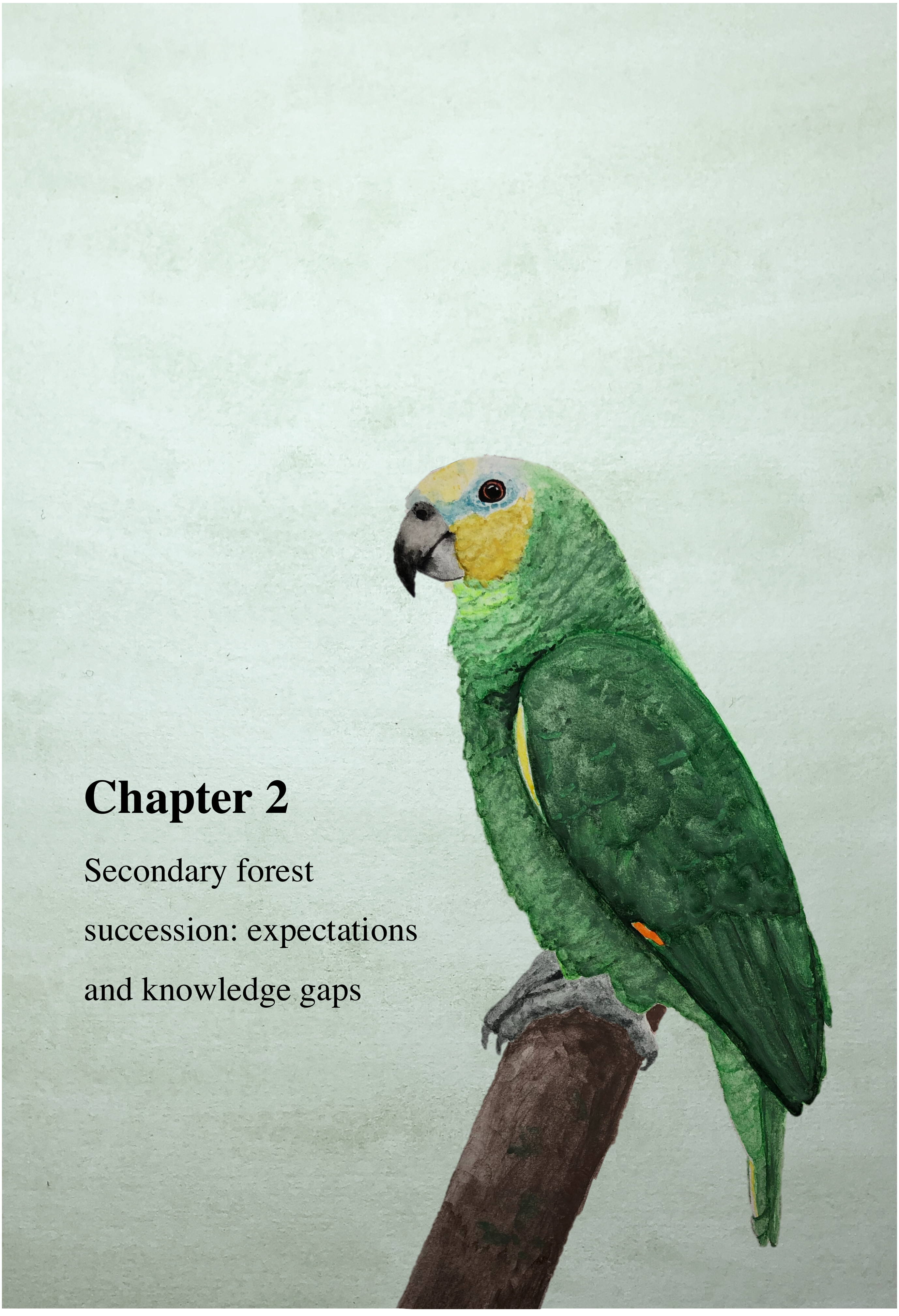
The objective of this thesis is to assess how species and functional diversity change over tropical secondary forest succession following cacao farming, and how generalised these patterns are across taxa in Trinidad. This thesis will also address whether these results align with expectations from succession theory and previous research. Within this, the following questions will be addressed:

1. How does taxonomic alpha-diversity and species composition change over secondary forest succession following cacao agroforest abandonment in Trinidad? (Chapter 4)
2. How does functional alpha and beta-diversity change with forest age following cacao agroforest abandonment in Trinidad (Chapter 5)
3. Do different taxa, and different facets and dimensions of biodiversity respond similarly over secondary forest succession following cacao agroforestry in Trinidad? (Chapter 6)
4. Are patterns of biodiversity change over secondary forest succession following cacao farming in Trinidad in line with expectations based on succession theory and previous research (Chapters 2 and 6)
5. What are the consequences of these changes in biodiversity over secondary forest succession following cacao agroforestry for conservation and land management? (Chapter 7)
6. What are future steps for improving our ability to monitor and assess forest change? (Chapter 7)

To address these questions, Chapter 4 quantifies how species diversity and composition change over succession, and Chapter 5 quantifies how functional diversity and functional trait composition change over succession. Chapter 6 compares trends across the facets and aspects of biodiversity and across taxa. Chapter 6 also assesses how trends in biodiversity change compare with expectations from the theory and previous research outlined in Chapter 2. The methods for these chapters are outlined in Chapter 3. Lastly, Chapter 7 summarises key findings and how they fit within global trends and discusses the applications of these findings for land management and conservation initiatives.

Chapter 2

Secondary forest succession: expectations and knowledge gaps



2.1 Introduction

Ecological succession (hereafter ‘succession’) refers to the transformation of an ecological community over time following natural or anthropogenic disturbance, or new land formation (Chazdon, 2014). Succession has been a central pillar in ecology since the turn of the 20th century (Glenn-Lewin, Peet and Veblen, 1992). Although many aspects of succession theory have been contested, it remains inextricably linked to many modern ecological theories, such as those regarding species coexistence and community assembly (Chang and Turner, 2019). Furthermore, understanding how ecological communities change over succession is a key challenge in conservation. For example, information on successional processes can help to predict the rate and trajectory of ecosystem recovery following disturbance, and inform decisions concerning which areas to protect and where intervention may be necessary (Bosselman and Tarlock, 1994).

The relative strengths of various drivers of succession, as well as the predictability and generalisability of successional processes, have been much debated (West, Shugart and Botkin, 1981; Glenn-Lewin, Peet and Veblen, 1992; Pulsford, Lindenmayer and Driscoll, 2014). Despite over a century of intensive study, there remains disagreement over theoretical frameworks, and incongruence in results from empirical research. Understand successional dynamics and the search for generalities is increasingly important, however, as the impacts of human activity become ever more acute and pervasive (Chapter 1; Meiners *et al.*, 2015; Chang and Turner, 2019).

The following chapter will discuss theories and findings from existing research regarding how ecosystems change over time through succession. Section 2.2 will cover the ongoing development of succession theory including information regarding links between taxa and between facets of biodiversity. Section 2.3 will address findings on how ecosystems change over succession from existing empirical research, focusing on patterns of biodiversity across taxa.

Box 2.1 Primary and secondary succession

Ecological succession is typically categorised as either “primary” following new land formation or complete land clearance, or “secondary” following partial land clearance with some soil properties remaining intact. Though the two are often treated as distinct categories, in natural systems the difference between primary and secondary succession is less discrete (Chazdon, 2014; Meiners *et al*., 2015). Chazdon (2014) outlines a conceptual framework for assessing the initial conditions of succession, where primary and secondary succession lie at opposite ends of a continuum based on species and resource availability. Secondary succession tends to have higher resource (eg. soil nutrients and water) and species (eg. seed rain, soil seed bank, and resprouting plant) availability compared to primary succession. Patches of land undergoing succession can fall onto different places on this primary-secondary succession gradient, depending on factors such as their geography and disturbance history, making categorisation difficult. Furthermore, resource and species availability can affect the rate and trajectory of succession (Pickett and Cadenasso, 2005), and thus successional processes can differ within both primary and secondary succession (Chapter 2.4; Chazdon, 2014).

This chapter will focus primarily on tropical secondary forest successional dynamics. Corlett (1994) defines secondary forests as those which have been mostly or entirely deforested naturally or anthropogenically, where some residuals (soil, organisms or propagules) survived, but where the effects of the disturbance are still evident (Corlett, 1994).

2.2 Succession: theory

Succession has been a primary focus of ecological research for more than a century. Ideas regarding succession appear in the works of pioneering naturalists such as Darwin (Darwin, 1859; Meiners *et al.*, 2015), and overarching theories of succession have been proposed, developed, and contested since the late 1800s (eg. Forbes (1880) and Cowles (1899); Connell and Slatyer, 1977; Johnson, 1979; West, Shugart and Botkin, 1981; Glenn-Lewin, Peet and Veblen, 1992). Much of our understanding of classical succession stems from research done on North American plant assemblages in the early 1900s (eg. work by Cowels, Clements, Gleason and others; Glenn-Lewin, Peet and Veblen, 1992). Classical succession theory, also referred to as Clementsian succession after Clements' (1916) seminal work, remained highly influential through the first half of the 20th century (Clements, 1916; Glenn-Lewin, Peet and Veblen, 1992).

Classical succession theory follows an equilibrium paradigm which suggests that plant assemblages will progressively and predictably converge towards a stable equilibrium following disturbance, (Clements, 1916, 1928, 1949; Cooper, 1926; Gleason, 1927; Odum, 1969; Glenn-Lewin, Peet and Veblen, 1992). Within this, Clements proposed succession as a process whereby (1) organisms colonise and (2) become established on disturbed land, (3) interact with each other through competition, and (4) modify their environment. This continually shifts the relative ability of species to survive until (5) the community reaches a stable climax (Clements, 1916).

However, this orderly and predictable classical understanding of succession has been widely criticized since the 1940s as being too simplistic and descriptive, and lacking support in empirical research (eg. (McCormick, 1968; Drury and Nisbet, 1971; Horn, 1971; Pickett, 1976; Connell and Slatyer, 1977). Succession seldom occurs so neatly in natural systems and the idea of a 'climax' state is illusory (Gleason, 1927; West, Shugart and Botkin, 1981; Chazdon, 2014; Ellison and Gotelli, 2021). It is now broadly accepted that ecosystems are dynamic and constantly changing, and there is rarely a clear point at which succession ends (Cowles 1901; Chazdon, 2014). While some elements of classical succession are still considered to hold true, many contemporary views of succession have been developed to refine classical theory, to apply a more quantitative approach, and to better account for the complexity in ecological processes.

The search for generalities in the patterns and processes of succession continues today with disagreement over theoretical frameworks and widely varying results from empirical research, even within the same ecosystem (West, Shugart and Botkin, 1981; Westoby, Walker and Noy-Meir, 1989; Tilman, 1990; Vandermeer *et al.*, 2004; Breugel, Martínez-Ramos and Bongers, 2006; Chazdon *et al.*, 2007; Feldpausch *et al.*, 2007; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Norden *et al.*, 2015). Furthermore, succession theory has historically focused on temperate ecosystems (West, Shugart and Botkin, 1981; Glenn-Lewin, Peet and Veblen, 1992), though research suggests that the rate and trajectory of succession varies across biomes (Section 2.4; Lugo and Brown, 1991; Lebrija-Trejos *et al.*, 2008; Lebrija-Trejos *et al.*, 2010; Gibson *et al.*, 2011). Thus, predicting how tropical ecosystems will change following disturbance based on successional theory can be especially difficult (Gibson *et al.*, 2011; Mora *et al.*, 2015). Other factors such as the intensity and frequency of disturbance, habitat connectivity, and biotic interactions can further alter successional processes and determine the successional pathway of an ecosystem (Section 2.4; Woods, 1989; Cubiña and Aide, 2001; Chazdon, 2003; Ingle, 2003; Hooper, Legendre and Condit, 2004; Derroire *et al.*, 2016; Rolim, Machado and Pillar, 2017).

Disagreement over succession theory largely stems from differences in the starting point of succession, the idea of a stable climax state that an ecosystem returns to following disturbance, the primary drivers of succession, and the spatial and temporal scale at which succession is viewed (West, Shugart & Botkin, 1981). Nonetheless, it is widely recognised that changing pressures from deterministic processes drive changes in biodiversity and community composition over succession (traditional niche-based theory; Brown and Lugo, 1990; Cequinel et al., 2018; Chang and Turner, 2019; Chazdon, 2014; Lebrija-Trejos et al., 2010a; Lohbeck et al., 2012). Deterministic process include environmental filtering, species traits, and interspecies interactions (Zhou *et al.*, 2014).

Environmental filtering occurs when species arrive at a given location but cannot survive due to the environmental conditions (also called "abiotic filtering"; Kraft *et al.*, 2015). Thus, local abiotic factors act as a filter where only species with phenotypic or behavioural traits that allow them to survive in a disturbed area can become established (Nobel and Slatyer, 1977; Bazzaz, 1991; Woodward and Diament, 1991; Kraft *et al.*, 2015). Similarly, species' traits (especially life history traits related to life strategy trade-offs such as the number and size of propagules or offspring, and rate of maturation) can affect the ability of species to colonise at different stages of succession as well as their relative fitness and competitive ability (West, Shugart and Botkin, 1981; Chu *et al.*, 2007; Zhang, Qi and Liu, 2018). Lastly, the biotic interactions of competition, facilitation and inhibition are also thought to strongly influence successional dynamics (West, Shugart and Botkin, 1981; Glenn-Lewin, Peet and Veblen, 1992; Pulsford, Lindenmayer and Driscoll, 2014; Meiners *et al.*, 2015).

The relative importance of these deterministic processes versus stochastic processes, such as random colonisations and extinctions, in driving successional dynamics has been the subject of long-standing dispute. For example, while traditional theory describes succession primarily as a product of deterministic processes resulting in stable communities, others such as Cowles (1901) and Gleason (1926) propose that stochastic processes are a major driver of successional change and assemblages are to some extent random collections of species (Cowles, 1901; Gleason, 1926).

There are some general features of succession that are well supported by empirical evidence (Section 2.3). The successional mechanisms of abiotic conditions, biotic interactions and species traits are commonly observed (West, Shugart and Botkin, 1981; Tilman, 1990; Glenn-Lewin, Peet and Veblen, 1992; Chu *et al.*, 2007; Cequinel *et al.*, 2018), and there is evidence that stochastic events play a role in shaping successional trajectories as well (Norden *et al.*, 2015; Ulrich *et al.*, 2016; Boukili and Chazdon, 2017; Marteinsdóttir, Svavarsdóttir and Thórhallsdóttir, 2018; Måren *et al.*, 2018). However, the extent to which each of these mechanisms influence successional processes varies over time and across systems.

This thesis aims to assess how patterns of taxonomic and functional diversity change over succession in the context of succession theory and research (Chapter 6), and using abandoned cocao plantations in Trinidad's Northern Range as a case study. The expectations presented for this thesis are informed by contemporary views of community assembly (Chang and HilleRisLambers, 2016) and succession, as driven by a combination of successional mechanisms. While neutral processes likely influence succession to some degree, they are not the focus of this work. The effects of starting point, which are not directly tested in this thesis, are summarised in Appendix 2.1 for completeness. The following sections delve further into deterministic successional mechanisms and consider how they may shape patterns of biodiversity over succession. My goal here is to highlight knowledge gaps and develop predictions that can be tested using my field study.

Successional mechanisms

Biotic interactions

Competition is often treated as a major driving force of successional processes in both classical and contemporary ideas on succession (eg. Clements, 1916; Hutchinson, 1951; Tilman, 1985, 1990; Meiners *et al.*, 2015). For example, Tilman (1985; 1990) put forward the resource-ratio hypothesis where different plant species have varying abilities to compete for certain limiting resources such as soil nutrients, light, and water (Tilman, 1985). Therefore, as the availability of two or more limiting resources changes over time, community composition will shift. Within this, Tilman found that the transition from grassland to oak woodland was primarily driven by a nutrient:light ratio hypothesis, where soil nutrients and light were the two primary limiting resources in the regeneration of these forests (Tilman, 1990).

Competition is commonly thought to promote greater functional diversity (Box 1.1; Chapter 3) through competitive exclusion (Hardin, 1960; Macarthur and Levins, 1967; Grime, 1973). Species with unique complementary suits of traits are potentially able to exploit new niches which can facilitate coexistence, while species with overlapping redundant traits may outcompete and competitively exclude each other (Brown and Lugo, 1990b; Lebrija-Trejos, Meave, *et al.*, 2010; Lohbeck *et al.*, 2012; Chazdon, 2014).

Contrary to this however, some research has found that competition can generate greater functional redundancy if certain traits are more competitively advantageous (Chesson, 2000; Mayfield and Levine, 2010; HilleRisLambers *et al.*, 2012; Godoy and Levine, 2014; Kraft *et al.*, 2015). Fitness differences between species, such as the relative ability of a species to compete for shared resources or endure a shared enemy, drive competitive dominance. Competitive exclusion can therefore result in greater trait convergence if certain traits give species a competitive edge (Mayfield and Levine, 2010; Godoy and Levine, 2014; Kraft *et al.*, 2015).

Along with competition, species can interact through facilitation when one species benefits another (Stachowicz, 2001). This can be either through commensalism or mutualism. For example, standing trees can stabilise the soil, moderate temperature and weather, and regulate soil nutrient and water cycling which can support seed germination (Jones, Lawton and Shachak, 1997). Similarly, mutualisms between mycorrhizal fungi and plants may influence successional processes by affecting the ability of plants to take up nutrients and species ability to tolerate harsh environmental conditions (Skujins, 1991; Emery, 2010). Facilitation is thought to positively effect both alpha and beta-diversity (Stachowicz, 2001; McIntire and Fajardo, 2014). For instance, facilitation can reduce stressors such as harsh environmental conditions which may support more species, and the modification and creation of new habitats can increase species turnover over time (McIntire and Fajardo, 2014).

Conversely, species can interact through inhibition, when one species hinders the growth or survival of another (Connell and Slatyer, 1977; Walker and Del Moral, 2011). For instance, one species can monopolise resources and in doing so inhibit the growth of other species. Within this, one species can have both facilitative and inhibitory effects simultaneously (Walker and Del Moral, 2011).

Alongside direct interactions between species, species can interact over time through priority effects where earlier colonisers can affect the ability of later colonisers to survive and thrive (Fukami, 2015). A classic example of this is when the first plants to colonise contribute to disturbed land, making it more habitable for future colonisers through facilitative habitat modification (eg. Clements (1916) and Egler (1954); Walker and Del Moral, 2011; Pulsford, Lindenmayer and Driscoll, 2014) and less habitable for other pioneer-type species (eg. facilitation model from Connell and Slatyer, 1977; Horn and MacArthur, 1972). Furthermore, species can have inhibitory priority effects, for example by producing allelochemicals that persist in the soil or by changing the soil chemistry (Emery, 2010).

Species' traits

Species' traits are generally agreed to play a role in shaping patterns of biodiversity and composition over succession as well by determining when different species can colonise disturbed land and their comparative fitness (West, Shugart & Botkin, 1981; Zhang, Qi and Liu, 2018). Disturbed and deforested land often has degraded soil (decreased organic matter) and lower soil stability, as well as greater soil evaporation, wind strength, temperature, and light exposure (Guariguata and Ostertag, 2001; Sanaphre-Villanueva *et al.*, 2017). These early successional conditions affect which species are able to colonise and become established (Finegan, 1996; Guariguata and Ostertag, 2001).

The harsher starting conditions favour pioneer-type species which typically have abiotic dispersal syndromes (Guariguata and Ostertag, 2001; Sanaphre-Villanueva *et al.*, 2017) and allocate fewer resources to permanent structures (eg. stems and branches; Garnier *et al.*, 2004). Thus, they grow and spread rapidly, but are short-lived. They are also typically light-demanding with high photosynthetic capacities, and generalists which can tolerate wide-ranging and harsher environmental conditions (Guariguata and Ostertag, 2001; Dent, DeWalt and Denslow, 2013; Lohbeck, Poorter, Martínez-Ramos, *et al.*, 2013; Lasky *et al.*, 2014; Craven *et al.*, 2015, 2018; Muscarella *et al.*, 2016; Boukili and Chazdon, 2017).

Unlike these pioneer species, those common in mature forests are often slow-growing, long-lived, shade tolerant, and successful competitors (Connell and Slatyer, 1977; Uhl and Jordan, 1984; Guariguata and Ostertag, 2001; Garnier *et al.*, 2004; Chazdon *et al.*, 2010). This change in the types of species which colonise at different stages of succession thus describes a continuum where early stages favour plant species with fast life history traits, and later stages favour those with slow life history traits. Therefore, changes in species' traits and relative fitness in disturbed areas over succession could facilitate turnover in species and functional trait composition.

The idea that only certain types of species can become established in the early stages of succession has been contested, however. For example, alongside neutral theory (Hubbell, 2001), the initial floristic composition model by Egler (1954), and the tolerance and inhibition models of succession proposed by Connell and Slatyer (1977) assume that any species can become established at the start of succession (Egler, 1954; Connell and Slatyer, 1977). In support of these ideas, there is some evidence that shade-tolerant species can colonise in the early stages of succession, but do not become dominant until later stages (Chazdon, 2014).

Environmental filtering

Environmental filtering limits the functional diversity of species within an assemblage, as only species with specific traits that allow them to cope with challenging environmental conditions can survive (Weiher and Keddy, 1995; Díaz *et al.*, 1999; Kraft *et al.*, 2015; Craven *et al.*, 2018). Research suggests that the strength of environmental filtering changes over space and time (Montgomery and Chazdon, 2002; Lohbeck, Poorter, Martínez-Ramos, *et al.*, 2013; Muscarella *et al.*, 2016; Craven *et al.*, 2018) and is greater in early successional stages (Lohbeck, Poorter, Martínez-Ramos, *et al.*, 2013; Blanchard *et al.*, 2021). The harsh environmental conditions at the start of succession can limit initial colonisations, which is thought to be a key stage in defining successional trajectories due to priority effects (West, Shugart and Botkin, 1981; Fukami, 2015; Marteinsdóttir, Svavarsdóttir and Thórhallsdóttir, 2018).

It is commonly predicted that environmental filtering as well as competition strongly influence the degree of functional redundancy and complementarity in an assemblage, where environmental filtering is stronger in the early stages of succession, and competition is stronger later in succession (Letcher, 2010; Lohbeck, Poorter, Martínez-Ramos, *et al.*, 2013; Blanchard *et al.*, 2021). For example, Lohbeck et al. (2013) found that environmental filtering primarily determines species dominance in woody plant assemblages early on when conditions are often harsher, while competitive exclusion becomes an increasingly stronger driver of community assembly as succession progresses. Over succession the land becomes more hospitable through biotic facilitation, but plants experience increasing competitive pressure for space, light, and other resources (Lohbeck, Poorter, Martínez-Ramos, *et al.*, 2013). Thus, there should be greater functional redundancy in younger forests, and greater trait complementarity in older forests.

Chazdon (2014), however, notes that environmental filtering can strongly influence successional dynamics later in succession. For example, light-demanding pioneer trees are excluded from mature forest stands since they cannot survive in the low-light conditions. Shade-tolerant species on the other hand can colonise earlier in succession, but do not dominate the canopy layer until later successional stages as they grow more slowly (eg. Kayes, Anderson and Puettmann, 2010). Other sources have likewise concluded that environmental filtering increases over succession (eg. Raevel, Violle and Munoz, 2012; Muscarella *et al.*, 2016; Craven *et al.*, 2018). Given this, greater functional redundancy should be expected in older forests, especially over secondary succession where some structural and soil properties remain intact (Chazdon, 2014).

Links between taxa

Most successional theory and research specifically focus on plant communities, though some work has considered patterns of successional change in non-plant taxa with mixed results. For example, Shelford (1911) found that changes in tiger beetles and pond fish assemblages were primarily driven by changes in the plant community over succession (Shelford, 1911). In contrast, Adams (1908) found that bird assemblages in North America were mostly influenced by a combination of biotic interactions and environmental variables (Adams, 1908).

Furthermore, Fox (1982) proposed the Habitat Accommodation model of succession for animal taxa based on Connell & Slatyer's (1977) Facilitation and Tolerance models of succession (Fox, 1982). The Habitat Accommodation model predicts that animal species will colonise disturbed land when the vegetation characteristics (eg. structure and composition) meet their habitat requirements. The animal species will decline if the plant community changes over succession in such a way that conditions become less favourable (Fox, 1982). While empirical testing of the Habitat Accommodation model of succession has likewise yielded varying results depending on the taxon studied (Fox, Taylor and Thompson, 2003; Lindenmayer *et al.*, 2008; Nimmo *et al.*, 2012; Smith, Michael Bull and Driscoll, 2013), it is expected that plant and animal community dynamics should be tightly linked (DeWalt, Maliakal and Denslow, 2003; Bowen *et al.*, 2007).

Overall, it is generally expected that changes in plant biodiversity and composition will be correlated with changes in other taxa. Plants are autogenic ecosystem engineers which disproportionately contribute to forest ecosystem functioning (Jones, Lawton and Shachak, 1994, 1997; Stachowicz, 2001). Trees and other plants create habitat, regulate local environmental conditions, contribute to nutrient cycling, soil formation and stabilisation, and provide resources for other species (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Weiher, 2011). It is thought that greater plant diversity provides more habitat and food resource heterogeneity, and can increase food stability over time, which may facilitate greater diversity in other taxa (Hooper *et al.*, 2000; Waldrop *et al.*, 2006; Sobek *et al.*, 2009; Haddad *et al.*, 2011; Tedersoo *et al.*, 2016; Brockerhoff *et al.*, 2017).

As plant community diversity and composition change over succession, the types and amounts of habitat and resources available for other organisms to exploit changes as well (DeWalt, Maliakal and Denslow, 2003; Bowen *et al.*, 2007). Therefore, animal populations should change in response to changes within the plant community. For example, older trees usually have more cavities (Santos Jr *et al.*, 2006), and tree cavity nesting bird species are often confined to older forests (Chazdon, 2014). Even within the plant community, greater tree diversity is thought to increase habitat heterogeneity, for example in light conditions, soil properties and resource availability and so positively affect ground vegetation diversity (Augusto et al., 2003; Lassau et al., 2005; Hobbie et al., 2006; Cesarz et al., 2007; Barbier et al., 2008; Sobet et al., 2009; Vockenhuber et al., 2011)

Furthermore, changes in animal assemblages such as invertebrates, mammals, and birds may affect plant communities through mechanisms including herbivory, seed predation and dispersal, and pollination (Gallagher, 2013; Schleuning, Fründ and García, 2014; Tedersoo *et al.*, 2016; Rolo, Olivier and van Aarde, 2017; Gardner *et al.*, 2019).

It is therefore expected that changes in biodiversity and composition will be correlated between taxonomic groups, as taxa interact with and influence how other taxa change over succession (van der Heijden *et al.*, 1998; Vogelsang, Reynolds and Bever, 2006; Hiiesalu *et al.*, 2014; Pellissier *et al.*, 2014; Rolo, Olivier and van Aarde, 2017; Catterall, 2018; Gardner *et al.*, 2019; Díaz-García *et al.*, 2020). Studies that compare trends in biodiversity change across taxa are scarce, however, and dynamic linkages between taxa over succession are complex and poorly understood (Section 2.3).

Links between facets and aspects of biodiversity

As well as between-taxa correlations, it is also expected that species and functional diversity will be positively correlated. It is hypothesised that the larger the local species pool is, the more likely there are to be species with complementary traits (Huston, 1997; Mayfield *et al.*, 2010) and that complementary traits between species can facilitate coexistence (Brown and Lugo, 1990b; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Lohbeck *et al.*, 2012; Chazdon, 2014). Several studies have found that species and functional diversity are positively correlated in various taxa and systems (eg. Heino, 2008; Bihn, Gebauer and Brandl, 2010), though the relationship is rarely perfectly proportional in nature, and functional richness should not exceed species richness due to the possible inclusion of functionally redundant species (Díaz and Cabido, 2001). Overall, however, empirical studies have yielded mixed results, and mechanisms such as environmental filtering can lead to trait overlap within an assemblage and affect the degree of correlation between taxonomic and functional diversity (Cadotte, Carscadden and Mirotchnick, 2011). It is commonly suggested that there is greater pressure from competition and more specialist species in older forests, which would further promote functional diversity over succession (Brown and Lugo, 1990b; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Chazdon, 2014) and thus a positive relationship with taxonomic diversity.

Summary of knowledge gaps and predictions from theory

Expectations for biodiversity change over succession based on these ideas and theoretical frameworks are tested in the following chapters of this thesis and used to contextualise the results of this research within ecological succession theory (Figure 2.1). These expectations highlight knowledge gaps and uncertainties in our theoretical understanding of succession (light colours and question marks in Figure 2.1).

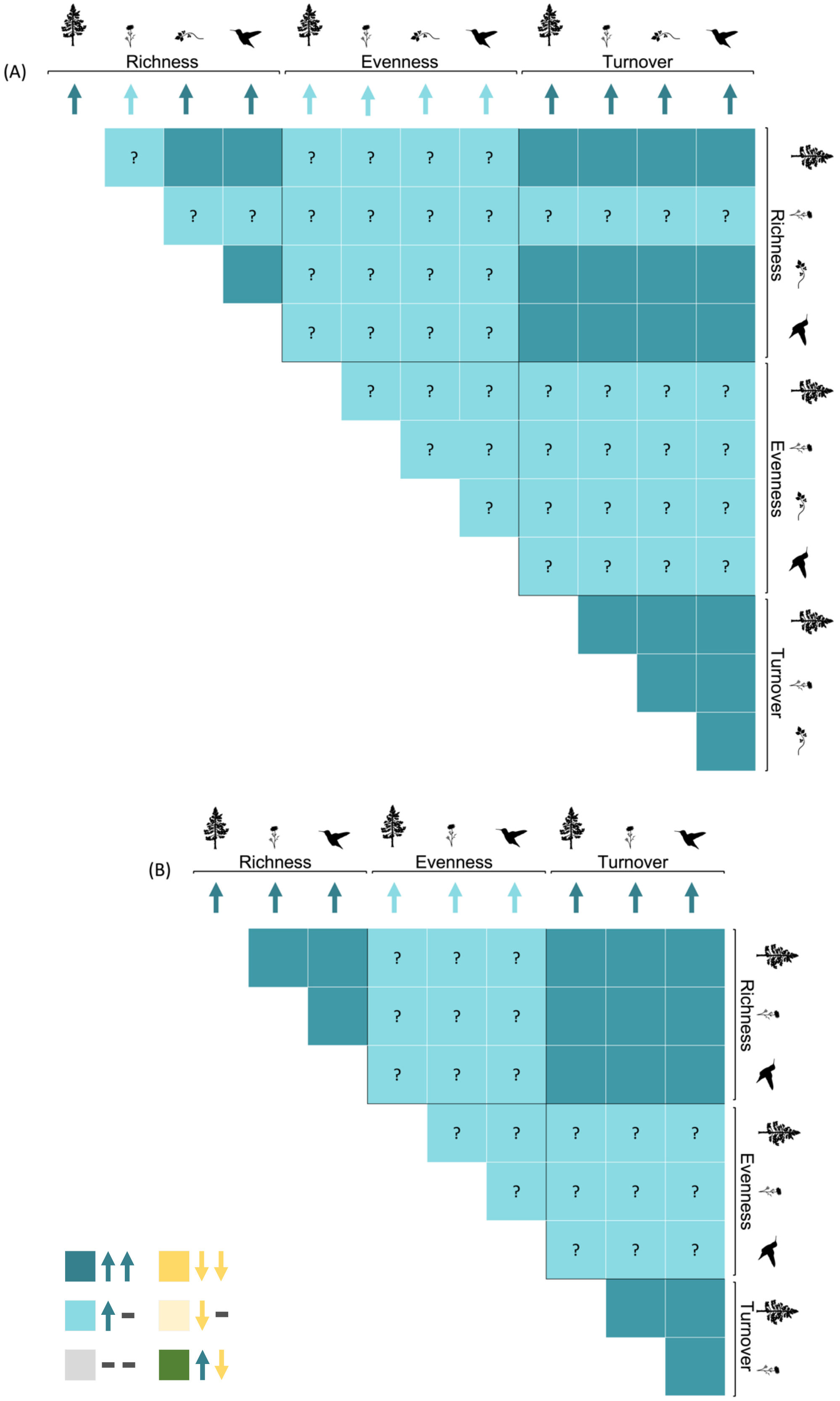


Figure 2.1 Expectations for (A) taxonomic and (B) functional diversity in tree, ground vegetation, epiphyte, and bird assemblages based on theory. Arrows indicate the directionality of the expected change for each aspect of taxonomic and functional diversity (richness, evenness and turnover) in each taxon over succession. The matrix represents the nature of the correlation between the taxa and facets of biodiversity. Blue indicates a positive trends and correlation. Question marks and lighter colours indicate uncertainty from lack of a clear theoretical framework.

The long history of succession research has led to a wealth of ideas and theories regarding how ecological communities change following disturbance, primarily within plant assemblages. There are many ongoing debates surrounding succession theory, especially regarding the primary drivers of succession. While the relative importance of different successional mechanisms remains uncertain and challenging to test, abiotic factors, species traits, biotic interactions, and stochastic events are all thought to play a role in shaping successional trajectories. How species alpha-diversity changes over succession is less clear and remains a key question in ecology.

For plant assemblages, and particularly tree assemblages, taxonomic and functional alpha-diversity are generally expected to increase over time. Most research and theory has focused specifically on species richness, however, and the shape of these relationships varies between theoretical frameworks. For example, many frameworks (eg. Clements (1916), Connell and Slatyer's (1977) facilitation model, Egler's (1953) relay floristics model, and many trait-based models of succession), predict that plant species alpha-diversity should increase rapidly with the first waves of colonisers, and quickly reach an asymptote. Some hypothesise that species and functional alpha-diversity should peak in mid-successional sere when pioneer and climax-type species co-exist (Schoonmaker and McKee, 1988). Other frameworks (eg. the tolerance and inhibition models of succession proposed by Connell and Slatyer (1977) and Egler's (1953) initial floristic composition) suggest that species richness should increase with the initial colonisers, and then decrease gradually as early pioneer species die.

It is also commonly proposed that competition is greater in later successional stages and that there are more species with specialist interactions (Brown and Lugo, 1990b; Lebrija-Trejos, Meave, *et al.*, 2010; Lohbeck *et al.*, 2012), and thus functional alpha-diversity should increase over succession. Environmental filtering may also limit species and functional alpha-diversity early in succession (Lohbeck, Poorter, Martínez-Ramos, *et al.*, 2013; Blanchard *et al.*, 2021), though the relative strength of environmental filtering and competition over succession is debated (Raevel, Violle and Munoz, 2012; Chazdon, 2014; Muscarella *et al.*, 2016; Craven *et al.*, 2018).

Furthermore, most theoretical frameworks agree that there is substantial change in the species which make up ecosystems over time (high species turnover; Chazdon *et al.*, 2010). For example, Clementsian succession and similar frameworks propose that species and functional composition should change gradually over time until reaching a stable climax (Clements, 1916). Further niche and deterministic models of succession predict that there is directional change in the types of species present within a community (high functional turnover). Species and functional competition are expected to change in line with changes in environmental conditions and resource availability over succession (Tilman, 1985). Early successional stages favour species with high dispersal and fast life cycles, while later successional stages favour species that are better competitors (Finegan, 1996; Guariguata and Ostertag, 2001; Sanaphre-Villanueva *et al.*, 2017; Zhang, Qi and Liu, 2018).

While these ideas have principally been applied to plant assemblages, other taxa are expected to change similarly over succession (Hooper *et al.*, 2000; DeWalt, Maliakal and Denslow, 2003; Waldrop *et al.*, 2006; Bowen *et al.*, 2007; Sobek *et al.*, 2009; Haddad *et al.*, 2011). Thus species and functional alpha-diversity are expected to increase, and composition is expected to change through time in other taxa as well.

Lastly, it is also expected that the facets and aspects of biodiversity (Box 1.1) will be positively correlated (Brown and Lugo, 1990b; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Lohbeck, Poorter, Martínez-Ramos, *et al.*, 2013; Chazdon, 2014). For example, the more species there are the more likely there are to be species with unique traits, and greater functional complementarity is thought to facilitate species coexistence (Brown and Lugo, 1990b; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Lohbeck, Poorter, Martínez-Ramos, *et al.*, 2013; Chazdon, 2014).

2.3 Succession: empirical evidence

As with theoretical frameworks, most empirical studies have been conducted on plant, and especially tree, community succession which have yielded varied results. There are some commonalities which can be drawn from this body of research, however. For example, studies often find that tree alpha-diversity, composition, and forest functions recover at different rates (Figure 2.2). In line with expectations from theory, studies support the idea that tree species richness and evenness (α-diversity) increase quickly over time as more species become established (Toky and Ramakrishnan, 1983; Lebrija-Trejos *et al*., 2010). For example, Abbas and colleagues (2019) found that species richness increased primarily within the first 20 years of tropical secondary forest succession in Hong Kong (Abbas et al., 2019).

Though the vegetation species richness may recover quickly (~4-35 years), species composition can remain altered long into succession (>100 years; Finegan, 1996; Chazdon *et al*., 2010; Derroire *et al*., 2016). For instance, Lebrija-Trejos and colleagues (2008) found that canopy height, crown cover and vegetation density recovered in under 15 years in secondary succession in Mexican dry-tropical forest following low-intensity agriculture. Species richness recovered within 40 years. Species composition became increasingly like that of old-growth forests, but had not completely converged over the 40 year chronosequence (Lebrija-Trejos *et al*., 2008). García-Montiel and Scatena (1994) found that humid tropical secondary forest near abandoned charcoal kilns, and forests that had previously been used for agroforestry, remained compositionally different from the surrounding old-growth forests after 100 years of natural succession (García-Montiel and Scatena, 1994). Riswan *et al*. (1985) likewise predict that compositional recovery of abandoned Indonesian pepper plantations should take over 150 years due to a prolonged pioneer-dominated phase, and the time needed for old-growth species to become established (Riswan, Kenworthy and Kartawinata, 1985).

A meta-analysis by Derroire and colleagues (2016) of 13 dry tropical forest chronosequences (<60 years since abandonment of pasture or shifting agriculture) similarly indicated that forest structure recovered rapidly and species diversity increased over secondary succession. The rate of species composition convergence with old-growth forests was much slower, however, and the authors suggest that the species composition may never fully recover (Derroire *et al*., 2016). In another meta-analysis of 600 secondary tropical forest studies by Martin, Newton, and Bullock (2013), tree species richness recovered within ~50 years while above and below-ground tree biomass recovered after ~85 years. Species composition remained altered, however, and many old-growth species were absent in the secondary forests (Martin, Newton, and Bullock, 2013).

While research on functional diversity change over succession is comparatively limited, some sources indicate that functional diversity follows a similar pattern to taxonomic diversity. For example, Craven and colleagues (2018) found that woody vegetation functional richness and functional dispersion both increase rapidly within the first 10 years of succession (Craven *et al.*, 2018). Whitfeld et al. (2014) also found that tree species and functional richness increased over 35 years of succession alongside changes in tree species composition following subsistence agriculture and other forms of land disturbance in New Guinea (Whitfeld *et al.*, 2014).

Other research on functional diversity change over succession has yielded varying results (eg. Lohbeck *et al.*, 2012; Sanaphre-Villanueva *et al.*, 2016). Muscarella et al. (2016), for example, found that tree height maximum height and sapling seed mass diversity decreased over 91 years of tropical secondary forest succession in Puerto Rico (Muscarella *et al.*, 2016). Bönke and colleagues (2014) found that there was little change in overall woody plant functional diversity (FD) over succession despite increases in Shannon diversity and Shannon evenness in subtropical forests in China. The lack of pattern was driven by contrasting trends in trait dissimilarity which decreased, and functional evenness which increased, over succession (Böhnke *et al.*, 2014)

Links between taxa

There are few studies which compare patterns of biodiversity change over succession across multiple taxa which makes comparisons between data and theory difficult. However, contrary to expectations from theory, studies have found that patterns of successional change are not consistent across taxa or with expectations from plant assemblage dynamics (J. Barlow *et al.*, 2007; Winter *et al.*, 2015; Tinya *et al.*, 2021). Barlow et al. (2007), for instance, found disparate patterns of biodiversity change between trees, mammals, insects, lizards, amphibians, and birds in response to disturbance in the Brazilian Amazon (J. Barlow *et al.*, 2007). Tinya and colleagues (2021) likewise found that patterns of biodiversity change varied across multiple plant and insect taxa in response to land management in Hungarian forests (Tinya *et al.*, 2021).

Conversely, some studies found similar results across taxa, and to findings from tree communities. In two meta-analyses by Dunn (2004a,b), for example, ant, lepidopteran, and bird species richness increased asymptotically with forest age over 30 years of succession, while species composition took far longer to recover post agriculture and pasture land abandonment (Dunn, 2004a,b).

There is evidence for links between tree and epiphyte dynamics. Though research on epiphytes is limited, studies have found that epiphyte diversity increases with tree diversity (Jüriado, Paal and Liira, 2003; Kapusta, Szarek-Łukaszewska and Kiszka, 2004) and with forest age (Neitlich and McCune, 1997; Brunialti *et al.*, 2010). Research has also highlighted that epiphytes are strongly influenced by humidity and shading (Kantvilas and Minchin, 1989; Kuusinen, 1994; Gustafsson and Eriksson, 1995; Campbell and Fredeen, 2004; Belinchón *et al.*, 2007; Fritz, Brunet and Caldiz, 2009; Moning *et al.*, 2009; Leppik, Jüriado and Liira, 2011). Cryptogenic epiphytes (lichens, mosses, liverworts, and algae) in particular, have varied tolerances and responses to bark chemistry, texture, and stability, and so are thought to be strongly influenced by tree composition and diversity (Ihlen, Gjerde and Sætersdal, 2001; Cleavitt, Dibble and Werier, 2009; Ellis, 2012).

Similarly, there is evidence that ground vegetation and tree species diversity are positively correlated and that ground vegetation alpha-diversity increases over succession (Nadrowski, Wirth and Scherer-Lorenzen, 2010; Vockenhuber *et al.*, 2011; Chamagne *et al.*, 2016). There have been relatively few studies specifically on the ground plant community, however, and some have found that ground vegetation alpha-diversity decreases due to more limited light levels in older forests (Kirby, 1988; Jennings, Brown and Sheil, 1999; Dölle and Schmidt, 2009; Hofmeister *et al.*, 2009).

In bird assemblages, some studies have found that taxonomic and functional alpha-diversity are greater in older forests (eg. Barlow et al., 2007; Barnagaud et al., 2017; Hobson and Bayne, 2000; Owen et al., 2020; Sayer et al., 2017; Sberze et al., 2010), and others that alpha-diversity remains constant with forest age (eg. Borges, 2007; Borges et al., 2021; Jarrett et al., 2021; Lee et al., 2020; Rocha et al., 2019; Sayer et al., 2017; Waltert et al., 2005). A study by Schwab and Sinclair (1994) in British Columbia found that breeding bird species richness increased non-linearly over succession with richness peaking at an early ‘shrub’ stage and the final climax stage of succession (Schwab and Sinclair, 1994). Scheick, Nietfeid, and Stelfox (1995) likewise found a non-linear relationship where old secondary forests had the greatest bird species richness, primary forests had the lowest species richness, and young secondary forests were in between (Schieck, Nietfeid, and Stelfox, 1995). Blake and Loiselle (2001) found that 4-year-old sites had greater bird species richness than old-growth forests in Costa Rica (Blake and Loiselle, 2001). Sayer, Bullock, and Martin (2017) found that bird species richness was greater in primary forests, functional evenness was greater in secondary forests, and functional dispersion and divergence remained relatively consistent with forest age (Sayer, Bullock and Martin, 2017). Most studies agree, however, that bird species and functional composition changes the most over succession and that there are more endemic, forest specialist, and insectivorous birds in older forests (Jarrett et al., 2021; Oksuz et al., 2021; Sayer et al., 2017; Waltert et al., 2005; Opposed to: Clavero et al., 2011).

The variability in the strength of correlations between taxa could be due to differences in their mobility. For example, flying vertebrates typically recover faster than non-flying vertebrates following disturbance (Barlow et al., 2007; Chazdon, 2014; Dunn, 2004b). A meta-analysis by Karthik and colleagues (2009) found that 70% of old-growth bird species recovered within 25 years of shifting cultivation abandonment (Karthik, Veeraswami and Samal, 2009). Furthermore, while changes in animal assemblages over succession are often predicted and interpreted through the lens of habitat-wildlife relationships, there are many other factors which can drive animal community dynamics (Le Borgne, Dupuch and Fortin, 2018). For example, predation risks as well as exploitative (consumption of limited shared resources), interference (restricting other organisms access to resources), and apparent competition (competing for survival from a shared predator) all shape the abundance and distribution of animal taxa (Le Borgne, Dupuch, and Fortin, 2018). Given the degree of complexity in animal population dynamics, it is unsurprising that research on successional change across taxa has yielded such mixed results.

Summary of knowledge gaps and predictions from research

As noted above, expectations for biodiversity change over succession based on this research are tested in the following chapters of this thesis (Figure 2.2). Research into biodiversity change is patchy across taxa and facets of biodiversity and results are often contradictory, leaving many knowledge gaps and uncertainties (light colours and question marks in Figure 2.2).

As with succession theory, most empirical research has focused on changes in tree or overall plant assemblages through succession. Most studies have found that species richness increases over time, especially in the early stages of succession, while species composition changes throughout succession (Riswan, Kenworthy and Kartawinata, 1985; García-Montiel and Scatena, 1994; Finegan, 1996; Lebrija-Trejos *et al.*, 2008; Chazdon *et al.*, 2010; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Martin, Newton and Bullock, 2013; Derroire *et al.*, 2016; Abbas *et al.*, 2019). Most studies measure species richness or indices such as Shannon diversity which include information on both richness and evenness, however, and thus it is more difficult to discern how tree species evenness will change based on research. Furthermore, research on functional alpha-diversity change in tree assemblages is comparatively limited and has produced varied results, though sources generally agree that there is change in functional composition over succession (Lohbeck *et al.*, 2012; Böhnke *et al.*, 2014; Muscarella *et al.*, 2016; Sanaphre-Villanueva *et al.*, 2016; Craven *et al.*, 2018).

Similarly, there is relatively little research on ground vegetation dynamics with studies on taxonomic alpha-diversity change yielding largely incongruous results (Kirby, 1988; Jennings, Brown and Sheil, 1999; Dölle and Schmidt, 2009; Hofmeister *et al.*, 2009; Nadrowski, Wirth and Scherer-Lorenzen, 2010; Vockenhuber *et al.*, 2011; Chamagne *et al.*, 2016). Most sources report that species and functional composition change over time, however, where understory vegetation progresses throughout succession and shade-tolerant undergrowth typically develops over time (Finegan, 1996).

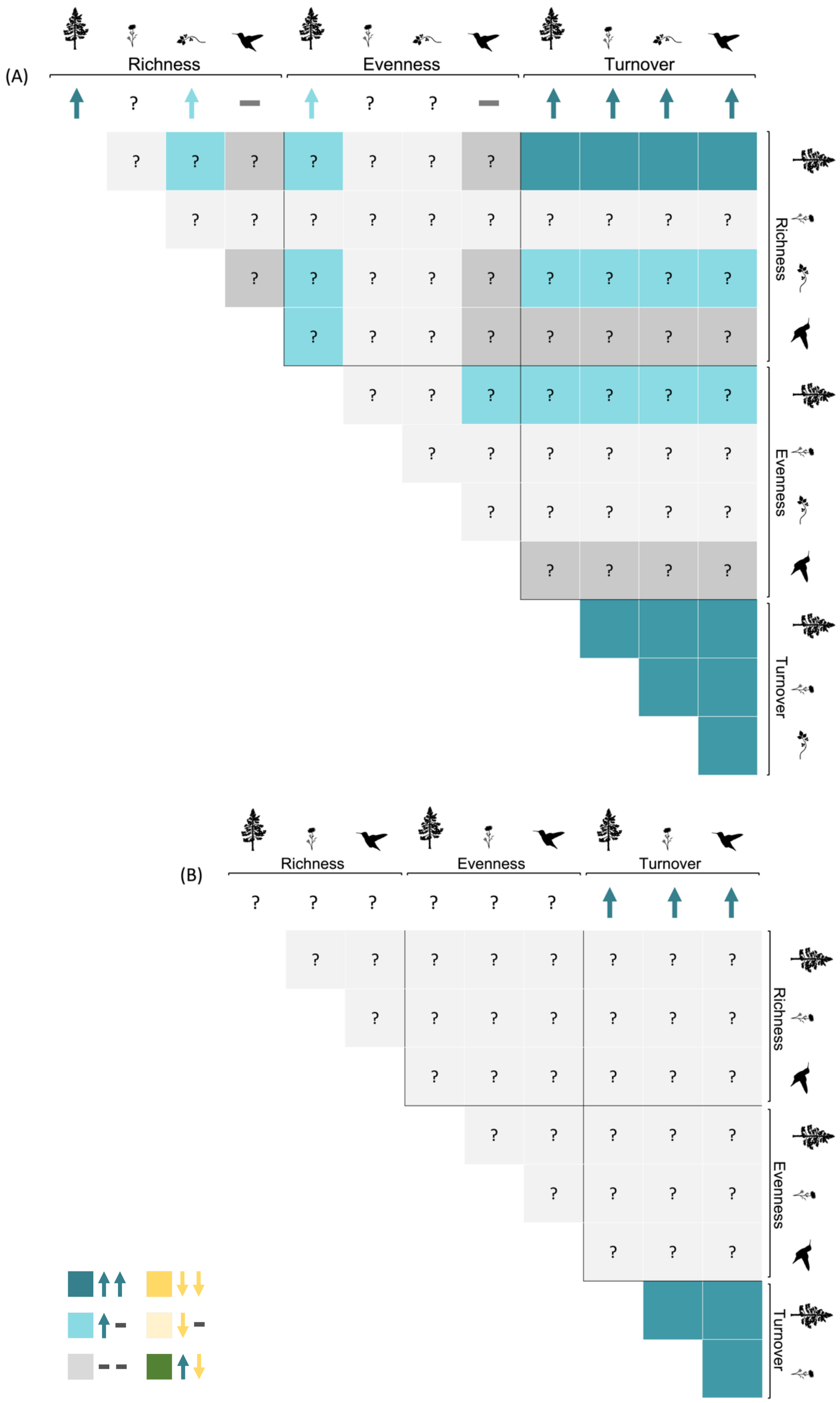


Figure 2.2 Expectations for (A) taxonomic and (B) functional diversity based on published empirical research. Arrows indicate the directionality of the expected change for each aspect of taxonomic and functional diversity (richness, evenness, and turnover) in each taxon over succession. The matrix represents the nature of the correlation between the taxa and facets of biodiversity. Blue indicates a positive trends and correlation. Question marks, grey and lighter colours indicate uncertainty from there being too few studies or studies with inconsistent results.

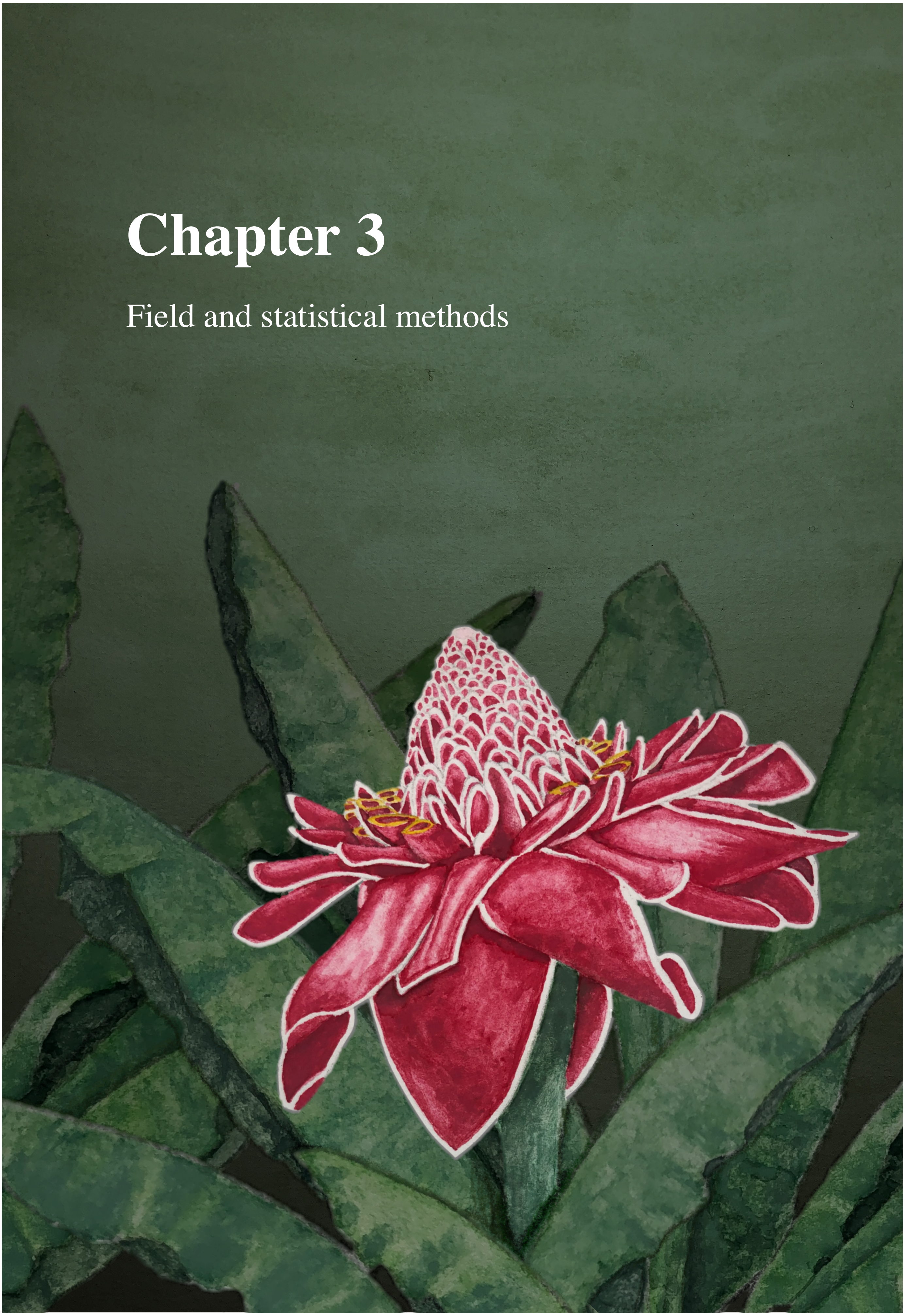
Patterns of biodiversity and composition in other taxa are also unclear and largely uncorrelated. There is evidence that epiphytes are highly dependent on tree community dynamics, and may change similarly as a result (Jüriado, Paal and Liira, 2003; Kapusta, Szarek-Łukaszewska and Kiszka, 2004; Ellis, 2012). Likewise, some studies found that lichen species richness increases over succession (Neitlich and McCune, 1997; Brunialti *et al.*, 2010). Also, being sensitive to bark and environmental conditions (Ihlen, Gjerde and Sætersdal, 2001; Cleavitt, Dibble and Werier, 2009; Ellis, 2012), change in epiphyte taxonomic and functional composition over time is expected alongside change in tree composition. Though, again, most studies focus on species richness and compositional turnover.

In contrast, many studies on birds have found that there is relatively little change in taxonomic alpha-diversity over succession (Waltert *et al.*, 2005; Borges, 2007; Sayer, Bullock and Martin, 2017; Rocha *et al.*, 2019; Lee *et al.*, 2020; Borges *et al.*, 2021; Jarrett *et al.*, 2021), though research has yielded widely varying results overall as well. This could be because birds are highly mobile species and thus may be more dependent on landscape-level features (Robert R Dunn, 2004; J. Barlow *et al.*, 2007; Chazdon, 2014). Most studies agree, however, that bird species and functional composition change most over succession, where there are commonly more rare, endemic, and sensitive species in older forests (Jarrett et al., 2021; Oksuz et al., 2021; Sayer et al., 2017; Waltert et al., 2005)

Overall, simple ecosystem functions tend to be regained early in succession, followed by species alpha-diversity. Species composition, functional trait composition, and complex functions take much longer (Chazdon, 2008). Canopy cover, canopy height, and most aboveground biomass can be regained within 30 years of succession (Finegan, 1996; Kennard, 2002; Chazdon, 2003; Lebrija-Trejos *et al.*, 2008). Tree density generally decreases over succession while stem diameter and basal area cover increase (Guariguata and Ostertag, 2001; Martin, Newton and Bullock, 2013). Complex functions, such as soil properties and fertility, and the types of species which make up forest ecosystems, can take centuries to recover (Álvarez-Yépiz *et al.*, 2008; Derroire *et al.*, 2016). Early functional recovery is supported when multiple species have overlapping functional roles (functional redundancy), thus allowing ecosystem processes to return even if not all the same species are present (Guariguata and Ostertag, 2001; Liu *et al.*, 2017).

Chapter 3

Field and statistical methods



3.1 Introduction

As outlined in Chapter 1, there are ongoing rapid changes in forest cover globally where the proportion of secondary and planted forests is rising relative to primary forests (Ehrlich and Pringle, 2008; Hansen *et al*., 2013; Vaast and Somarriba, 2014; Semper-Pascual *et al*., 2019; FAO and UNEP, 2020; Global Forest Watch, 2020). This is driven in large part by land conversion for agriculture, timber plantations, and other purposes. Tropical regions, which are especially biodiverse, are currently experiencing the highest levels of deforestation and land conversion (Lambin *et al*., 2001; Geist and Lambin, 2002; Gibson *et al*., 2011; Mora *et al*., 2015).

Cacao is a major crop in tropical regions and the cacao industry is growing rapidly (Vaast and Somarriba, 2014; Borda *et al*., 2021). The conversion of land to farm cacao, however, is considered a major contributor to tropical deforestation (Vaast and Somarriba, 2014; Borda *et al*., 2021). Understanding the effects of agricultural expansion on biodiversity and how forests recover over time through succession requires urgent attention, especially in swiftly changing tropical landscapes. Further research regarding the contributions of secondary and agricultural forests make to biodiversity conservation and identifying conservation solutions that can support both people and nature are also essential.

To address these questions (further detailed in Chapter 1.5), fieldwork was conducted in Trinidad and Tobago to assess biodiversity change over secondary forest succession following cacao agroforest abandonment. As described in Chapter 1, Trinidad represents a case study of a landscape shaped by the cacao industry. The legacy of Trinidad's long cacao farming history remains evident in the patchwork forested matrix which covers the Northern Range. Though cacao production decreased in the mid-late 20th century, cacao production has been increasing again and there are many cacao farmers in Trinidad and Tobago today (approximately 3,500 farmers in 2014; Bekele, 2004; NATT, 2018). The following chapter outlines the field and analysis methods used for the research based in Trinidad detailed in Chapters 4-6; these approaches were piloted in small field study in Fife (Scotland; Box 3.1).

Box 3.1 Field methods for pilot research in Scotland

A pilot study was conducted to test the field and analysis methods in eight forest patches in Fife, Scotland. These sites include mixed timber plantations ranging from 20 to 62 years old, and two patches of woodland which were c. 90 years old. The ages of the sites were determined using the Ordnance Survey Historic Map Archive and documentation from landowners (Dr Edward Baxter and Patrick Bowden-Smith). All the forest patches were between 1-5ha with over 50% canopy cover and trees over five metres tall. The sites were predominantly surrounded by agricultural fields and pastureland. The surveys were conducted between July and September 2018 with the help of Anna Kellner.

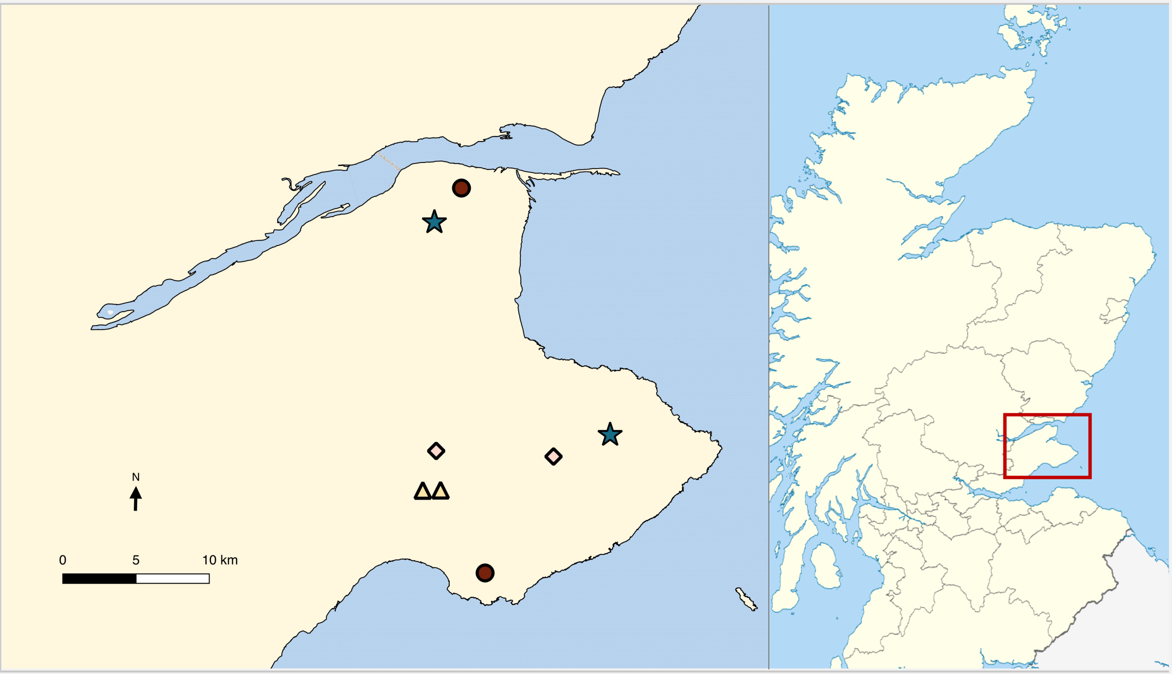


Figure 3.1 Map of surveyed forest sites in Fife, Scotland. There were two under 30 year old sites (red circles), two sites between 40-50 years old (pink diamonds), two sites which were 62 years old (yellow triangles) and two >90 year old forest sites (dark blue stars).

Trees

Trees were surveyed using five 50m transect lines for each site. The transects were randomly placed and oriented within each site using a random number table. The path of

Continued

Box 3.1 Field methods for pilot research in Scotland (continued)

the transect was diverted by 90 degrees if an impassable barrier was encountered. All trees (woody vegetation >6cm in diameter at breast height (DBH) and >3m in height) within five metres on either side of the transect line were measured and identified to species level. For this, the circumference of each tree trunk was measured using a tape measure at approximately 1.3m from the ground. For multi-stemmed trees, the DBH of all major stems (>6cm DBH) were measured, and the overall DBH for each multi-stemmed tree was quantified using the equation:

$$overall\ DBH = \sqrt{\sum DBH_n{}^2}$$

where DBH_n is the diameter for stem *n* of a multi-stemmed tree. Lastly, the height of each tree was estimated. Species were identified with the aid of field guides (Corbet, 1998; Russell, Cutler and Walters, 2014; Sterry, 2015; Press, 2016), and samples and detailed pictures were taken of the trees where necessary to identify species. Data collected in the field was supplemented with existing functional and life history trait data (Chapter 3.3).

Ground vegetation

Ground vegetation in this study is defined as all plants growing on the ground excluding the tree and shrub layers (woody vegetation >0.5m in height). The ground vegetation was surveyed using a standard 10-pin point quadrat with the pins approximately 0.5cm in diameter and spaced 5cm apart. Twenty point quadrat surveys were conducted in each site. Every plant species (including grasses, herbs, tree and shrub seedlings, bryophytes, and forbs) that touched a pin was recorded as one individual of a given species, so that each species was recorded only once per pin. A point quadrat was used because they are less subjective than frame quadrats and provide abundance data rather than percent cover. As with the trees, species were identified using field guides (Stary and Jirásek, 1975;

Continued

Box 3.1 Field methods for pilot research in Scotland (continued)

Phillips and Grant, 1980; Smith, 1980; Fitter, Fitter and Ferrer, 1984; Sutton, 1988; Corbet, 1998; Crawford, 2002; Porley, 2008; Sterry, 2008; Wildlife Trusts, 2010; Godfrey, 2014), and samples and pictures were taken where necessary to confirm species identifications.

Epiphytes

Epiphytes (plants and lichens growing on trees including lianas, vines, orchids, ferns, lichens, and bryophytes) were surveyed using the same standard 10-pin point quadrat on each tree surveyed. The quadrat was placed vertically on the tree trunk at approximately 1.3m from the ground. The direction the quadrat faced on a tree trunk was randomly assigned using a random number table (a random number generated between 1-8 to indicate the eight major compass directions). All epiphytes were identified using field guides (Phillips and Grant, 1980; Smith, 1980; Corbet, 1998; Crawford, 2002; Dobson, 2005b, 2005a, 2013, 2017; Walewski, 2007; Porley, 2008; Wolseley *et al.*, 2013; Godfrey, 2014), and samples and pictures were taken where necessary.

Birds

Bird surveys were done using a point distance survey method (Gregory, Gibbons and Donald, 2004; Buckland, Marsden and Green, 2008; Thomas *et al.*, 2013). Five survey points were randomly placed within each site at least 50m apart. Bird surveys were conducted near dawn (5:30-7:30am) when birds are more active. All birds seen or heard within the 15-minute survey period were identified to species level and their estimated distance from the surveyor recorded. The minute (1-15) in which an individual was detected was recorded to generate species accumulation curves. Whether the bird was seen or heard, their behaviour (perched or flying), the number of individuals if grouped, and the confidence in the species identification was also noted. Individual birds were counted only once. Binoculars were used, and sound recordings were taken using a Tascam DR-05X handheld recorder during each survey to verify any uncertain species identifications.

Continued

Box 3.1 Field methods for pilot research in Scotland (continued)

ID guides and pre-existing recordings of known bird species further aided species identifications (Corbet, 1998; Hume, 2014; Harrap, 2015). Any other animals, including humans, detected during the survey period and their distance to the survey point were recorded as possible confounding factors. Surveys were not conducted in extreme weather (wind, fog, or rain) which substantially reduced visibility or changed the bird's behaviour.

Environmental data

Environmental and topographic data were collected in each site: altitude was measured using a calibrated GPS, canopy cover was measured using a spherical densiometer, and the land gradient was measured using an inclinometer. Information on weather conditions was also recorded at the start of each 50m transect. The dominant matrix habitat was recorded as well. Additional data compiled from other sources were used to supplement environmental data recorded in the field. qGIS was used to measure the geographical distance between site pairs (QGIS Development Team, 2021).

3.2 Analysis methods: Taxonomic diversity

Taxonomic and functional alpha and beta-diversity (Figure 1.2) were measured in the tree, bird, epiphyte, and ground vegetation communities in order to obtain a more complete understanding of how biodiversity changes over forest succession across taxa. While most studies have focused on taxonomic diversity, functional diversity is now often measured as well. Measuring functional diversity alongside taxonomic diversity provides a more comprehensive view of biodiversity and ecosystem functioning (Box 1.1; Díaz and Cabido, 2001; Weiher, 2011; Cadotte, 2017). Taxonomic diversity is measured by identifying and recording the species which make up an assemblage, while functional diversity is measured by quantifying species' functional traits (traits which relate to a certain ecosystem function, such as leaf nitrogen content and soil nutrient cycling; Figure 1.2).

The following analysis methods were applied to the Trinidad data to assess changes in taxonomic and functional alpha and beta-diversity with forest age in subsequent chapters. The pilot study conducted in Fife (Scotland) was used as an example of the analysis methods described below (pilot study details in Box 3.1).

Taxonomic alpha-diversity

Here, Hill numbers of the order q: species richness (q=0), Shannon diversity (q=1), and Simpson diversity (q=2; Hill, 1973) are used to quantify taxonomic diversity. The three orders present a coherent statistical framework. Species richness is simply the number of species present in an assemblage. Shannon diversity incorporates information on both species richness and evenness (how evenly the relative abundances of species within an assemblage are; Maurer & McGill, 2011). Lastly, Simpson diversity is a measure of species evenness (Maurer & McGill, 2011).

Table 3.1 Equations and descriptions of taxonomic alpha-diversity indices. *S* is the number of species in an assemblage and P_i is the relative abundance of species *i*.

Index	Formula	Description
Species richness	S	The number of species in an assemblage (Maurer & McGill, 2011).
Shannon diversity	$\Sigma p_i \ln p_i$	A measure encompassing both the number and the relative abundances of species (Maurer & McGill, 2011).
Simpson diversity	$\frac{1}{\Sigma p_i^2}$	The evenness of species relative abundances in an assemblage (Maurer & McGill, 2011).

Extrapolated rarefaction curves generated using the iNEXT package (Chao *et al.*, 2014; Hsieh, Ma and Chao, 2020) are then used to obtain species richness, Shannon, and Simpson diversity estimates for a consistent sample size for each taxon and each site (Appendix 3.1 extrapolated rarefaction curves for each site, taxon, and order). Extrapolated rarefaction allows for fair comparisons between sites, which is especially important when using metrics such as species richness and Shannon diversity that are strongly influenced by sampling effort (Chao *et al.*, 2004; Magurran, 2004). All the diversity values in the Fife pilot study are estimated for a sample size of 100 individual trees, 100 individual ground plants, 100 individual epiphytes, and 50 individual birds. These sample sizes were chosen because the rarefaction curves for each site and taxon neared an asymptote, and the confidence intervals were small.

Pilot study: Taxonomic alpha-diversity example results

To illustrate the use of these indices, OLS linear regressions were used to assess whether there was significant change in species alpha-diversity over succession for each taxon using the Fife pilot study data. The alpha-diversity indices for the pilot study were calculated using the iNEXT rarefaction/extrapolation approach for a sample size of 100 individual trees, 100 individual ground plants, 100 individual epiphytes, and 50 individual birds across all sites.

There was no significant change in tree species richness with forest age ($F_{(1,6)}$= 1.092, adj R^2= 0.15, p=0.34), though there was a significant increase in Shannon ($F_{(1,6)}$= 17.95, adj R^2= 0.75, p=0.005) and Simpson diversity over succession ($F_{(1,6)}$= 24.01, adj R^2= 0.80, p=0.0027). There was no significant change in ground vegetation species richness ($F_{(1,6)}$= 1.03, adj R^2= 0.15, p=0.35), Shannon ($F_{(1,6)}$= 1.001, adj R^2= 0.002, p=0.97) or Simpson diversity with forest age ($F_{(1,6)}$= 0.52, adj R^2= 0.08, p=0.50). Conversely, epiphyte species richness ($F_{(1,6)}$= 23.86, adj R^2= 0.80, p=0.003), Shannon ($F_{(1,6)}$= 13.56, adj R^2= 0.69, p=0.01), and Simpson diversity ($F_{(1,6)}$= 6.00, adj R^2= 0.50, p=0.05) all significantly increased over succession. Lastly, there was no significant change in bird species richness ($F_{(1,6)}$= 0.09, adj R^2= -0.15, p=0.78), Shannon ($F_{(1,6)}$= 0.15, adj R^2= -0.13, p=0.71), or Simpson diversity with forest age ($F_{(1,6)}$= 0.19, adj R^2= -0.13, p=0.68).

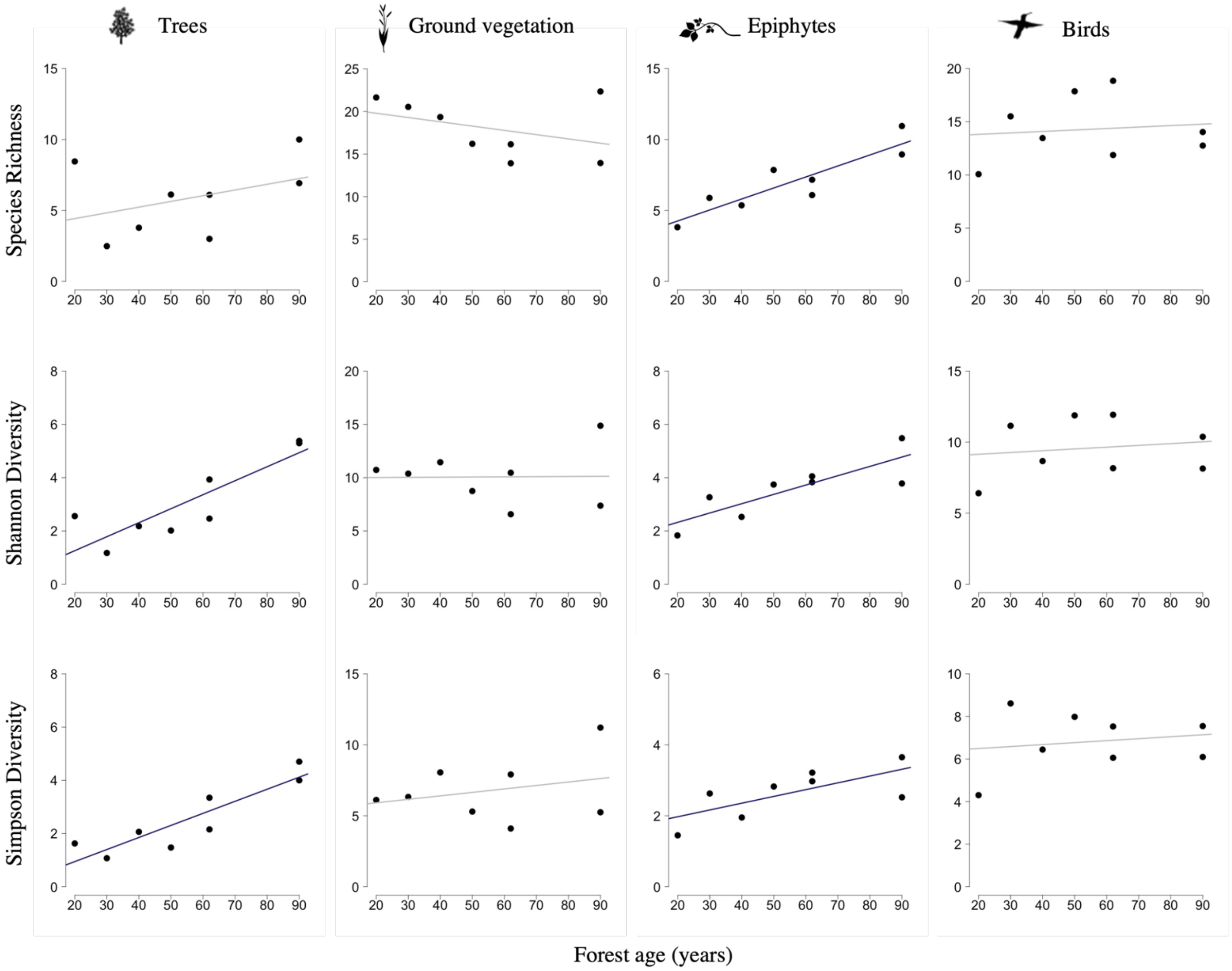


Figure 3.2 Linear regressions of species richness, Shannon, and Simpson diversity with forest age for each taxon (trees, ground vegetation, epiphytes, and birds) from Fife pilot study. Blue lines indicate a significant change in the alpha-diversity indices with forest age.

Taxonomic beta-diversity

Pairwise compositional dissimilarity between sites was quantified using the Chao-corrected Jaccard index (Chao-Jaccard; *dis.chao* function, CommEcol package; Melo, 2019). Jaccard dissimilarity ranges between 0 and 1, where values closer to 1 indicate greater compositional dissimilarity between site pairs. This index corrects for unseen species and under-sampling by weighting for the rare species shared between site pairs (Table 3.2; Chao *et al*., 2004).

Table 3.2 Equation and description of the taxonomic beta-diversity index Chao-corrected Jaccard. n represents the individuals in assemblage X, and m represents the individuals in assemblage Y. X_i is the frequency of species i in assemblage X. Y_i is the frequency of species i in assemblage Y. f_{1+} and f_{2+} are the number of shared species with only one individual, and with only two individuals in assemblage X respectively (they may have any frequency >0 in assemblage Y; add 1 if there are none). f_{+1} and f_{+2} are the number of shared species with only one individual, and with only two individuals in assemblage Y respectively (they may have any frequency >0 in assemblage X; add 1 if there are none). Lastly, D_{12} is the frequencies of the species observed in both assemblages X and Y (shared species).

Index	Formula	Description
Chao-Jaccard	$\hat{U} = \sum_{i=1}^{D_{12}} \frac{X_i}{n} + \frac{(m-1)}{m} \frac{f_{+1}}{2f_{+2}} \sum_{i=1}^{D_{12}} \frac{X_i}{n} \, I\,(Y_i = 1)$ $\hat{V} = \sum_{i=1}^{D_{12}} \frac{X_i}{m} + \frac{(n-1)}{n} \frac{f_{1+}}{2f_{2+}} \sum_{i=1}^{D_{12}} \frac{X_i}{m} \, I\,(Y_i = 1)$ $\frac{\hat{V}\hat{U}}{\hat{U} + \hat{V} - \hat{U}\hat{V}}$	An abundance-based Jaccard index corrected for unseen shared species (by using the frequencies of observed rare shared species; Chao *et al.*, 2004, 2006). This equation provides Jaccard similarity, but dissimilarity can be calculated by subtracting the obtained value from one (as is done in the dis.chao function of the CommEcol package).

Pilot study: Taxonomic beta-diversity example results

Again using the pilot study as an example, quantile regressions were employed to test whether sites which were farther apart in age were also more compositionally dissimilar (50th quantile; Figure 3.4; Koenker, 2013). Quantile regressions are more robust to outliers and unequal variance (heteroscedasticity) compared to standard linear regressions (Cade and Noon, 2003; John, 2015).

There was no significant change in tree compositional change with increasing age difference between sites ($T_{(1,26)}$= 0.01, p=0.98). Thus, the tree composition was similar between sites close in age and those distant in age. There was likewise no significant change in vegetation ($T_{(1,26)}$= 0.66, p=0.51), epiphyte ($T_{(1,26)}$= 0.34, p=0.74), or bird compositional dissimilarity with age difference between sites ($T_{(1,26)}$= 0.07, p=0.94).

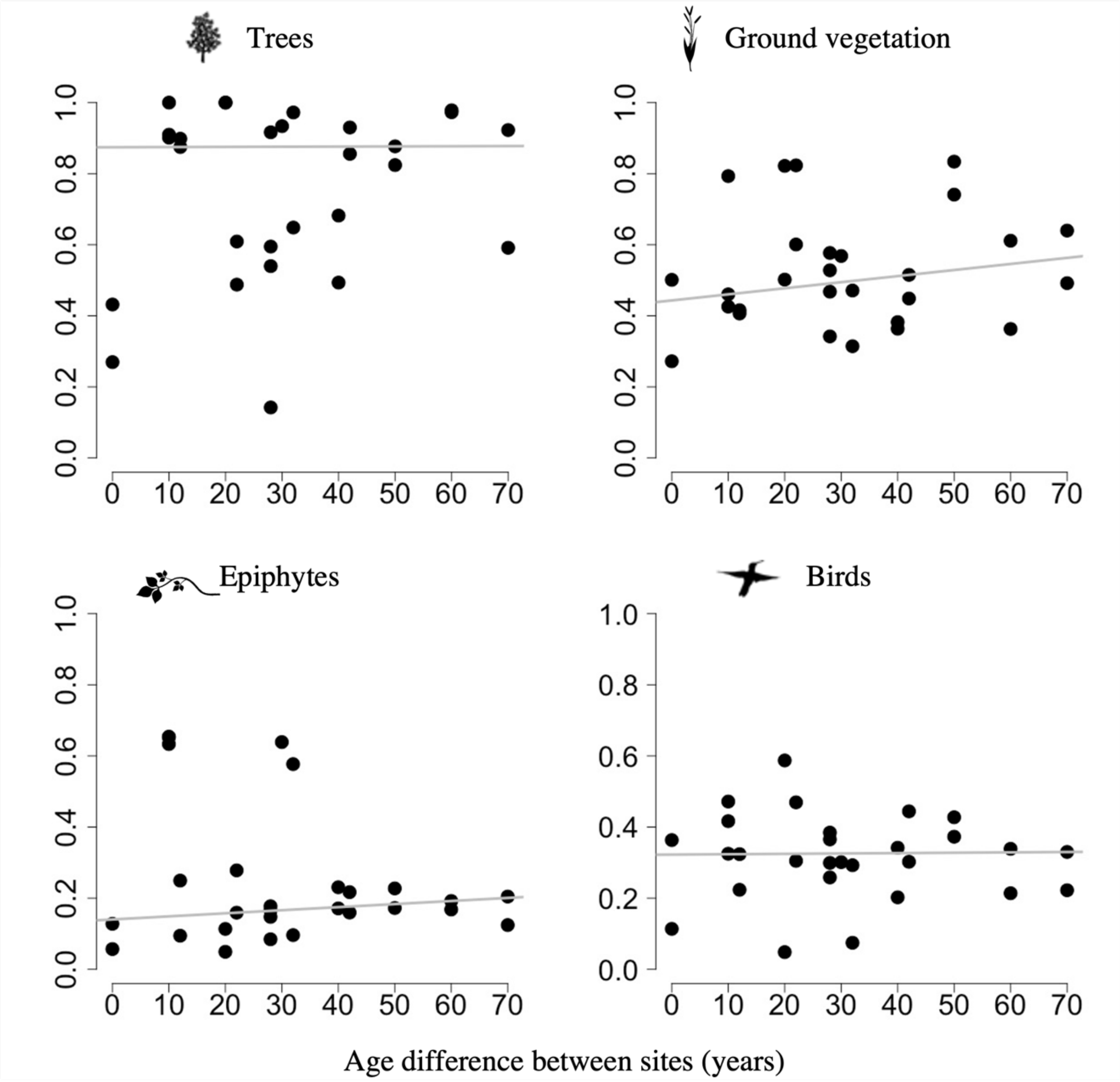


Figure 3.3 50th quantile regressions of tree, ground vegetation, epiphyte and bird species compositional change (Chao-Jaccard) with age difference between sites for Fife pilot study data. Grey lines indicate no significant change in species composition with age difference between sites.

3.3 Analysis methods: Functional diversity

Functional diversity was measured using comparable metrics to those used for taxonomic diversity. Functional diversity analyses are strongly influenced by trait choice. Traits were chosen based on those which were considered most relevant to habitat provision and life history, those which had high-quality data for most species, and those which were most comparable across the taxa. Numeric traits were used where possible, and categorical traits were transformed onto a numeric scale (Appendix 5.1) to avoid generating negative eigenvalues in PCoA, which diminishes the quality of the functional space used in functional diversity analyses (Laliberté, Legendre and Shipley, 2014).

Data on tree and bird assemblages from the Fife pilot study were used to illustrate these analysis methods. The traits used for the bird functional diversity analyses were: primary trophic guild, body length (cm), longevity (years), average number of eggs per clutch, maximum wingspan (cm), and sexual dimorphism (functional trait information from: Hume, 2014; BirdLife International, 2020). The traits used in tree functional diversity analyses were: maximum height at maturity (m), average leaf length (cm), flower colour, propagule length (cm), and primary dispersal mode. Functional trait information was compiled from guide books and other sources (McGinley *et al.*, 1990; Sullivan, 1994; Herman, Stange and Quam, 1996; Weeda, 2003; Wall, Borchert and Gworek, 2006; Batkhuu and Udval, 2013; Gilman and Watson, 2015; Sterry, 2015; De Jaegere, Hein and Claessens, 2016; San-Miguel-Ayanz *et al.*, 2016; Baxter, 2018; Kubínová *et al.*, 2018).

Functional alpha-diversity

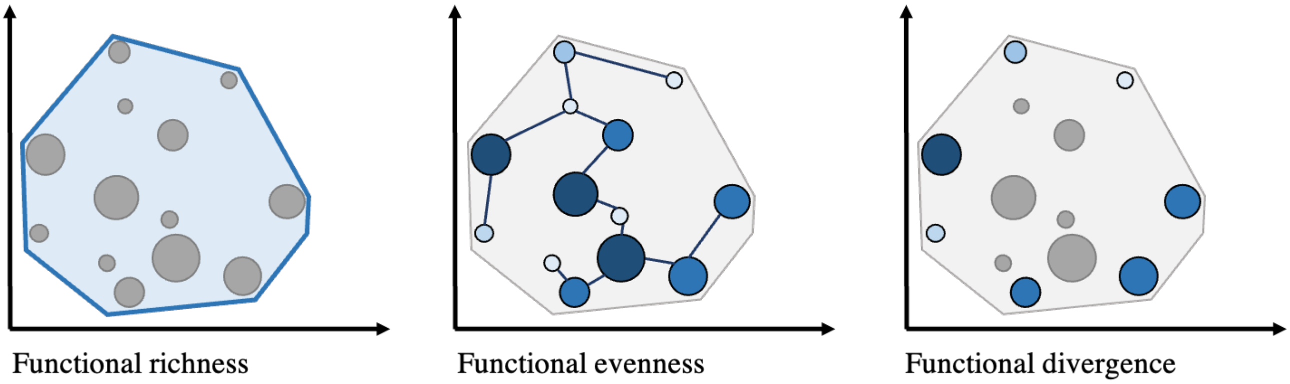


Figure 3.4 Hypothetical schematic to explain the different functional alpha-diversity measures used in this thesis. Functional richness quantifies how much of the functional trait space is taken up by the species in an assemblage. Functional evenness quantifies how even the distances between species in trait space are (using a minimum spanning tree), as well as how even the relative abundances of species in an assemblage are. Functional divergence quantifies how many species have extreme trait values, and how populated those species are, relative to the species towards the centre of trait space.

Three measures of functional α-diversity were quantified for each taxon: functional richness, functional evenness, and functional divergence (as outlined in: Cornwell, Schwilk & Ackerly, 2006; Villéger, Mason & Mouillot, 2008; Mouchet et al., 2010; Weiher, 2011; Figure 3.4). Functional richness (FRic or CHV) is a measure of how much multidimensional functional trait space is occupied by the species in an assemblage. In other words, it is the volume of the convex hull surrounding the species in trait space for each assemblage. Functional evenness is a measure of how evenly spread-out species are in functional trait space, and how evenly abundant species are. This metric uses a minimum spanning tree, where the evenness of the distances between species in trait space is measured. Lastly, functional divergence indicates the relative proportion of species on the edge of functional trait space relative to the centre of the convex hull. For this measure, the more species that have extreme trait values, the higher the functional divergence will be. There have been many functional diversity metrics proposed, and little consensus over which are best (Petchey and Gaston, 2006). This framework was chosen, however, as it is commonly used, intuitive, and the three metrics are independent and provide information on different aspects of functional diversity change.

Table 3.3. Equations and descriptions of functional alpha-diversity indices. EW_l is the weighted evenness for branch *l* between two species on the MST. *dist*(i,j) is the Euclidean distance between species *i* and *j* (the two species at either end of a given branch on the MST). PEW_l is the partial weighted evenness of the assemblage. *V* is the species on the vertices (extreme ends) of the convex hull. G_k is the coordinates of the centre of gravity for the *V* species. X_{ik} is the coordinate of species *i* on trait *k*. dG_i is the distance to the centre of gravity for each species in the assemblage. *T* is the number of traits / dimensions of the functional space. $\overline{dG}$ is the mean distance between the species in the assemblage and the centre of gravity. Δd is the sum of abundance weighted deviances. Lastly, $\Delta|d|$ is the absolute abundance weighted deviances from the centre of gravity for the species in an assemblage.

Index		Formula	Description
Functional richness	FRic	V(C1)	Volume of the minimum convex hull (minimum convex polytope) surrounding the species of a given assemblage in trait space calculated for all the species across all assemblages being compared (the species pool) as outlined in (Barber, Dobkin and Huhdanpaa, 1996) (Villéger, Mason and Mouillot, 2008; Villéger, Grenouillet and Brosse, 2013)
Functional evenness	FEve	$EW_l = \frac{dist(i,j)}{P_i + P_j}$ $PEW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l}$ $\frac{\sum_{l=1}^{s=1} \min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	A measure encompassing both the evenness of species abundances and the evenness in the distribution of species throughout trait space using a minimum spanning tree (MST) (Villéger, Mason and Mouillot, 2008).

Functional divergence	FDiv	$g_k = \frac{1}{V}\sum_{i=1}^{V} x_{ik}$ $dG_i = \sqrt{\sum_{k=1}^{T}(x_{ik} - g_k)^2}$ $\overline{dG} = \frac{1}{S}\sum_{i=1}^{S} dG_i$ $\Delta d = \sum_{i=1}^{S} P_i \times (dG_i - \overline{dG})$ $\Delta\lvert d\rvert = \sum_{i=1}^{S} P_i \times \lvert dG_i - \overline{dG}\rvert$ $\frac{\Delta d + \overline{dG}}{\Delta\lvert d\rvert + \overline{w}dG}$	A measure encompassing the number and abundance of species on the vertices (outer edges) of a convex hull. It is a measure of how many species and individuals have extreme trait values within an assemblage (Villéger, Mason and Mouillot, 2008).

Pilot study: Functional alpha-diversity example results

There was no significant change in tree functional richness ($F_{(1,6)}$= 0.30, adj R^2= -0.11, p=0.60), divergence ($F_{(1,6)}$= 0.05, adj R^2= -0.16, p=0.83), or evenness with forest age ($F_{(1,6)}$= 5.41, adj R^2= 0.39, p=0.06). There was likewise no significant change in bird FRic ($F_{(1,6)}$= 0.43, adj R^2= -0.09, p=0.54), FDiv ($F_{(1,6)}$= 2.32, adj R^2= 0.16, p=0.18), or FEve over succession ($F_{(1,6)}$= 0.33, adj R^2= -0.11, p=0.59).

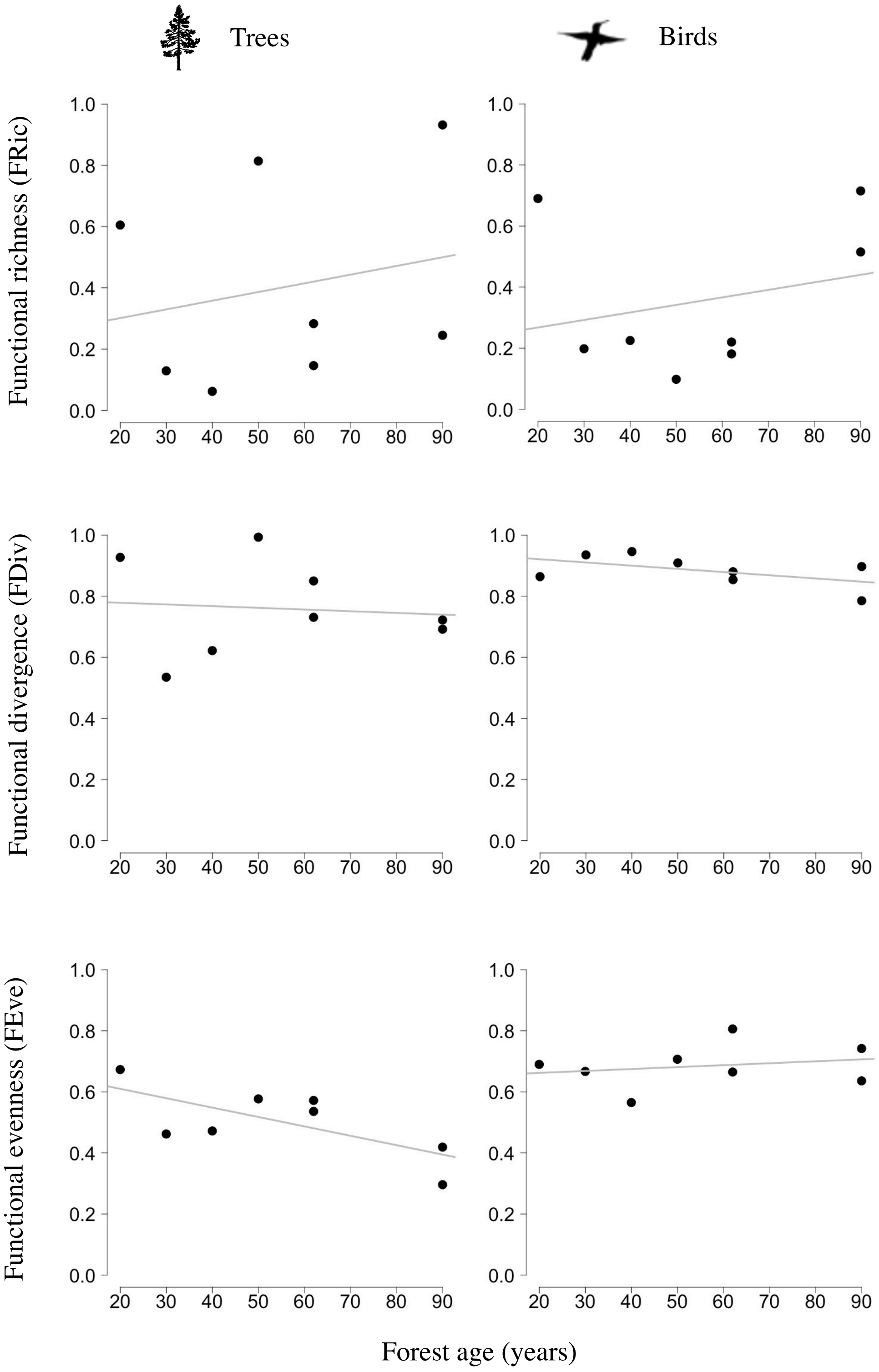


Figure 3.5 Functional richness, evenness, and divergence with forest age in tree, ground vegetation and bird assemblages. Grey lines indicate no significant change in functional alpha-diversity with forest age.

Functional beta-diversity

Table 3.4. Equation and description of the functional turnover component of the functional beta-diversity index. $V(C1)$ is the volume of convex hull around species in assemblage X. $V(C2)$ is the volume of convex hull around species in assemblage Y. $V(C1 \cap C2)$ is the intersection of the convex hulls around assemblages X and Y.

Index		Formula	Description
Functional turnover	FTurn	$\frac{2 \times \min(V(C1), V(C2)) - 2xV(C1 \cap C2)}{2 \times \min(V(C1), V(C2)) - V(C1 \cap C2)}$	A measure of how different the functional trait composition is between two assemblages (Villéger, Grenouillet and Brosse, 2013).

The functional beta diversity index was used to quantify dissimilarity in functional trait composition between sites (Villéger, Grenouillet & Brosse, 2013). This is also an intuitive index which assesses the overlap in functional trait space between two assemblages and decomposes functional beta diversity into its turnover and nestedness components.

Pilot study: Functional beta-diversity example results

As with taxonomic turnover, 0.5 quantile regressions were employed to assess whether functional turnover significantly increased with age-difference between sites for the Fife pilot study data. The same traits were used in the functional alpha and beta-diversity analyses.

The quantile regressions show that there was no significant change in the tree functional trait composition with age difference between sites ($T_{(1,26)}$= 0.17, p=0.86). Contrary to this, there was a significant decrease in bird functional trait turnover with increasing age difference between sites ($T_{(1,26)}$= -2.73, p=0.01).

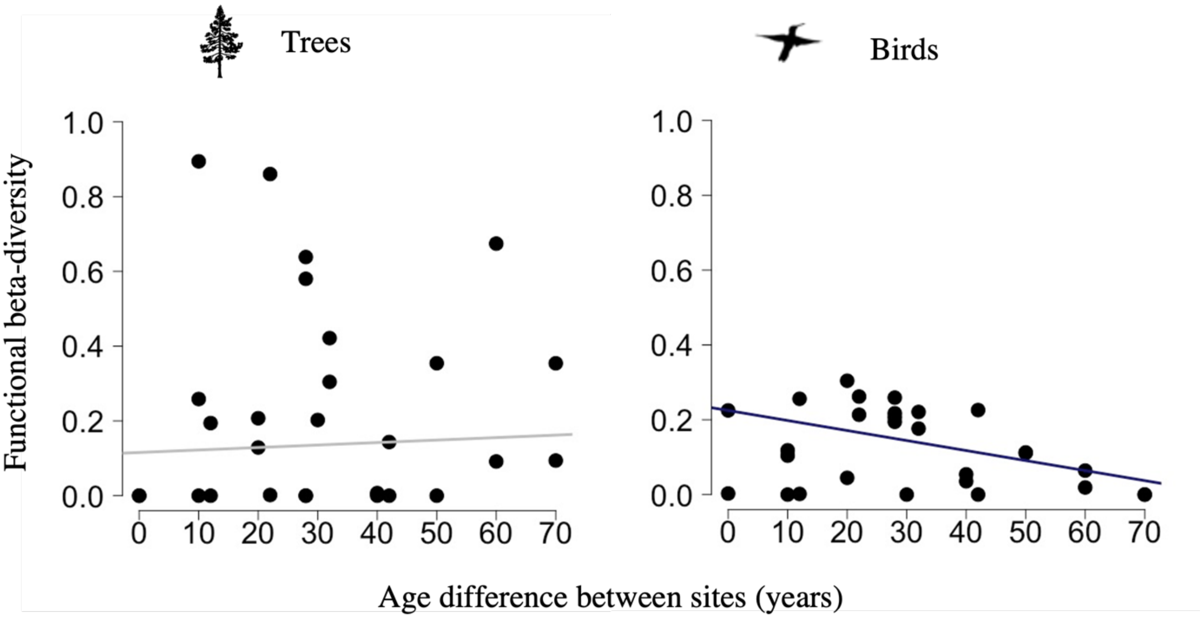


Figure 3.6 50th quantile regressions of tree and bird functional turnover with age difference between sites. Blue lines signify a significant change in functional trait composition with site age difference.

These results confirm that the approach adopted is tractable and that it yields ecologically interpretable results. They show, for this system, that the magnitude and direction of temporal change over secondary succession varies across assemblages, and also differs amongst the metrics.

3.4 Trinidad field study

For the field study conducted in Trinidad and Tobago, 28 forest sites located in valleys across the southern slopes of the Northern Range mountains of Trinidad were surveyed (Figure 3.7). These included active cacao agroforests, secondary forests, and primary forests. The active cacao agroforests were planted predominantly with cacao, but shade trees such as mountain immortelle (*Erythrina peoppigiana*), and other crop trees such as mango (*Mangifera indica*) and citrus (*Citrus sp.*) were commonly present (Seedial, 2009; Seedial, 2013). The secondary forests were at various stages of regeneration following cacao agroforest abandonment (20-100 years). The primary forest sites had no indication or record of anthropogenic or natural

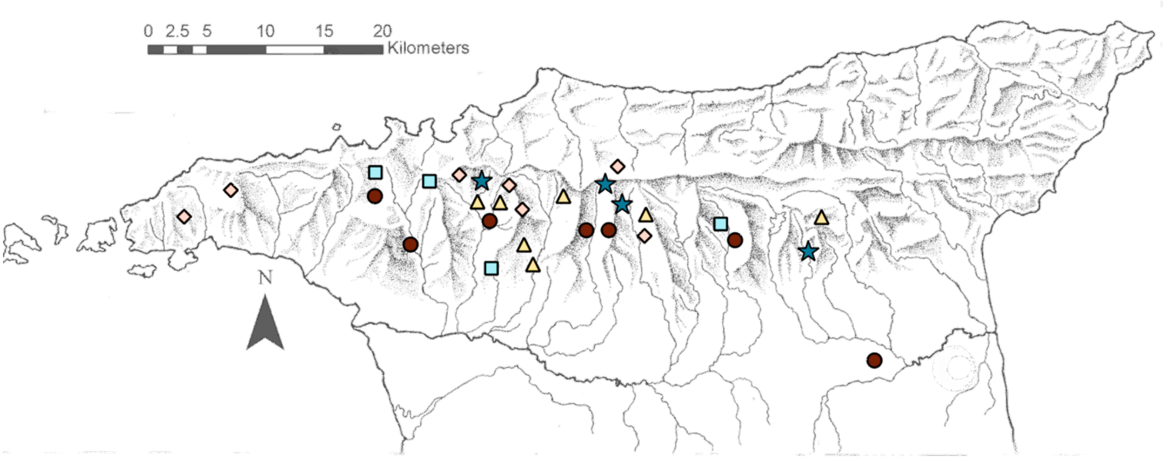


Figure 3.7 Map of field sites in Trinidad. There were seven active sites (red circles), seven 25–50 yo (pink diamonds), seven 60–80 yo (yellow triangles), four >100 yo (light blue squares) secondary forests, and four primary forest sites (dark blue stars).

disturbance, and had not been disturbed in local memory. Active cacao agroforests were given an age of zero. Secondary forest sites ranged from c.20 to 100 years old where time since abandonment was used as a proxy for successional age. Primary sites were given a conservative age of 200 years old and were used as a baseline for beta-diversity comparisons. Overall, this chronosequence represents c. 100 years of succession. All surveys conducted in Trinidad were done with the help of a field team and local experts.[1]

The aim with site selection was to capture the full chronosequence from active agroforest to primary forest, with replication. Specific sites were chosen based on where we could obtain reliable land use history information, as well as where we could obtain permission to survey. Information on the age and history of each site was based on local knowledge, historic records, and expert knowledge (Table 3.5). Land history, forest type, matrix habitat type, land gradient, and altitude were kept as similar as possible between sites. All the sites were between 1-5ha with over 50% canopy cover and trees over five metres tall. The sites were situated in lower montane seasonal evergreen forest and were mostly under 250m in altitude

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[1] Field team: Dan Jaggernauth, James Josaphat, Nicholas Manchouck, Keshan Mahabir with help from Dr Amy Deacon, Dr Aidan Farrell, Dr Alex Sansom, Dr Mark Hulme, Shane Ballah, Vicki Balfour, and Dr Linton Arneaud

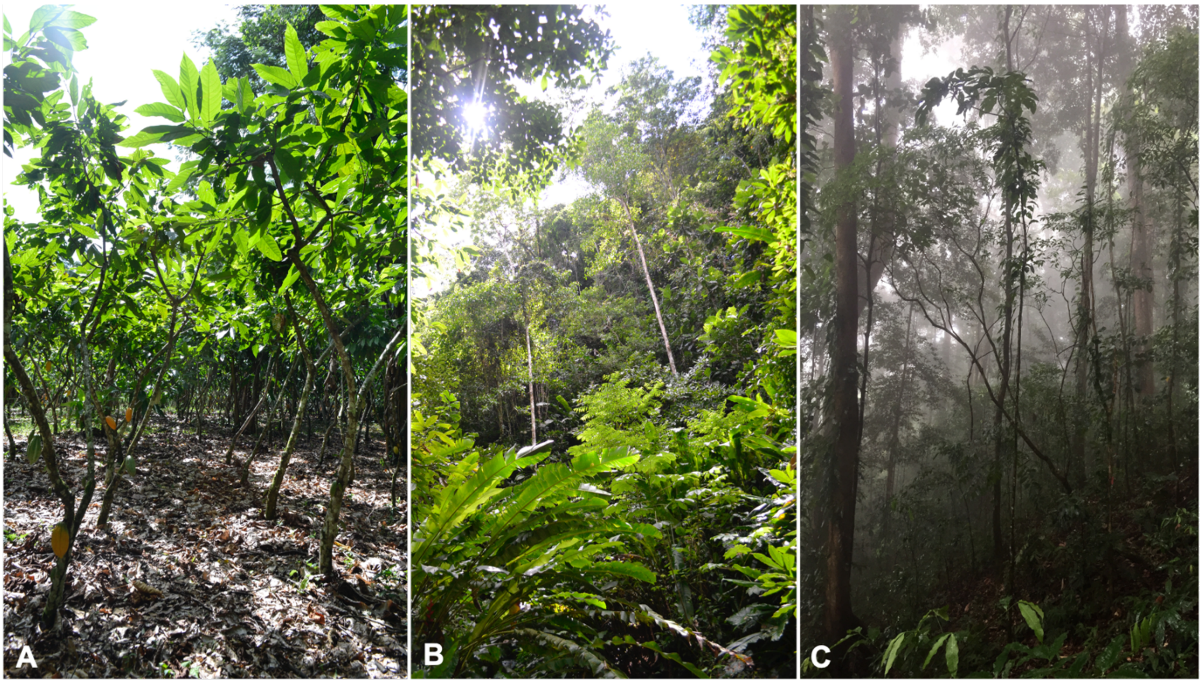
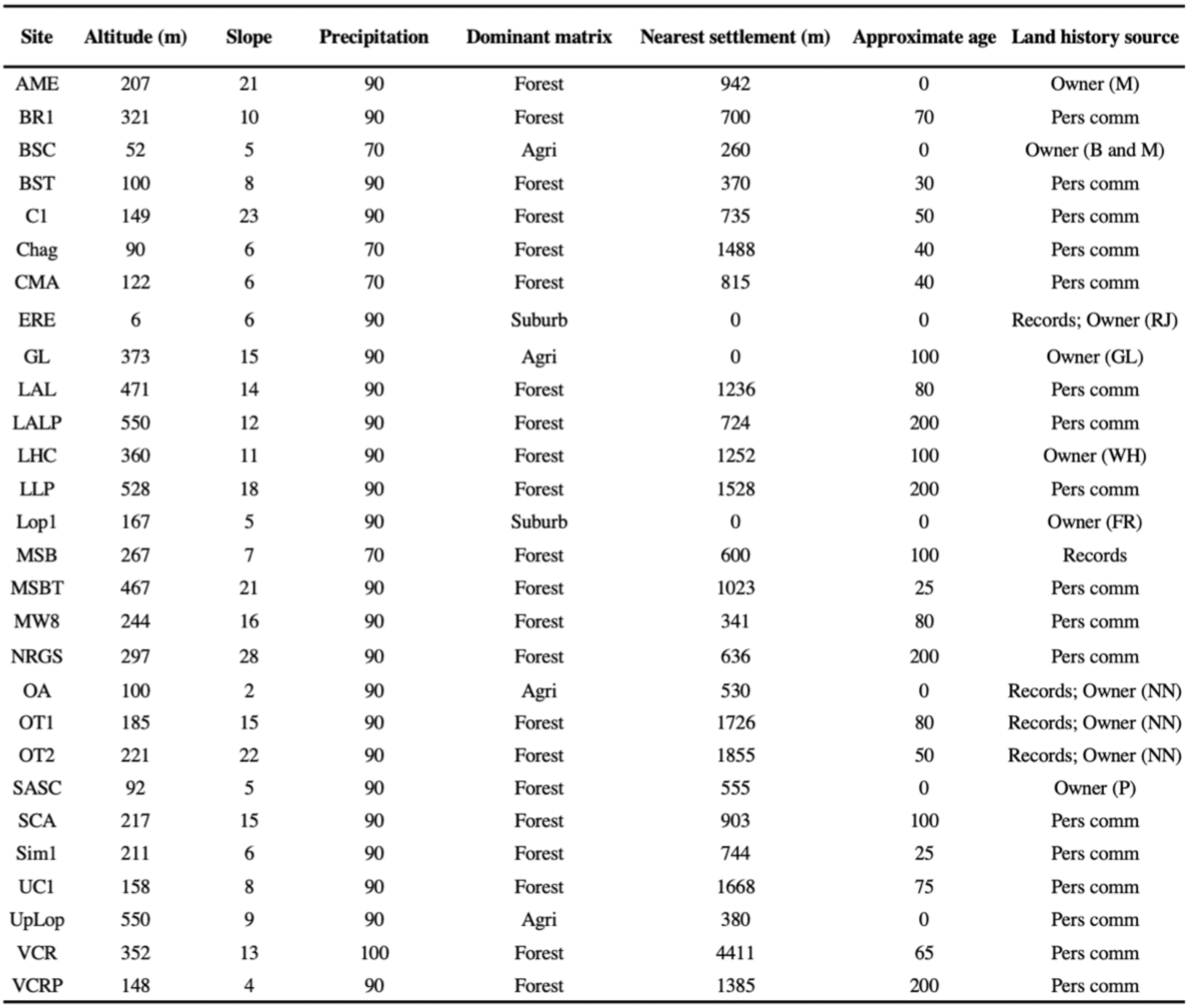


Figure 3.8 Examples of (A) an active cacao agroforest, (B) a secondary forest and (C) a primary forest in Trinidad's Northern Range.

with some higher altitude sites (Kenefick et al., 2013). While older sites tended to be at higher altitudes for historical reasons, the altitudinal difference between sites was small (<550m). One active cacao agroforest was located just south of the Northern Range but was managed similarly to other active agroforests in this study. Sites were spread out latitudinally so that similarly aged sites were not geographically clustered (Figure 3.7).

Each site was mostly surrounded by similar habitat. The primary forest sites were situated within larger tracts of primary forest where the size and shape were chosen to be comparable to the active and abandoned agroforests. Historic estates were large with many adjacent plots of cacao (De Verteuil, 2000). Thus, the secondary forest patches were surrounded by similar plots of abandoned agroforests that had once been part of the same estate. The plot boundaries were determined based on local knowledge and landmarks, such as the crotons (usually *Cordyline fruticosa*) which are commonly used as cacao agroforest boundary markers. The active cacao agroforest plots were likewise surrounded by other active agroforests managed by different landowners. The minimum distance between sites was approximately 0.8km (qGIS development team, 2021).

Table 3.5 Site information. Personal communication and records from site property managers Nikita Nath (NN), Francisco Rodriguez (FR), Gregory Leotaud (GL), Wayne Hutchinson (WH), Barry and Mary (B and M), Paul (P), Ramish Jadoo (RM) and Martin (M).



Site	Altitude (m)	Slope	Precipitation	Dominant matrix	Nearest settlement (m)	Approximate age	Land history source
AME	207	21	90	Forest	942	0	Owner (M)
BR1	321	10	90	Forest	700	70	Pers comm
BSC	52	5	70	Agri	260	0	Owner (B and M)
BST	100	8	90	Forest	370	30	Pers comm
C1	149	23	90	Forest	735	50	Pers comm
Chag	90	6	70	Forest	1488	40	Pers comm
CMA	122	6	70	Forest	815	40	Pers comm
ERE	6	6	90	Suburb	0	0	Records; Owner (RJ)
GL	373	15	90	Agri	0	100	Owner (GL)
LAL	471	14	90	Forest	1236	80	Pers comm
LALP	550	12	90	Forest	724	200	Pers comm
LHC	360	11	90	Forest	1252	100	Owner (WH)
LLP	528	18	90	Forest	1528	200	Pers comm
Lop1	167	5	90	Suburb	0	0	Owner (FR)
MSB	267	7	70	Forest	600	100	Records
MSBT	467	21	90	Forest	1023	25	Pers comm
MW8	244	16	90	Forest	341	80	Pers comm
NRGS	297	28	90	Forest	636	200	Pers comm
OA	100	2	90	Agri	530	0	Records; Owner (NN)
OT1	185	15	90	Forest	1726	80	Records; Owner (NN)
OT2	221	22	90	Forest	1855	50	Records; Owner (NN)
SASC	92	5	90	Forest	555	0	Owner (P)
SCA	217	15	90	Forest	903	100	Pers comm
Sim1	211	6	90	Forest	744	25	Pers comm
UC1	158	8	90	Forest	1668	75	Pers comm
UpLop	550	9	90	Agri	380	0	Pers comm
VCR	352	13	100	Forest	4411	65	Pers comm
VCRP	148	4	90	Forest	1385	200	Pers comm

In this study, factors which could affect patterns of biodiversity such as environmental variables and land management history were controlled for as much as possible through site choice. Environmental data were also collected in the field to control for the effects of these external factors (Table 3.5). Altitude was measured as the average of five measurements taken at random points in each site using a GPS. The slope was also measured as the average of five measurements taken at random points using an inclinometer. Annual average precipitation was based on values from Spiers et al. (2008). The dominant matrix (the land cover most abundant in the area immediately surrounding each site) was recorded. Lastly, the nearest settlement is the distance from the centre of each site to the nearest settlement with >5 houses and a paved road. Approximate age is the age of each forest site since abandonment as indicated by historic records, the property owner, local experts, and personal comments from residents with knowledge of the area. Field data was supplemented with existing functional trait data for functional diversity analyses (Chapter 5).

The chronosequence approach used in this study assumes that the management practices used in the active agroforests are similar to those used in the abandoned agroforests when they were actively cultivated, that patterns of biodiversity are primarily driven by forest age, and that the forests are transforming over succession at a similar rate. Local knowledge and local records, including those in the National Archives of Trinidad and Tobago, confirm that the agroforests were managed similarly.

As outlined in Chapter 1.4, standard cacao agroforest management in Trinidad involves pruning the cacao trees so that they remain short and easy to harvest from. Management also commonly includes removing epiphytes and suppressing the ground vegetation (Seedial, 2009). The sites surveyed for this research followed traditional management systems which include shade and other crop trees (Chapter 1.4).

The field methods used in this research were the same as those outlined for the pilot study (Box 3.1), with some exceptions. All epiphytes were identified to species level, except for some mosses which were only able to be identified to genus level, and lichens which were assigned to morphospecies (Appendix 3.2 photo library of morphospecies). Samples and detailed pictures were taken of the trees, ground vegetation, and epiphytes, and the species identifications were confirmed by the National Herbarium of Trinidad and Tobago where necessary. Samples of each lichen species were submitted to the herbarium so that species could be identified using chemical analyses in future. Bryophytes were identified with the help of a local expert, Shane Ballah.

Additionally, instead of using point counts, birds were surveyed using a single transect spanning the longest orientation of each site (found using qGIS; QGIS development team, 2021). The transects were set at least 50m from the site edge to avoid counting birds outside of the site. The bird surveys were conducted in the early morning (7-9am) when birds are more active between late April to early August (2019) to coincide with the start of the wet season and the main bird breeding season (Snow & Snow, 1963, ffrench, 1985; Kenefick et al., 2013). All birds that were seen or heard over the survey period on either side of the transect line were recorded. Birds heard behind the surveyors were not recorded to avoid double counting.

When a large flock of birds was encountered, the number of birds of each species was estimated and the distance and direction to the centre of the flock was recorded. Binoculars and sound recordings were used to aid in identifying species. Domesticated captive birds (*Numida meleagris* and *Gallus sp*.) were recorded, but not included in analyses. Bird behaviour (on the ground, flying over, flying low, perched, eating, or nesting) and the method of detection (seen, heard, or both) were recorded. Whether a bird was directly interacting with the site was recorded as well. Birds up to 200m away were recorded and the full dataset was used for analyses in the following chapters. Results using truncated data which included only birds within 50m of the transect line are available in Appendix 3.3 for comparison.

The transects were walked three times, 20 minutes apart. The first transect was used in analyses, while the two repetitions were used to assess the repeatability and precision of the bird surveys (Appendix 3.4). A GPS was used to ensure the transects were walked at a consistent walking speed between repetitions and between sites. Surveys were not conducted in extreme weather that reduced visibility and altered bird behaviour (rain, wind, or fog). Environmental variables including habitat descriptions, weather conditions, and visibility (estimated as the distance to which objects were visible and not obscured by foliage etc) were recorded at the start of each bird survey. All the bird surveys were conducted with assistance from Dan Jaggernauth and Nicholas Manchouck.

Chapter 4

Taxonomic diversity over tropical secondary forest succession

4.1 Introduction

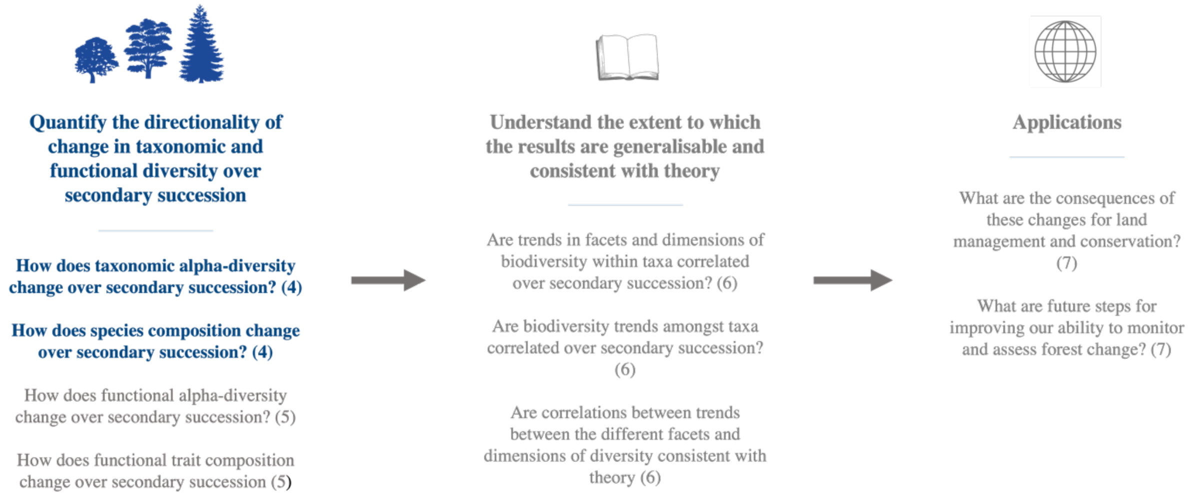


Figure 4.1. Schematic of questions being addressed in this thesis. Questions highlighted in blue are the focus of this chapter.

Biodiversity is under unprecedented threat due to growing anthropogenic pressures on ecosystems globally (Chapter 1;Magurran and Dornelas, 2010; Isbell *et al*., 2017; Blowes *et al*., 2019). Habitat loss and transformation are major drivers of this ongoing biodiversity crisis (Ehrlich and Pringle, 2008; Semper-Pascual *et al*., 2019). While deforestation rates have slowed over the last decade, the proportion of secondary and planted forests continues to increase while primary forest cover declines (Ellis, Antill and Kreft, 2012; Martin, Newton and Bullock, 2013). Tropical regions are experiencing high rates of deforestation and conversion of land for agriculture (Gibson *et al*., 2011; Mora *et al*., 2015). As the proportion of converted and disturbed land continues to grow relative to primary forests, agricultural and secondary forests are becoming increasingly important biodiversity reservoirs. Thus, understanding how tropical forests regrow on abandoned agricultural land is crucial for conservation. The conversion of primary forest for farming cacao is one widespread form of land conversion in the tropics (Ruf and Schroth, 2004), though the effects of cacao farming on tropical biodiversity has received little attention compared to other forms of land conversion.

The following chapter will assess how taxonomic alpha and beta-diversity change over c. 100 years of tropical secondary forest succession following cacao agroforest abandonment in Trinidad, using the methods detailed in Chapter 3 (Figure 4.1). The chapter will also address whether the rate of taxonomic diversity change varies over succession, as well as how some basic structural characteristics of the forests change over time. Taxonomic diversity is the most studied dimensions of biodiversity and provides important insight into how forests change; this perspective will be developed further in Chapters 5 and 6.

Unlike other forms of agriculture or disturbance, traditionally grown ‘shade-cacao’ agroforests have standing trees with a mostly closed canopy and multiple canopy layers, which can create similar habitats and microclimates to older forests and attract seed dispersing animals (details on farming methods in Chapters 1 and 3; Finegan, 1996; Franklin *et al*., 2002; Chazdon, 2003; Sandor and Chazdon, 2014; Derroire *et al*., 2016). This suggests that cacao agroforests and similar agroforestry systems like coffee and vanilla may retain some characteristics and functions of older forests, and may recover old-growth characteristics more rapidly than would be expected following other forms of disturbance and land use.

Species (i.e. taxonomic) alpha-diversity is expected to increase through time in all taxa investigated in this system; simple functional characteristics such as forest structure are also expected to recover over time, especially in the early stages of succession. These predictions are based on succession theory and findings from research, where species colonise abandoned areas and accumulate over time as forests regenerate (Chapter 2; DeGraaf, Geis and Healy, 1991; Finegan, 1996; Calvo and Blake, 1998; Keller, Richmond and Smith, 2003; Rey-Benayas, Galván and Carrascal, 2010; Buechley *et al*., 2015; Derroire *et al*., 2016; Arroyo-Rodríguez *et al*., 2017). It is also expected that species composition will change significantly over succession in all taxa as the biotic and abiotic conditions, such as environmental filtering and competitive regimes, change within a forest over time (Chapter 2; Guariguata and Ostertag, 2001). To test these predictions, I first ask how forest structure changes through succession by assessing canopy cover, tree height, and DBH. I then present the results for taxonomic alpha and beta-diversity change over succession for each taxon. The methods for this chapter are described in Chapter 3.

4.2 Structural characteristics

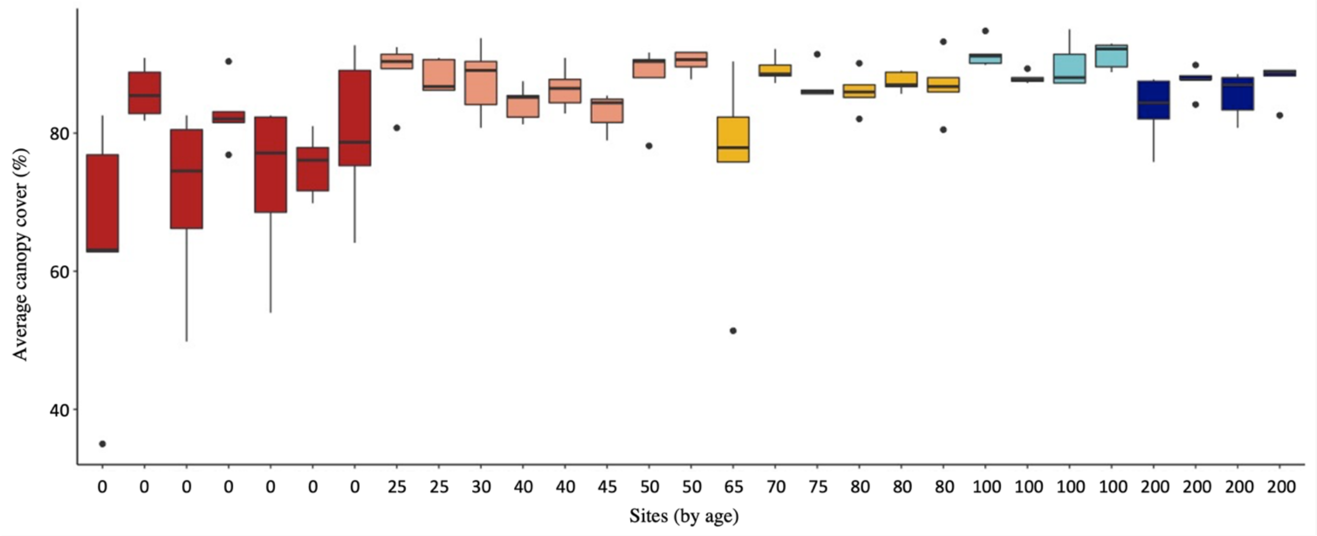


Figure 4.2. Canopy cover with forest age. Boxes represent the median value (horizontal line) with the interquartile range (box), the minimum and maximum values excluding outliers (vertical lines), and outliers (points). Red boxes are active sites, orange boxes are 25–50 yo secondary forest sites, yellow boxes are 60–80 yo secondary forests, light blue boxes are >100 yo secondary forests, and dark blue boxes are primary forest sites.

Results from my research show that the forest canopy develops and becomes more structurally complex over succession. Five measure of canopy cover were taken in random locations at each site using a spherical densiometer (Chapter 3). Boxplots were used to assess changes in canopy cover with forest age (ggplot package in R; R Core Team, 2021; Wickham *et al*., 2021). Active cacao agroforests had a higher degree of variation in canopy cover than secondary and primary forest sites, but all sites had >50% cover (Figure 4.2). Canopy closure occurred early, within the first 20 years of succession, with the result that young secondary forests had a similar percentage canopy cover to primary forests (Figure 4.2). Overall, there was little difference in canopy cover between most secondary forests, actively cultivated cacao agroforest sites, or the primary forest sites.

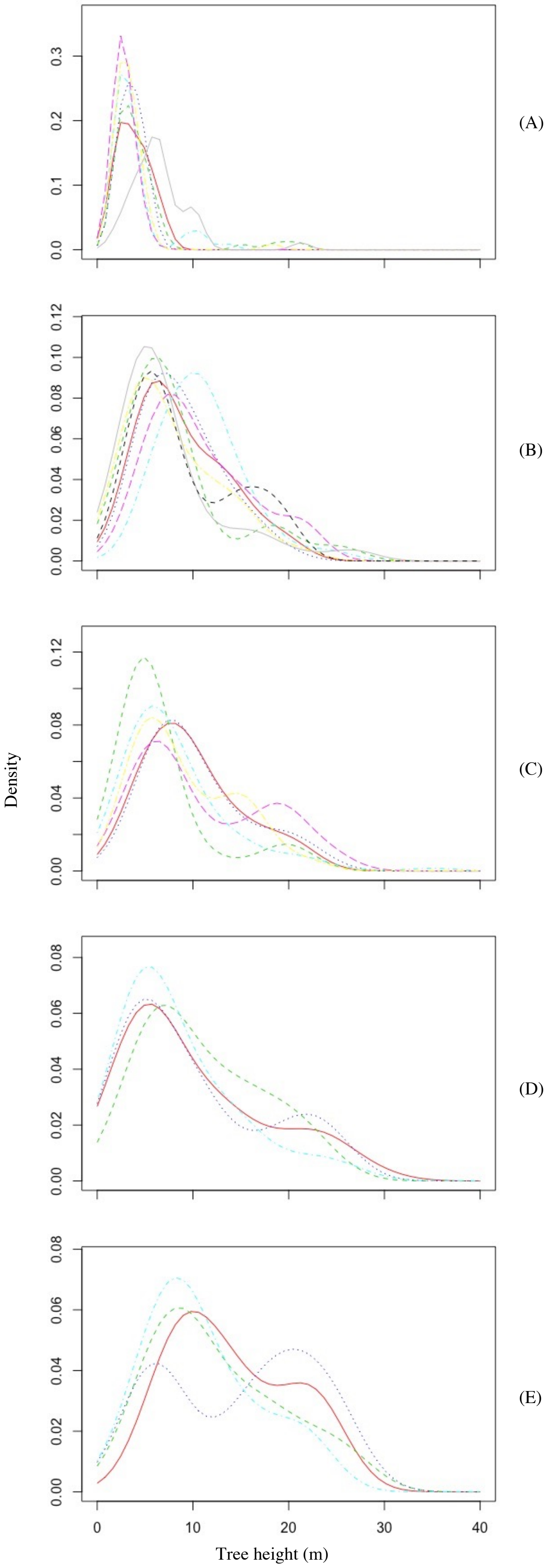


Figure 4.3 Kernel density plot of tree height for each site where the probability density function (density) represents the number of trees which have a given height value in an assemblage (probability density per each height unit). Each line represents a different site: (a) Active cacao agroforests, (b) 20-45, (c) 50-80, (d) >100, (e) primary forest.

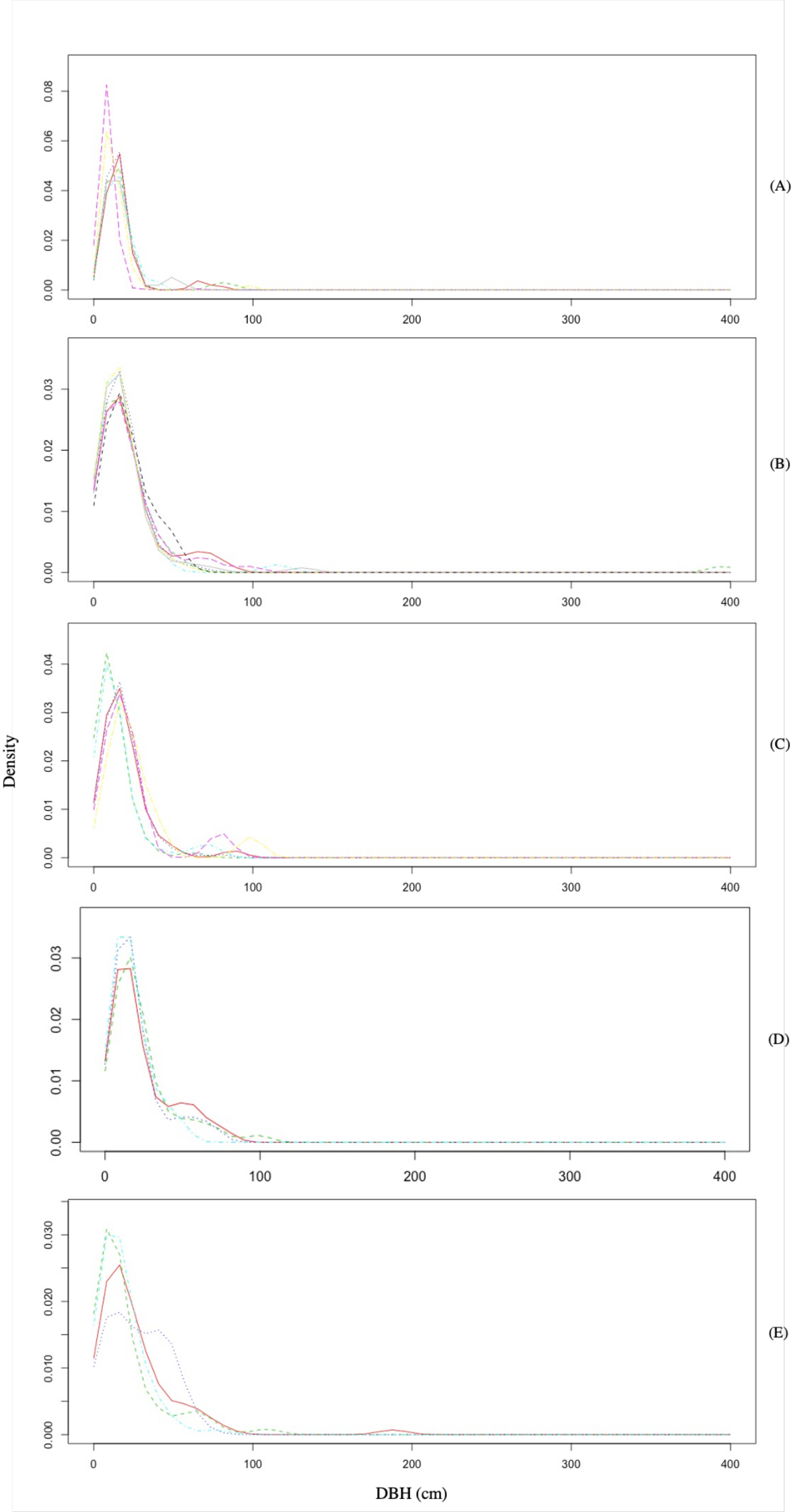


Figure 4.4 Tree diameter at breast height (DBH). The probability density function (density) represents the number of trees which have a given DBH value in an assemblage (probability density per unit DBH). Each line represents a different site: (a) Active cacao agroforests, (b) 20-45, (c) 50-80, (d) >100, (e) primary forest.

Forest structure was further evaluated by examining tree height. The height of each tree surveyed in this study was estimated in the field, and kernel density plots were used to assess changes in canopy height and structure (Chapter 3; sm package in R statistical software; Bowman and Azzalini, 2021; R Core Team, 2021). Canopy structure became increasingly bimodal with forest age, indicating the growth of taller trees and the emergence of multiple canopy layers as the forests recover (Figure 4.3). Lastly, the circumferences of all the trees surveyed were also measured in the field and the DBH of each tree was calculated from these values (Chapter 3). The change in tree trunk size (DBH) was less pronounced than in tree height, but also increased with forest age and became more bimodal (Figure 4.4).

4.3 Alpha-diversity

Taxonomic alpha-diversity was quantified using Hill numbers of the order q: species richness (q=0), Shannon diversity (q=1), and Simpson diversity (q=2; Chapter 3; Hill, 1973). Species richness is the number of species present in an assemblage. Simpson diversity emphasises species evenness (how even the relative abundances of species within an assemblage are). Shannon diversity provides an intermediate perspective of assemblage diversity as it draws on both species richness and evenness.

GLM linear regressions of the alpha-diversity indices and forest age were used to assess whether there were significant changes in species alpha-diversity over succession for each taxon (Figure 4.5; Table 4.1; taxonomic alpha-diversity analysis method detailed in Chapter 3.2). GLMs were further conducted without primary sites (Appendix 4.2) and used to control for the effects of environmental variables (altitude, annual average precipitation, and distance to the nearest settlement; Chapter 3). Environmental variables were used if the addition increased AIC scores. Lastly, the analyses also tested for break points and, if there was a significant break point which improved model fit, this was taken as evidence that the rate of alpha-diversity change varied over succession (segmented package in R statistical software; Muggeo, 2017; R Core Team, 2021).

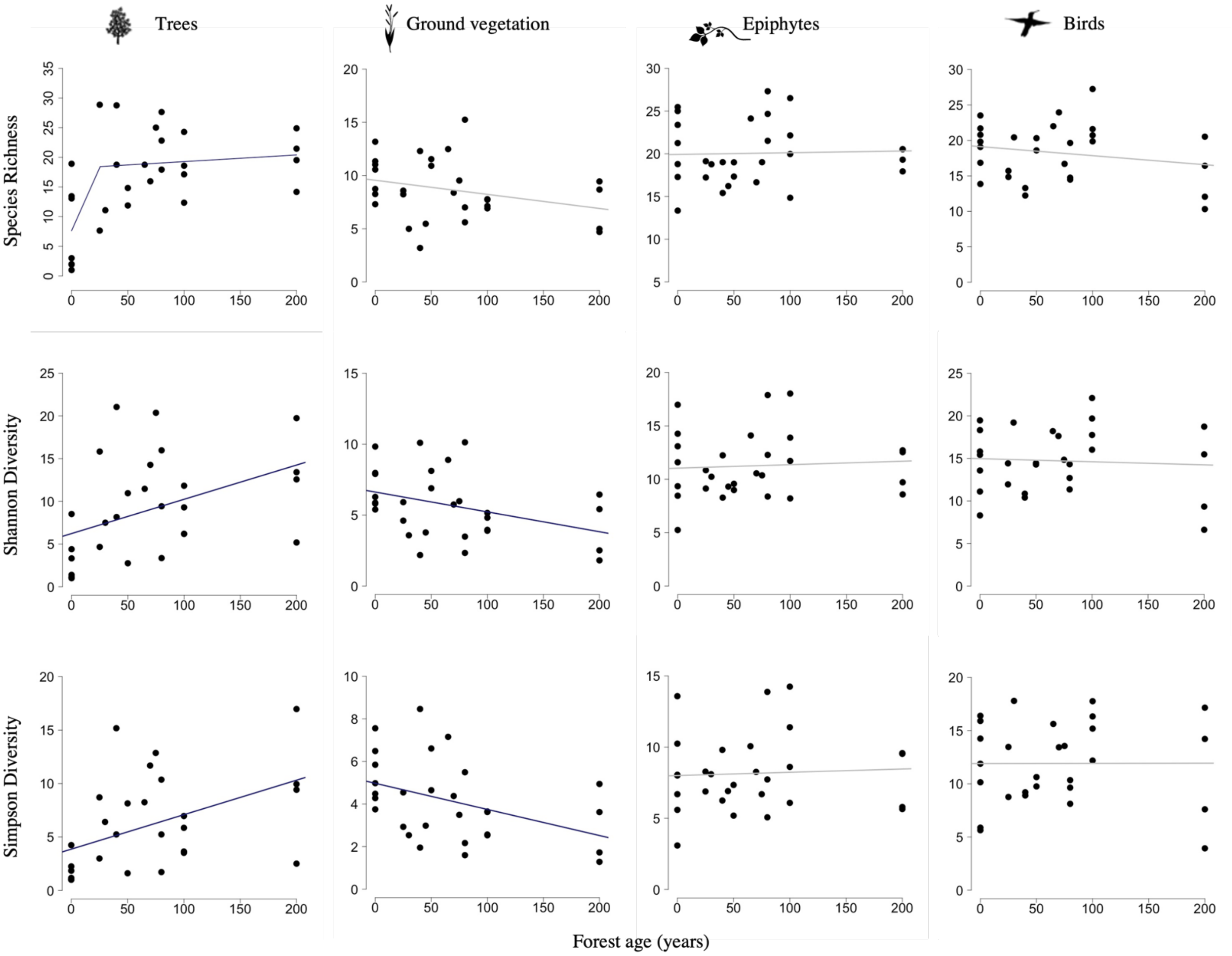


Figure 4.5 Species richness, Shannon diversity and Simpson diversity with forest age in tree, ground vegetation, epiphyte and bird assemblages. The points represent the field sites, and blue lines indicate statistically significant trends (regression information is detailed in Table 4.1).

As expected, there was a significant increase in tree species richness (p=0.02), Shannon diversity (p=0.02), and Simpson diversity with forest age (p=0.01; Table 4.1). There was a significant break point in tree species richness at 25.4 years indicating that tree species richness increased more rapidly early on in succession (Figure 4.5; Table 4.1).

Also, in line with expectation, there was a significant decrease in ground vegetation Shannon (p=0.02) and Simpson diversity with forest age (p=0.02), but there was no significant change in ground vegetation species richness (p=0.12).

There was no significant change in epiphyte species richness (p=0.33), Shannon diversity (p=0.67), or Simpson diversity over time (p=0.26).

There was also no statistically significant change in bird richness (p=0.30), Shannon (p=0.75) or Simpson estimates over succession (p=0.99). There was one fewer degree of freedom in the bird surveys due to there being one fewer site included in these analyses (Chapter 3).

No other regressions had significant breakpoints, and environmental variables reduced the model fit in these analyses. The potential issue of multiple comparisons is noted here. These statistics are therefore included to provide intuitive information of the fitted linear trend of each time series, rather than presented in a classical hypothesis-testing context.

Table 4.1 GLM linear regression results for alpha-diversity measures with forest age. Sites is the number of sites (n) included in each analysis.

Taxon	Model	Breakpoints	df	Sites	adj R^2	F value	P value
Trees	Richness ~ Forest age	25.4 years	1 on 27	29	0.16	6.47	0.02
	Shannon ~ Forest age	—	1 on 27	29	0.14	5.61	0.03
	Simpson ~ Forest age	—	1 on 27	29	0.17	6.57	0.02
Birds	Richness ~ Forest age	—	1 on 26	28	0.01	1.13	0.30
	Shannon ~ Forest age	—	1 on 26	28	-0.03	0.10	0.75
	Simpson ~ Forest age	—	1 on 26	28	-0.04	<0.01	0.99
Vegetation	Richness ~ Forest age	—	1 on 27	29	0.05	2.63	0.12
	Shannon ~ Forest age	—	1 on 27	29	0.11	4.56	0.04
	Simpson ~ Forest age	—	1 on 27	29	0.14	5.72	0.02
Epiphytes	Richness ~ Forest age	—	1 on 27	29	0.04	0.97	0.33
	Shannon ~ Forest age	—	1 on 27	29	0.01	0.19	0.67
	Simpson ~ Forest age	—	1 on 27	29	0.05	1.35	0.26

4.4 Beta-diversity

The Chao-Jaccard index was used to quantify compositional dissimilarity between sites. This index corrects for under-sampling and unseen species by weighting for rare species that are shared between site pairs (Chapter 3.2; Chao *et al.*, 2006). A 0.5 quantile regression was then used to relate Chao-Jaccard compositional dissimilarity to age difference and environmental distance between sites in pairwise comparisons for each taxon (Koenker, 2013). Age difference is the difference in time since abandonment between sites, where actively cultivated sites have an age of zero and primary sites are given a conservative age estimate of 200 years old. Environmental distance was quantified using non-metric multi-dimensional scaling (NMDS) on the environmental variables: annual average precipitation (Fick and Hijmans, 2017), average site altitude, distance to the nearest settlement (measured as distance to the nearest settlement with >5 houses and a paved road using QGIS), and average land gradient (Chapter 3; metaMDS function in the vegan package in R; Oksanen *et al.*, 2010). NMDS provided a measure of the pairwise environmental distance between sites in multidimensional Euclidean space. Environmental variables were chosen based on their relative weight and independence in determining environmental distance between sites, and their ecological relevance. Quantile regressions were used because they are more robust to outliers and unequal variance (heteroscedasticity) than GLM linear regressions (Cade and Noon, 2003; John, 2015).

A 0.5 quantile regression found a significant increase in Chao-Jaccard compositional dissimilarity between tree assemblages with increasing age difference between site pairs ($p < 0.001$) and with increasing environmental distance ($p = 0.01$; Table 4.2; Figure 4.6). Out of all the taxa, the regression model fit tree assemblages best with a markedly higher R^2 value. There was likewise a significant change in ground vegetation composition with increasing age difference between sites ($p < 0.001$), but not with environmental distance ($p = 0.69$). A 0.5 quantile regression also found bird compositional dissimilarity increased with age difference between site pairs ($p < 0.001$), but not with environmental distance ($p = 0.10$). Lastly, there was no significant change in epiphyte composition with age difference between sites ($p = 0.31$), or with environmental distance between site pairs ($p = 0.77$)

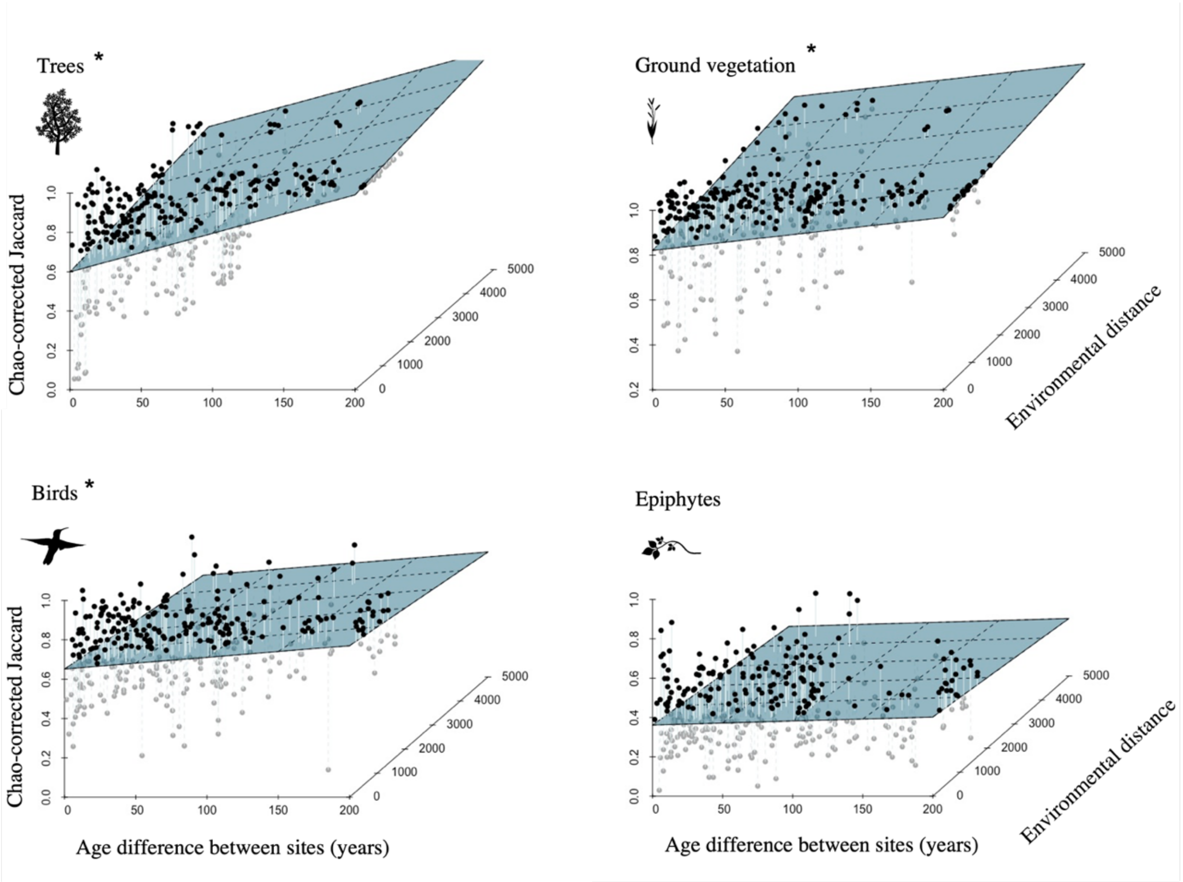


Figure 4.6 Species compositional change (Chao-Jaccard) with age difference and environmental distance between site pairs. 'Age difference' is the pairwise difference in age between sites, and 'environmental distance' is the pairwise distance between sites in environmental Euclidean space. The Euclidean space was built using the environmental variables: average site altitude, distance to the nearest settlement, annual average precipitation, and average land gradient. Asterisks indicate statistically significant change in species composition with forest age from a 0.5 quantile regression (regression information is detailed in Table 4.2).

Table 4.2 Results from 0.5 quantile regression of Chao-corrected Jaccard with age difference and environmental distance between site pairs. P-values are given for age difference (A) and for environmental distance (E).

Taxon	Model	df	Sites	adj R^2	F value	P value A	P value E
Trees	Chao-Jaccard ~ Age difference + Environmental distance	2 on 404	29	0.28	74.86	<0.001	0.01
Birds	Chao-Jaccard ~ Age difference + Environmental distance	2 on 375	28	0.06	13.37	<0.01	0.10
Vegetation	Chao-Jaccard ~ Age difference + Environmental distance	2 on 404	29	0.05	10.71	<0.001	0.69
Epiphytes	Chao-Jaccard ~ Age difference + Environmental distance	2 on 404	29	0.05	10.71	0.31	0.77

Principal Coordinates Analysis (PCoA) was used to visualise forest age groupings in multidimensional space based on differences in species composition (Chao-corrected Jaccard) between sites (pcoa function in the ape package in R; Figure 4.7; Paradis *et al.*, 2022). For the trees, active cacao agroforests and primary forests had unique species composition, while the secondary forests largely overlapped in species composition regardless of forest age. A similar pattern was seen in the bird and ground vegetation assemblages, where active agroforests and primary forests were more compositionally unique. The distinction between age categories was less clear in epiphyte assemblages.

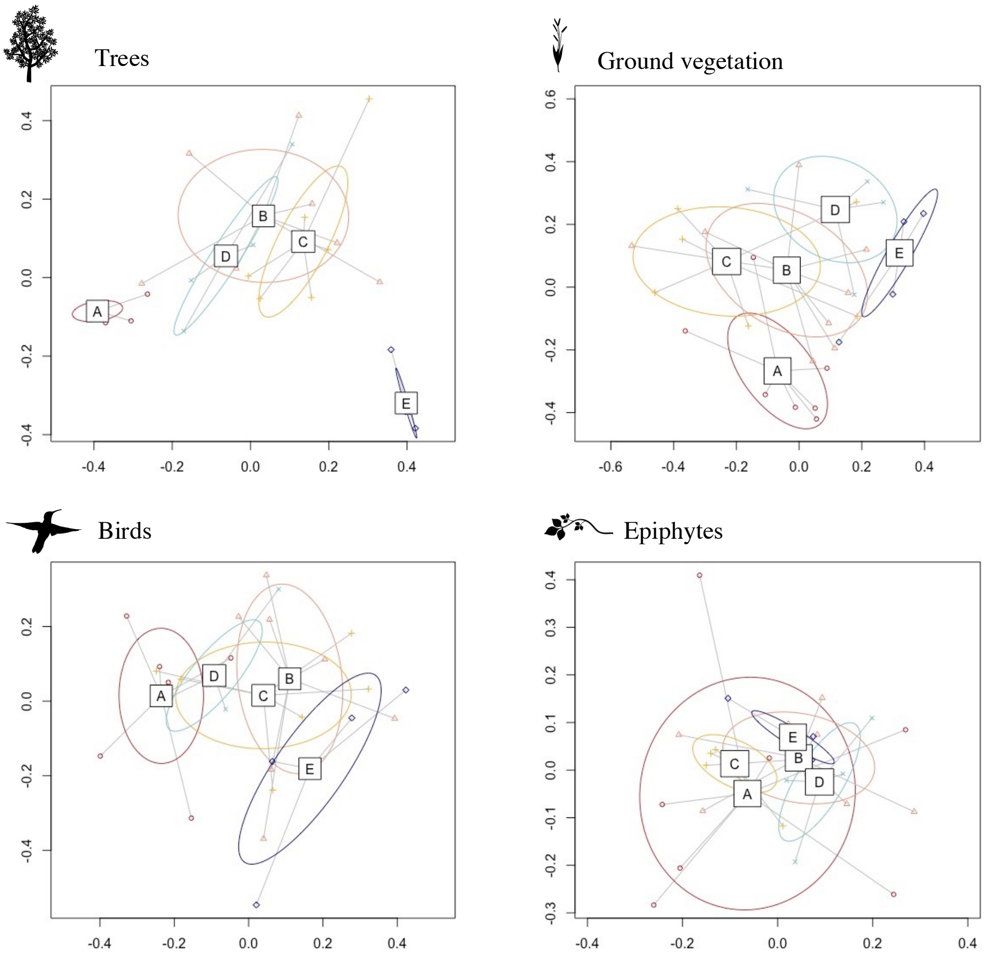


Figure 4.7 Species composition comparisons between age groups. PCoA of species composition between sites based on chao-corrected Jaccard dissimilarity. X and Y axes are the first and second PCoA axes respectively. A (red) are active sites, B (pink) are 25–50 yo secondary forest sites, C (yellow) are 60–80 yo secondary forests, D (light blue) are >100 yo secondary forests, and E (dark blue) are primary forest sites.

Bubble plots were used to further illustrate changes in species composition with forest age (inkspot function in the rioja package in R; Figure 4.8; bubble plots with all species in Appendix 4.1; Juggins, 2020). Some species were more common in active cacao farms, young secondary forests, or in older forests. Other species were more ubiquitous and present across sites regardless of successional age. Active cacao agroforests and young secondary forests were primarily composed of agricultural trees such as cacao, mountain immortelle (*Erythrina poeppigiana*), mango (*Mangifera indica*), breadfruit (*Artocarpus altilis*), citrus (*Citrus sp*. including *C. sinensis* and *C. paradisi*), and coconut (*Cocos nucifera*). Older secondary and primary forests had more native forest tree species such as toporite (*Hernandia Sonora*), sandbox (*Hura crepitans*), cooperhoop (*Brownea coccinea*), white mahoe (*Heliocarpus trichopodus*), angelin (*Andira inermis*), roughleaf (*Curtella americana*), and mature stranglers including *Clusia flavida* and *Ficus* species.

Common bird species such as blue-grey tanagers (*Thraupis episcopus*), palm tanagers (*Thraupis palmarum*), bananaquits (*Coereba flaveola*), and spectacled thrushes (*Turdus nudigenis*) were abundant, especially in active agroforests and young secondary forests. Forest species including white-bearded manakins (*Manacus manacus*), long-billed gnatwrens (*Ramphocaenus melanurus*), red-eyed vireos (*Vireo olivaceus*), and rufous-breasted hermits (*Glaucis hirsutus*) were more common in older secondary and primary forests.

For ground vegetation, grasses including *Axonopus compressus, Bambusa vulgaris, Cyperus luzulae,* and *Cyperus rotundus*, and herbs such as *Fleurya aestuans*, *Vanto somundipus*, *Eryngium foetidum* and *Centropogon cornatus* were more common in active agroforests and young secondary forests. Saplings of agricultural trees including mountain immortelle and avocado (*Persea americana*) were also present mostly in active agroforests and young secondary forests. Plant species such as the fern *Adiantum obliqum*, the herb *Heliconia spathocircinata*, and sandbox and palm saplings (including *Aiphanes minima* and *Attalea maripa*) were most common in secondary forests. Ferns such as *Sticherus bifidus* and *Adiantum latifoliuim*, vines such as *Philodendron giganticum* and *Monstera adonsonii*, and herbs such as *Ischnosiphon arouma* and *Stromanthe tonckat* were more common in older forests. Species such as the shrubs *Piper aduncum* and *Pachystachys coccinea*, the vine *Philodendron lingulatum* and herbs including *Heliconia bihai* and *Costus scaber* were ubiquitous across forest sites.

Most epiphytes were common across sites regardless of age including liverworts such as *Plagiochila adiantum*, *Neckeropsis undulata,* and *Lejeuneaceae* species, mosses such as *Calymperes afzelii* and *Sematophyllum* species, vines such as *Peperomia rotundifolia* and *Philodendron lingulatum*, and lichens such as *Coenogonium linkii*. Younger sites tended to have more lichens and bryophytes such as *Plagiochila adiantum*, *Papillaria* and *Goutiella* species, though the vine *Monstera dubai* and the orchid *Polystachya concreta* were only found in active agroforests. Older sites had more vines and lianas such as *Philodendron acutatum, P. ornatum, P. venosum, P. rudgeanum,* and *Desmoncus polycanthos*. Older forests also had more of the strangler tree *Clusia rosea*.

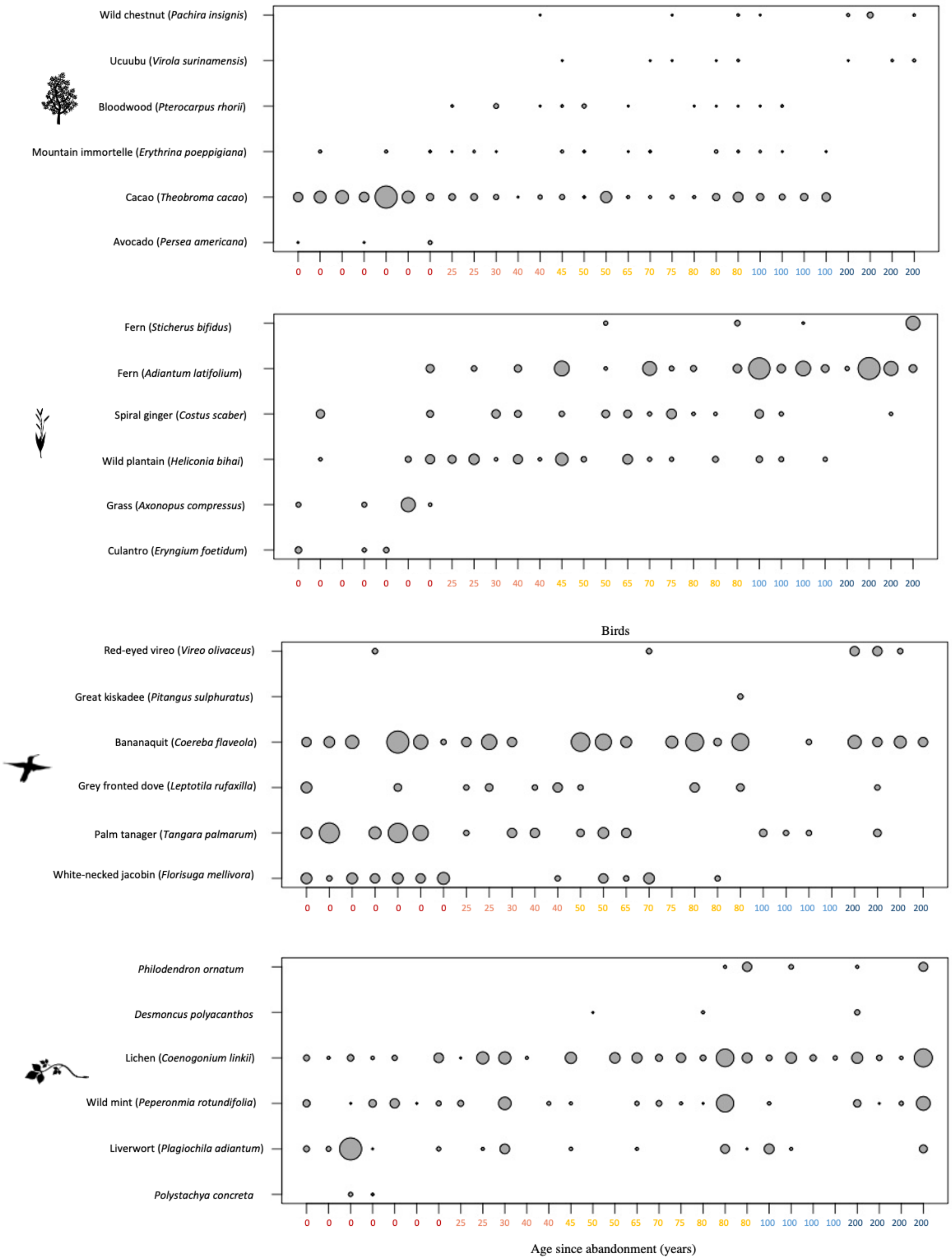


Figure 4.8 Bubble plots as a visual example of how species composition changes over time. The size of each circle represents the abundance of a given species (rows) in a given forest site (columns with age increasing from left to right). Some species are more common in active agroforests, in young secondary forests or in older forests, while others are ubiquitous across sites. Plots with all species are available in Appendix 4.1.

4.5 Discussion

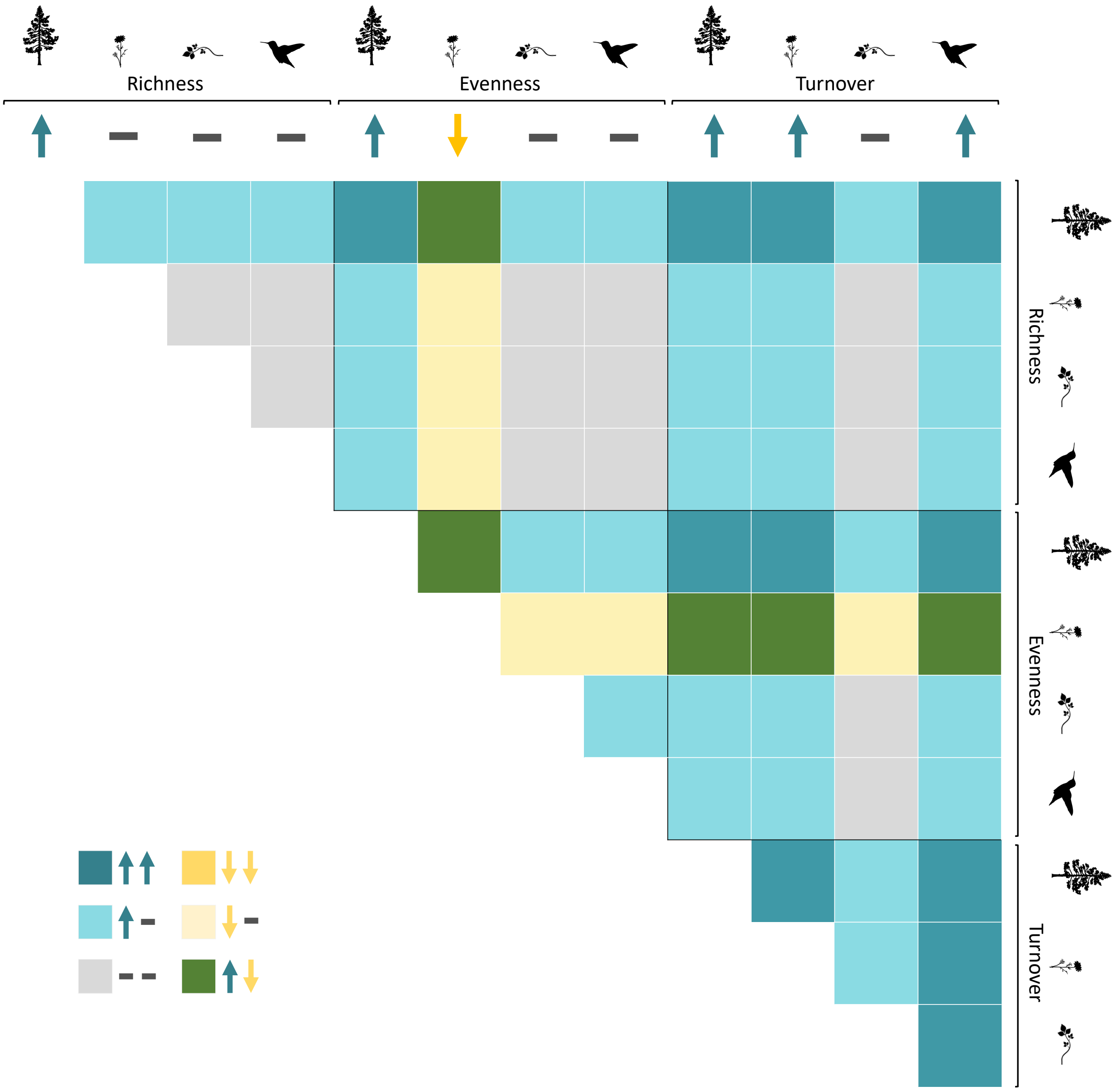


Figure 4.9 Summary figure of the taxonomic diversity results. Upward arrows (dark blue) indicate a positive trend with forest age, and yellow downwards arrows are negative trends. Grey dashes indicate no statistically significant change in the diversity measure over succession. The coloured grid indicates the relationship between different taxa and aspects of biodiversity. Dark blue indicates a strong positive relationship and light blue squares indicate conflicting trends with one of the pair increasing and one showing no significant change. Yellow indicates a strong negative trend, and light yellow squares indicate conflicting trends with one of the pair decreasing and one showing no change. Green squares represent opposing trends. Grey squares indicate that both the taxon and aspects of biodiversity being compared did not change over succession.

The aim of this chapter was to assess how forest structure and taxonomic diversity change over tropical secondary forest succession following cacao agroforest abandonment in Trinidad. Results from these analyses found that forests become more structurally complex over time, but that canopy cover recovered early in succession. This is in line with other studies that have found that structural characteristics and simple functions can recover early in succession (~15-50 years; Kubota, Katsuda and Kikuzawa, 2005; Lebrija-Trejos *et al.*, 2008; Derroire *et al.*, 2016). The standing trees and complex structure of cacao agroforest may facilitate the recovery of these simple functional attributes.

Alpha-diversity

As expected, there was a significant increase in tree species richness and evenness over succession. The increase in tree species richness was significantly greater within the first 25 years of succession. This is in line with other studies which have found tree species richness recovers quickly (within about 4–40 years; Finegan, 1996; Muñiz-Castro, Williams-Linera and Martínez-Ramos, 2012; Derroire *et al.*, 2016), though the results in this chapter also indicate that species richness continues to increase at a slower rate over c. 100 years of succession in these forests.

While there was no significant change in ground vegetation richness, Shannon and Simpson diversity significantly decreased over succession. These results are contrary to the expectation that ground vegetation alpha-diversity should increase over time alongside tree diversity and habitat heterogeneity. Conversely, these results support the concept that there is stronger environmental filtering due to greater canopy closure and lower light availability at ground level in older forests, which limits ground vegetation diversity (Laska, 1997; Lebrija-Trejos, Meave, *et al.*, 2010; dos Santos-Junior *et al.*, 2017). Some studies have also found that ground vegetation species alpha-diversity decreases over succession (Laska, 1997; Rasingam and Parthasarathy, 2009; dos Santos-Junior *et al.*, 2017). For example, Laska (1997) found that secondary forest sites had greater shrub species richness compared to primary forest in Costa Rica (Laska, 1997). Rasingam and Parthasarathy (2009) similarly found that disturbed forest sites in India had higher understory plant species richness than undisturbed forest sites (Rasingam and Parthasarathy, 2009). Likewise, dos Santos-Junior and colleagues (2017) found that herbaceous ground vegetation species richness was higher in secondary forest than primary forest in Brazil (dos Santos-Junior *et al.*, 2017). Other studies on ground vegetation taxonomic diversity over secondary forest succession have yielded mixed results, however (Costa and Magnusson, 2002).

There was no significant change in bird alpha-diversity with forest age. This is in line with expectations based on research where many studies have similarly found no change in bird alpha-diversity over succession (Chapter 2; Borges, 2007; Borges et al., 2021; Jarrett et al., 2021; Lee et al., 2020; Rocha et al., 2019; Sayer et al., 2017; Waltert et al., 2005). Theory, however, predicts that bird alpha-diversity should increase, and other studies have found that bird species richness increases over time, especially early on in succession (<20 years; Keller, Richmond and Smith, 2003; Dunn, 2004; Acevedo-Charry and Aide, 2019). The stability of bird species richness and evenness through succession in this study may be because the basic structural characteristics and functions of a forest often recover quickly and can be sustained with few tree species (Finegan, 1996; Kennard, 2002; Chazdon, 2003; Lebrija-Trejos *et al.*, 2008; Derroire *et al.*, 2016). Thus, the trees that are already established in cacao agroforests could be maintaining core structural features of a forest such as providing shade and shelter through the early stages of succession. The maintenance of forest structure in cacao agroforests and young secondary forests, including the presence of epiphytic plants, can support invertebrate abundance and diversity as well (Díaz *et al.*, 2012; Mottl *et al.*, 2019). This could provide an ample food source for insectivorous birds. Many of the crop trees in cacao agroforests and secondary forests regenerating from agroforestry are fruiting trees, which provide a food source for frugivorous birds. Furthermore, all the sites in this study were situated within a forest matrix consisting of many different forest types. Research indicates that highly mobile animals tend to recover more quickly than other taxa following disturbance (Barlow et al., 2007; Chazdon, 2014; Dunn, 2004b). Birds can easily move between forest patches, and other studies have found that cacao agroforests can act as habitat corridors for birds in fragmented landscapes, especially when there is a diverse array of native shade trees (Clough *et al.*, 2009; Cabral, Faria and Morante-Filho, 2021).

There was likewise no significant change in epiphyte alpha-diversity over succession. Other studies have found that epiphyte diversity is higher in older forests across epiphytic taxa, with the exception of vine and liana species richness which are commonly higher in secondary forests than in primary forests (Dewalt, Schnitzer and Denslow, 2000; Martin, Sherman and Fahey, 2004; Chazdon, 2008; Ellis, 2012; Martin, Newton and Bullock, 2013). Some of the change in epiphyte diversity may have been missed in this study because lichens were identified as morpho-species rather than species. It could also be that, unlike other forms of land conversion, the residual shade trees and crop standing trees in actively cultivated agroforests provide space for epiphytes to grow. Many cacao farmers remove lianas and vines from the cacao trees to improve crop yields (Bekele, 2004; NATT, 2018), but most lichens and bryophytes (slow-spreading taxa) are left untouched. In this study there were larger epiphytes on the cacao trees despite this management, including small vines such as *Peperomia rotundifolia* and *Monstera dubai*, the orchid *Polystachya concreta,* and resurrection ferns (*Pleopeltis polypodioides*).

Beta-diversity

There was significant turnover in tree, ground vegetation, and bird species composition over time. Tree composition changed both with age difference and environmental distance between sites which suggests that tree composition is a product of both the location and the age of the forest. Significant compositional change in the ground vegetation and bird assemblages over time was also detected, but not with environmental distance between site pairs. It was expected that species composition would change with forest age across taxa due to stochastic events and as the relative strength of successional drivers, such as environmental conditions and competitive regimes, vary over succession driving shifts in the comparative fitness of species (West, Shugart and Botkin, 1981; Glenn-Lewin, Peet and Veblen, 1992; Lebrija-Trejos, Meave, *et al.*, 2010; Lohbeck *et al.*, 2012; Chazdon, 2014; Cequinel *et al.*, 2018; Chang and Turner, 2019). The PCoA plots (Figure 4.7) show that active agroforests and primary forests have distinct species composition in these taxa. This is in line with other studies which indicate that it can take centuries for the species composition of secondary forests to converge with that of primary forests (Finegan, 1996; Derroire *et al.*, 2016; Rozendaal *et al.*, 2019).

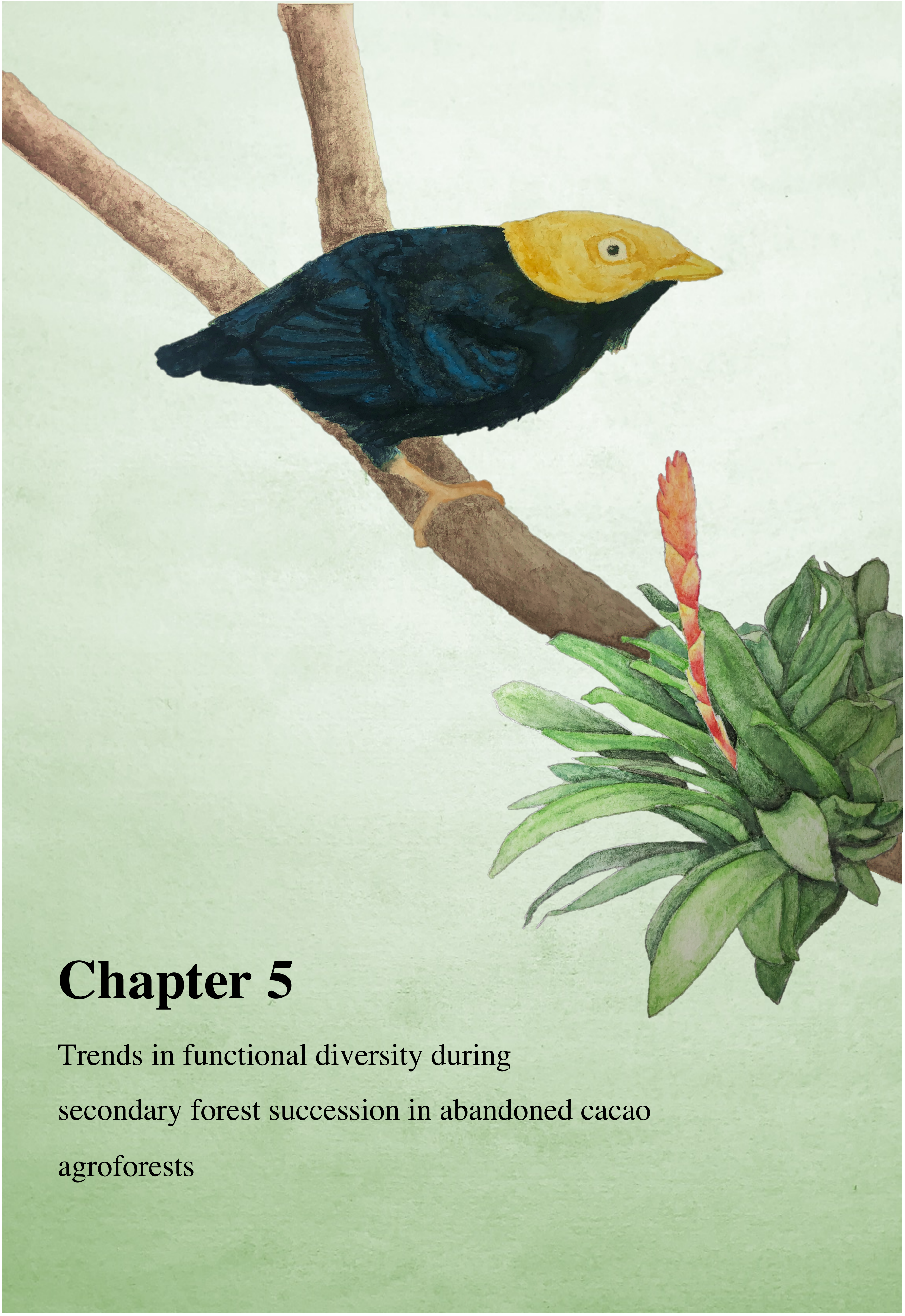
There was no significant change in epiphyte composition either over time or with environmental distance, however. Many species were present across sites regardless of forest age, especially lichen species (Figure 4.8, Appendix 4.1). Lichens and bryophytes are sensitive to air quality, atmospheric nitrogen content, humidity, and other microclimate conditions, and are often used as indicator taxa (Benzing, 1998; Sett and Kundu, 2016; Shi *et al.*, 2017). Studies have shown that some cryptogenic lichens can be tightly linked to certain tree bark properties and tree species (Ihlen, Gjerde and Sætersdal, 2001; Cleavitt, Dibble and Werier, 2009; Ellis, 2012). The consistency of lichen, bryophyte, and other epiphyte alpha and beta-diversity could be because epiphytes were surveyed within a relatively narrow band at the same height on each the tree trunk. Epiphyte populations commonly form vertical stratification patterns on trees due to environmental gradients from ground and canopy levels such as in light availability and humidity (Nieder et al., 1999; Krömer et al., 2007). Furthermore, the mature trees present in cacao agroforests can form vertical structural habitats similar to those in older forests and can survive for decades after a cacao farm is abandoned, thus allowing epiphytes to become established from the starting point of succession. The results suggests that the microclimates necessary for the epiphyte species recorded in this study were maintained throughout succession, and that the epiphytic species in these forests were robust to changes in the environment and tree composition with forest age.

Conclusion

Notwithstanding the complexity of the observed trends in biodiversity, it is clear that habitat heterogeneity created through Trinidad's history of cacao farming can support greater overall landscape-level biodiversity (gamma-diversity; Box 1.1; Chapter 3). The Northern Range of Trinidad is a patchwork landscape of different habitat types which support different species, thereby increasing the cumulative diversity of the region (Tscharntke *et al.*, 2002; Peintinger, Bergamini and Schmid, 2003; Fischer and Lindenmayer, 2005; Socolar *et al.*, 2016). The turnover in tree, bird, and ground vegetation composition between forest patches at different stages of succession contributes to the richness of the species pool and maintenance of gamma-diversity.

Furthermore, active cacao agroforests and young secondary forests sustained high levels of alpha-diversity across taxa. This suggests that disturbed and actively managed agroforests can be important, though often undervalued, reservoirs of tropical biodiversity. While cacao farming is often cited as a major driver of tropical deforestation (Vaast and Somarriba, 2014; Borda *et al.*, 2021), findings from this research and those of others suggest that sustainably managed cacao agroforests have the potential to support wildlife as well as livelihoods (Calvo and Blake, 1998; Buechley *et al.*, 2015; Rajab *et al.*, 2016; Arroyo-Rodríguez *et al.*, 2017; Young, 2017; dos Santos *et al.*, 2021; Brodbeck, Hapla and Mitloehner, 2022; Schuler *et al.*, 2022).

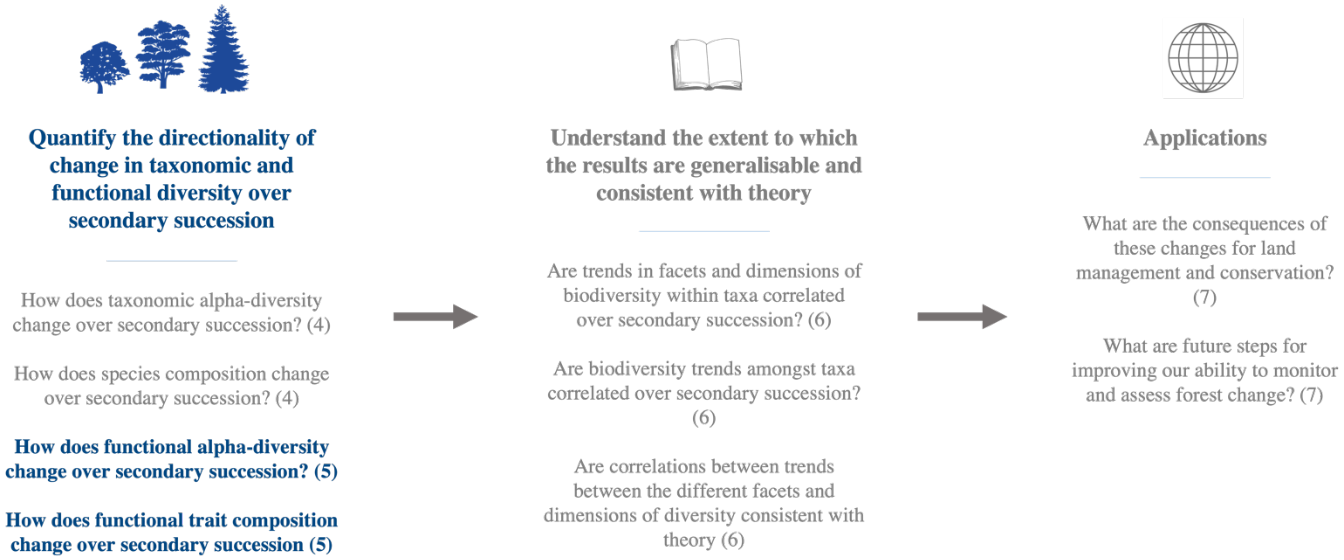
While it is essential to protect primary forests due to their ability to support diverse ecological assemblages and the slow recovery of species composition in disturbed forests, these findings highlight the value and potential of agroforests and secondary forests in sustaining biodiversity, especially in tropical regions. Agroforests and secondary forests enrich regional gamma biodiversity and provide conservation solutions that support both people and nature (Mace, 2014). These ideas will be explored further in Chapters 6 and 7.



Chapter 5

Trends in functional diversity during secondary forest succession in abandoned cacao agroforests

5.1 Introduction



Quantify the directionality of change in taxonomic and functional diversity over secondary succession

How does taxonomic alpha-diversity change over secondary succession? (4)

How does species composition change over secondary succession? (4)

How does functional alpha-diversity change over secondary succession? (5)

How does functional trait composition change over secondary succession (5)

Understand the extent to which the results are generalisable and consistent with theory

Are trends in facets and dimensions of biodiversity within taxa correlated over secondary succession? (6)

Are biodiversity trends amongst taxa correlated over secondary succession? (6)

Are correlations between trends between the different facets and dimensions of diversity consistent with theory (6)

Applications

What are the consequences of these changes for land management and conservation? (7)

What are future steps for improving our ability to monitor and assess forest change? (7)

Figure 5.1. Schematic of questions being addressed in this thesis. Questions highlighted in blue are the focus of this chapter.

Compositional turnover within ecological communities has accelerated globally, with anthropogenic changes to the environment implicated as a cause (Chapters 2 and 4). For example, turnover occurs when species shift their distribution due to changes in their environment, when species are introduced to new locations, or if a species becomes locally extinct (McKinney, 2006; Hobbs, Higgs and Harris, 2009; Dornelas *et al*., 2014; Magurran, 2016). In forests across the world, species composition is changing as more land is converted from primary forest to secondary and planted forests (Hansen *et al*., 2013; FAO and UNEP, 2020; Global Forest Watch, 2020).

As discussed in Chapter 1, forests provide many important functions and services that are beneficial to humans including providing habitat and resources for wildlife, contributing to soil formation, stabilisation and nutrient cycling, and capturing carbon (Hansen *et al*., 2013; FAO and UNEP, 2020; Cox *et al*., 2022). The maintenance of key processes and interactions within ecosystems is an indicator of ecosystem wellbeing and is essential for maintaining the services we rely on (Díaz *et al*., 2018; FAO and UNEP, 2020). The consequences of ongoing rapid changes in species composition for ecosystem functioning, however, remain unclear.

While most research has focused on taxonomic diversity, research on functional diversity has been increasing (Díaz and Cabido, 2001). Functional diversity is measured by quantifying species' functional traits (i.e. phenotypic and behavioural traits related to an ecosystem function; Chapter 2). While the links between biodiversity and ecosystem functioning are debated, functional diversity is thought to provide important insights into ecosystem functioning that taxonomic diversity alone cannot (Grime, 1997; Tilman *et al.*, 1997; Chapin *et al.*, 1998; Tilman, 1999; Loreau, 2003).

For example, taxonomic diversity indices treat all species equally, but not all species are functionally equivalent. Each have different traits which shape their interactions within an ecosystem (Díaz and Cabido, 2001; Weiher, 2011; Cadotte, 2017). While more closely-related species tend to have more similar traits, divergent and convergent evolution can cause some closely-related species to have distinct traits and some distantly-related species to share similar traits (Weiher, 2011; Schweiger *et al.*, 2018). The contributions a species makes to ecosystem functioning vary as well, depending on their relative ability to perform certain ecological roles, such as the influence of leguminous plant species on soil nutrients (Fargione et al., 2007; Cadotte, 2017).

Moreover, the functional diversity represented within a community can affect the proclivity and capacity of certain ecosystem functions (Tilman et al., 1997; Weiher, 2011; Schweiger et al., 2018). Traits which are dominant within a community commonly influence ecosystem processes the most. Accordingly, both species and functional trait composition shape ecosystem functioning. Assessing changes in functional diversity can therefore generate a deeper understanding of how ecosystems are changing over time, especially in regard to the maintenance of ecosystem functions and services.

This chapter explores how functional diversity in tree, ground vegetation, and bird assemblages change in secondary forests regenerating on abandoned cacao farms in Trinidad (Chapters 3 and 4). Functional alpha-diversity measures the range and abundance of traits expressed by the species within an assemblage, while functional beta-diversity measures changes in the composition of functional traits between assemblages (Chapter 3.3).

Empirical research on functional diversity change over secondary forest succession is limited, but it is expected that functional diversity will increase over succession, particularly in plant assemblages, based on succession theory (Chapter 2). For example, it is thought that environmental filtering limits plant functional alpha-diversity early in succession, while greater pressure from competition promotes functional alpha-diversity later in succession. In line with this, other research on tropical forest succession has found that functional diversity increases as forests accumulate species over time, and that older forests commonly have more specialist species and biotic interactions which contributes to functional diversity across taxa (Arroyo-Rodríguez *et al.*, 2017; Sayer, Bullock and Martin, 2017; Jarrett *et al.*, 2021; In temperate systems: Oksuz, Palmeirim and Correia, 2021).

Most studies show that bird and plant functional composition change through succession to include more specialist and sensitive species as species composition changes, and environmental conditions and competitive regimes shift to favour different types of species (Sayer, Bullock and Martin, 2017; Jarrett *et al.*, 2021; In temperate systems: Oksuz, Palmeirim and Correia, 2021). Theory likewise predicts that species composition will shift from being dominated by fast spreading and growing, but short-lived "pioneer" species which can tolerate harsh early-successional conditions, to slow-growing and spreading, but long-lived "climax" species which are better competitors (Dewalt, Schnitzer and Denslow, 2000; Guariguata and Ostertag, 2001; Garnier *et al.*, 2004; Dent, DeWalt and Denslow, 2013; Lohbeck, Poorter, Lebrija-Trejos, *et al.*, 2013; Lasky *et al.*, 2014; Sanaphre-Villanueva *et al.*, 2017; Craven *et al.*, 2018)

There have also been some mixed results regarding functional beta-diversity, however. While many tropical studies have supported the view that functional beta-diversity changes over succession (eg. Lohbeck *et al.*, 2012; Bhaskar, Dawson and Balvanera, 2014; Whitfeld *et al.*, 2014; In temperate systems: Purschke *et al.*, 2013), other work has revealed that functional diversity and composition are more stable than taxonomic composition (Böhnke *et al.*, 2014; Blanco *et al.*, 2021). Blanco and colleagues (2021), for example, found that mammal functional composition remained relatively stable compared to taxonomic composition over evolutionary timescales, where functional composition only changed in response to dramatic perturbations. The maintenance of functional diversity over time could result from there being enough trait overlap to buffer changes in species composition and ensure niches remain filled (Bai *et al*., 2004; Tilman, Reich and Knops, 2006; Griffin *et al*., 2009; Loreau and de Mazancourt, 2013; Hautier *et al*., 2015; Isbell *et al*., 2015). Species may also be replaced like-with-like due to existing functional structures where new species fill vacated niches (Roopnarine & Banker, 2021).

The aim of this chapter is to assess the rate and nature of functional alpha and beta-diversity change over c. 100 years of tropical secondary forest succession following cacao farming (Figure 5.1). I assess changes in functional richness, evenness, and divergence (alpha-diversity), as well as changes in functional turnover. The chapter also asks how individual traits change with forest age for each taxon, and whether this fits with expectations of a shift from pioneer to climax-type species. To do this, changes in the abundance of relevant traits including plant dispersal syndromes and bird trophic guilds are assessed over succession.

5.2 Alpha-diversity

This research was conducted in 29 forest sites in Trinidad including active cacao agroforests, secondary forests regenerating from abandoned cacao agroforests, and primary forests (Chapter 3). Trees, ground vegetation, epiphytes, and birds were surveyed in these sites, though epiphytes were excluded from functional diversity analyses as lichens were assigned morphospecies and so do not feature in this chapter.

Functional alpha-diversity was quantified using the metrics FRic for functional richness, FEve for functional evenness, and FDiv for functional divergence (Chapter 3.3; Villéger, Mason and Mouillot, 2008). FRic is a measure of the amount of space taken up by the species of a given assemblage in multi-dimensional trait space. FEve is a measure of both how evenly species are distributed in multi-dimensional trait space, and how even species' relative abundances are. FDiv quantifies the number and abundances of species at the edges of trait space with extreme trait values, relative to those towards the centre of trait space (Chapter 3.3; Figure 3.4).

The plant traits used in these analyses for the tree and ground vegetation assemblages were: maximum height at maturity (m), average leaf length (cm), primary dispersal mode, and dominant flower colour (Appendix 5.1; Trait data compiled from: Hendrix and Marquis, 1983; Little and Skolmen, 1989; Anderson, 1990; Sheridan, 1994; Scariot, Lleras and Hay, 1995; Milliken and Ratter, 1998; Quesnel and Farrell, 2000; Hewitt, 2005; Plowman, 2012; Ramirez, Jhala and Singh, 2012; Kuete, 2014; Kachhiyapatel, Patel and Rajput, 2016; Aximoff, Soares and Bernadello, 2020; Kattge *et al.*, 2020; CABI, 2021; EOL, 2021; Fern, 2021; GBIF.org, 2021; Kew, 2021; NC State University, 2021; Nparks, 2021; Piertro and Beltramini, 2021; Smithsonian, 2021; University of Florida, 2021). The bird traits used were: primary trophic guild, body length (cm), generation time (years), average number of eggs per clutch, sexual dimorphism, forest dependence, and the forest strata (ground, canopy, aerial, etc) which a species predominantly occupies (trait data compiled from: ffrench, 1973; Kenefick, Restall and Hayes, 2013; Wilman *et al.*, 2014; Acevedo-Charry and Aide, 2019; BirdLife International, 2020).

For all the functional diversity analyses, functional trait space quality was tested using the function qual_funct_space in R statistical software (Villéger, Mason and Mouillot, 2008; R Core Team, 2021). This was used to select the optimal number of dimensions for the functional diversity analyses of each taxon. The functional diversity analyses require there to be more species than functional traits in order to generate a minimum convex hull (Chapter 3; FRic and FDiv; Villéger, Mason and Mouillot, 2008). As such, four active cacao agroforest sites were removed from the tree functional diversity analyses because there were too few tree species (BSC, ERE, OA, and SASC; < 3 species).

As with the taxonomic diversity analyses presented in Chapter 4, GLM linear regressions were used to test whether there were significant changes in functional alpha-diversity over succession for birds, trees, and ground vegetation. These analyses were conducted both with and without primary forest sites to ensure these sites did not have undue influence over the results of the regressions (Appendix 4.2). Environmental variables (altitude, distance to settlements, and annual average precipitation; Chapter 3) were also tested in these analyses to control for their effects. Environmental variables were included if doing so increased AIC scores. Lastly, the regressions were checked for significant break points to assess whether the rate of alpha-diversity change varied over succession (segmented package in R statistical software; Muggeo, 2017; R Core Team, 2021).

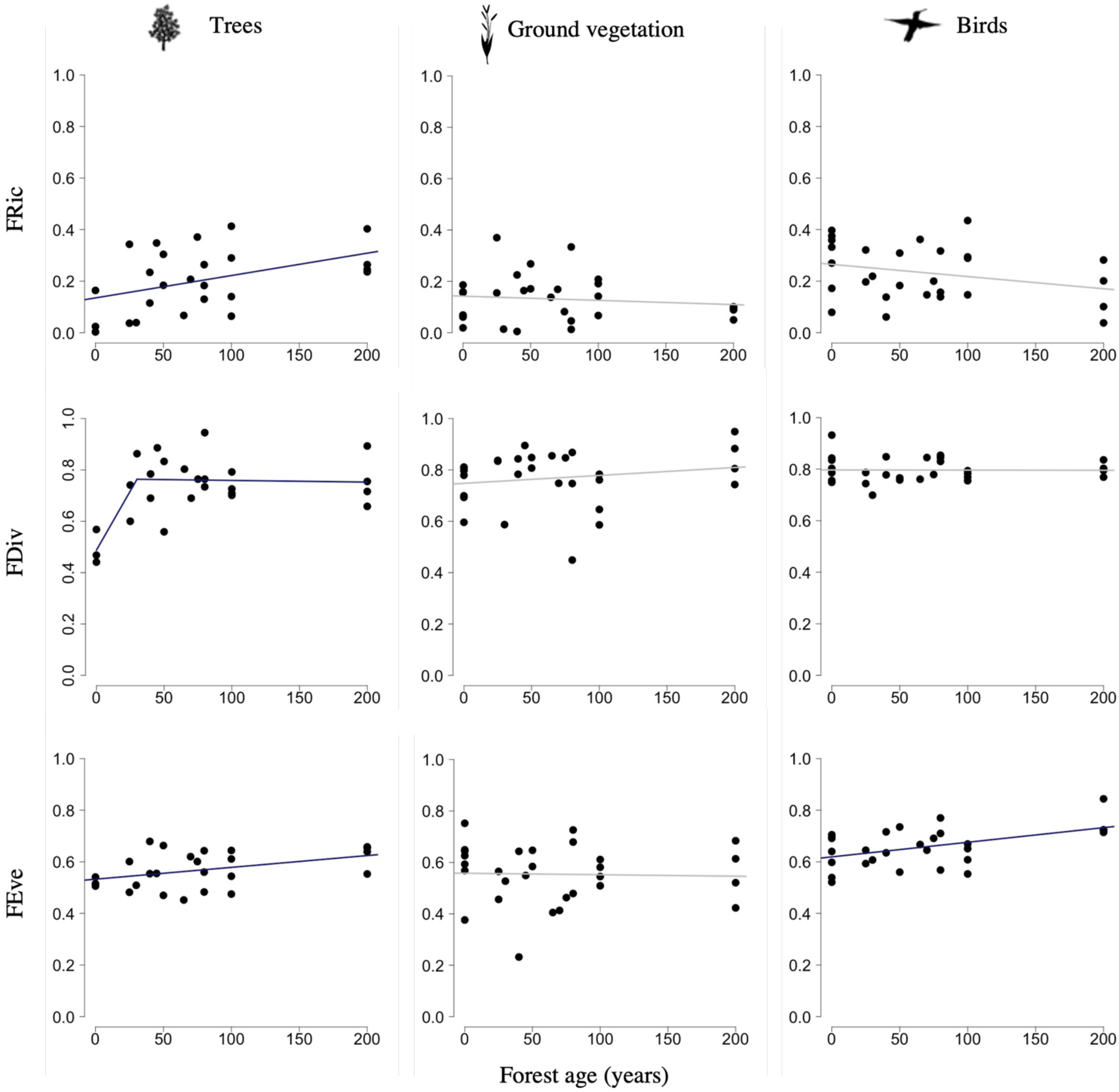


Figure 5.2 Functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve) with forest age in tree, ground vegetation and bird assemblages. Blue lines indicate statistically significant trends (regression information is detailed in Table 5.1).

The results of these analyses found that tree functional richness (p=0.03), divergence (p=0.004), and evenness all increased significantly with forest age (p=0.04; Table 5.1; Figure 5.2). There was a significant break point in tree functional divergence, where the rate at which FDiv increased was greater in the early stages of succession (<30 years). Contrary to this, there was no significant change in ground vegetation alpha-diversity over time (Table 5.1). Lastly, bird functional evenness increased significantly over succession (p=0.01), but there was no significant change in bird functional richness or divergence (Table 5.1). There were no other significant breakpoints in ground vegetation or bird functional alpha-diversity regressions, and the environmental variables did not improve AIC scores for any of the taxa.

Table 5.1 GLM regression results for functional alpha-diversity measures with forest age. Sites is the number of sites (n) included in each analysis.

Taxon	Model	Breakpoints	df	Sites	adj R^2	F value	P value
Trees	FRic ~ Forest age	—	1 on 23	25	0.16	5.50	0.028
	FDiv ~ Forest age	30 years	1 on 23	25	0.08	3.06	0.004
	FEve ~ Forest age	—	1 on 23	25	0.13	4.57	0.043
Vegetation	FRic ~ Forest age	—	1 on 27	29	-0.02	0.36	0.554
	FDiv ~ Forest age	—	1 on 27	29	<0.01	0.89	0.353
	FEve ~ Forest age	—	1 on 27	29	-0.04	0.03	0.868
Birds	FRic ~ Forest age	—	1 on 26	28	0.04	2.27	0.144
	FDiv ~ Forest age	—	1 on 26	28	-0.04	<0.01	0.962
	FEve ~ Forest age	—	1 on 26	28	0.21	8.22	0.008

5.3 Beta-diversity

Functional beta-diversity was quantified as functional turnover using the methods outlined by Villéger, Grenouillet, and Brosse (Chapter 3; Villéger, Grenouillet and Brosse, 2013). Functional turnover is a measure of dissimilarity in functional trait composition between site pairs (the degree to which two assemblages do not overlap in functional trait space; Villéger, Grenouillet and Brosse, 2013).

Also in line with the taxonomic diversity analyses presented in Chapter 4, 0.5 quantile regressions were used to relate functional turnover to age difference and environmental distance in pairwise site comparisons within the tree, ground vegetation, and bird assemblages (Koenker, 2013). Age difference is the difference in time since abandonment between site pairs, where actively cultivated agroforests were given an age of zero, and primary forests were given a conservative age estimate of 200 years old. Environmental

Quantile regressions were again chosen as they are more robust to outliers and heteroscedasticity than standard linear regressions (Cade and Noon, 2003; John, 2015)

The results of these quantile regressions showed that tree functional trait composition changed significantly with both increasing age difference (p=0.05; Table 5.2) and increasing environmental distance between sites (p=0.02). There was likewise significant turnover in ground vegetation functional trait composition with age difference (P<0.001) and environmental distance between sites (p=0.03). There was no significant change in bird functional trait composition with either age difference or environmental distance, however (Table 5.2).

Table 5.2 Results from 0.5 quantile regression of functional turnover (FTurnover) with age difference and environmental distance between site pairs. P-values are given for age difference (A) and for environmental distance (E).

Taxon	**Model**	**df**	**Sites**	**adj R^2**	**F value**	**P value A**	**P value E**
Trees	FTurnover ~ Age difference + Environmental distance	2 on 273	25	0.02	3.62	0.047	0.008
Vegetation	FTurnover ~ Age difference + Environmental distance	2 on 375	29	0.13	30.09	<0.001	0.031
Birds	FTurnover ~ Age difference + Environmental distance	2 on 375	28	0.05	10.71	0.272	0.137

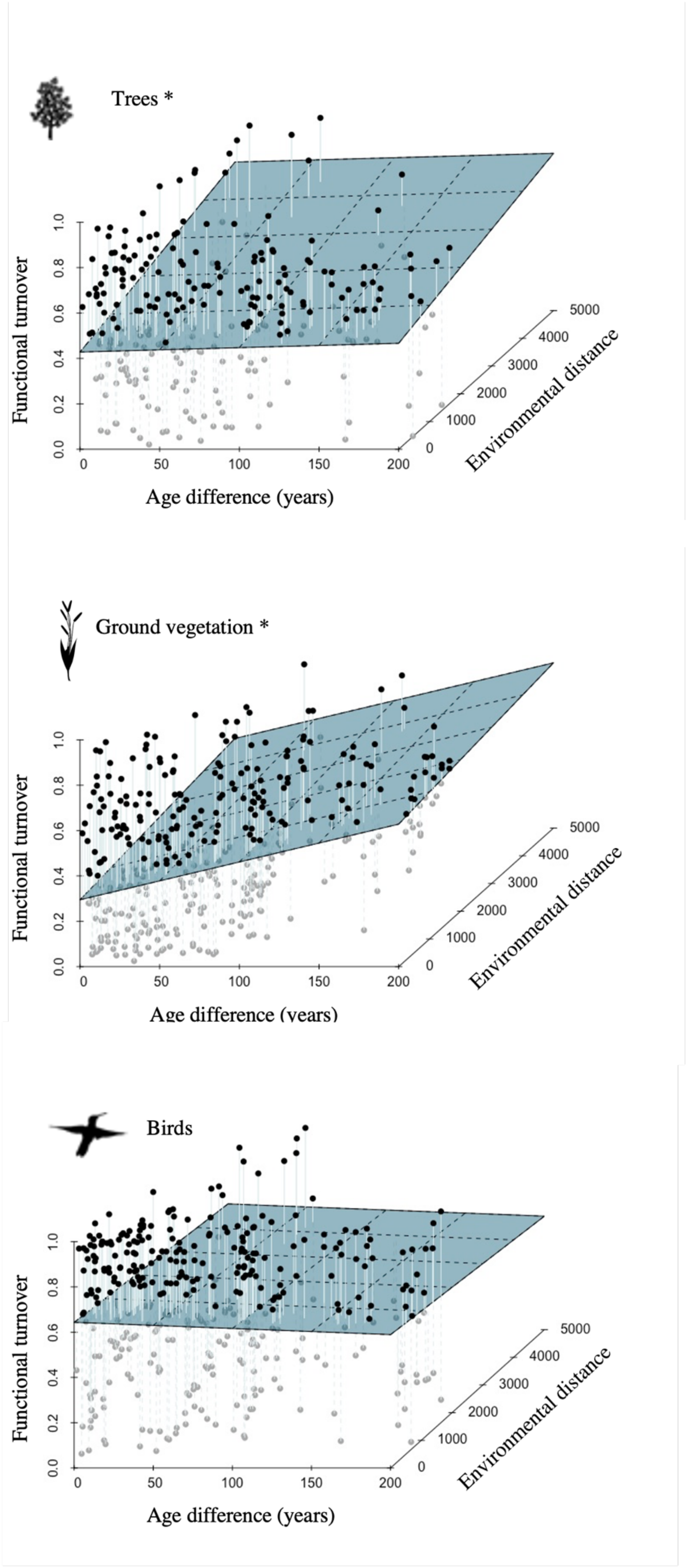
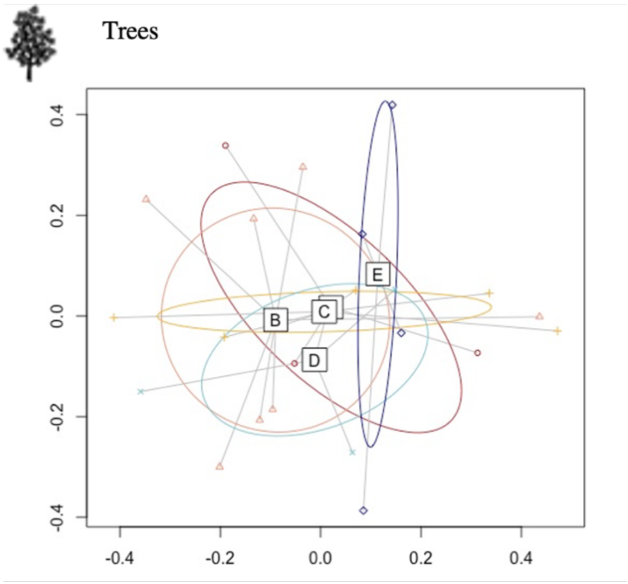
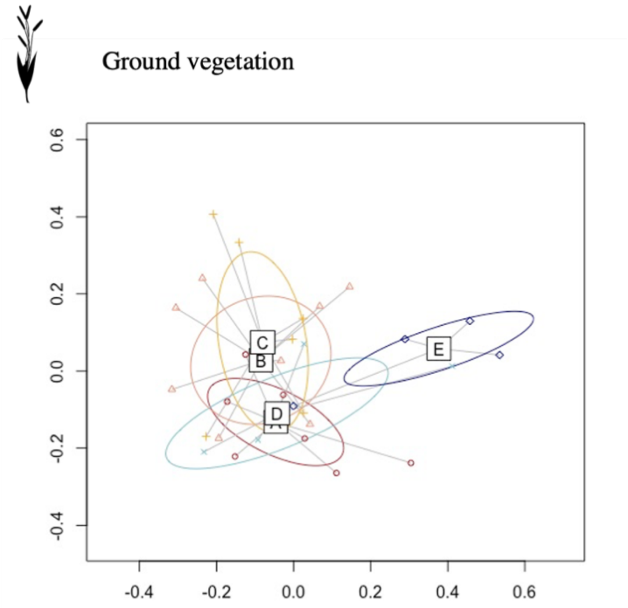


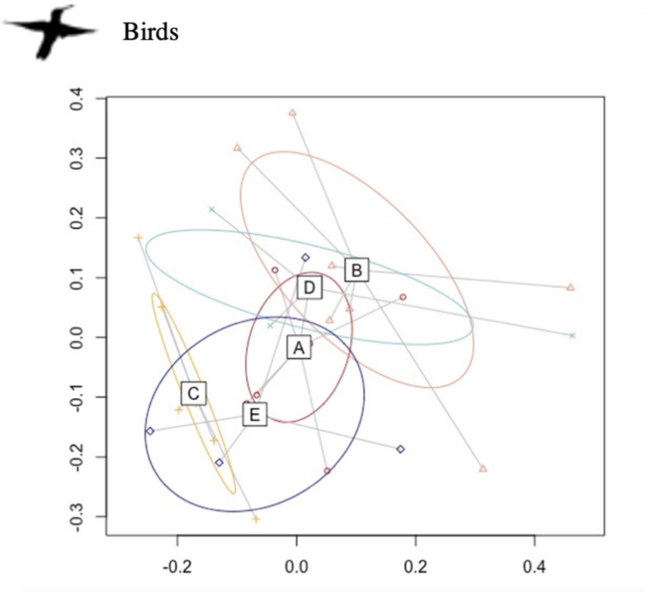
Figure 5.3 Functional trait turnover with age difference and environmental distance between site pairs. Age difference is the pairwise difference in age between sites, and environmental distance is the pairwise distance between sites in Euclidean space built using the environmental factors: annual precipitation, average site altitude, distance to the nearest settlement and average land gradient. Asterix indicate statistically significant change in functional trait composition with forest age from a 0.5 quantile regression.



Trees



Ground vegetation



Birds

Figure 5.4 Functional trait compositional turnover between age groups. PCoA of functional composition between sites based on Functional Turnover (Villéger, Grenouillet and Brosse, 2013). X and Y axes are the first and second PCoA axes respectively. A (red) are active sites, B (pink) are 25–50 yo secondary forest sites, C (yellow) are 60–80 yo secondary forests, D (light blue) are >100 yo secondary forests, and E (dark blue) are primary forest sites.

Lastly, PCoA was used to visualise age groupings in multidimensional functional trait space (PCoA function in the ape package in R; Fig 5.4; Paradis *et al.*, 2022). As with taxonomic diversity, primary forest sites were slightly further from the other sites across taxa which suggests the functional composition of these assemblages was more distinct from active cacao agroforests and secondary forests, especially for ground vegetation. Overall, there was a high degree of compositional overlap between the active cacao agroforests and secondary forests.

5.4 Functional trait composition

Trends in ecologically meaningful functional traits were individually assessed to illustrate change in functional composition in greater detail.

Trees

Locally weight least squares (loess) regressions were used to examine changes in the relative abundance of dispersal methods within plant assemblages over succession. Loess is a non-parametric regression which creates a smoothed line through the data points (Cleveland and Devlin, 1988). Loess plots were chosen as they can illustrate more nuanced patterns of change compared to standard linear regressions.

First, each plant species was categorised according to its predominant mode of seed dispersal: anemochory (wind), hydrochory (water), autochory (falling or explosive dispersal), and zoochory (animal dispersal; Data on dispersal syndromes from TRY database; Kattge *et al.*, 2020). The proportion of individual trees which utilise each of these four dispersal syndromes was quantified and illustrated using a loess plot (geom_smooth function in the ggplot2 package in R; Wickham *et al.*, 2021). The results showed that, while there is little change in abiotically dispersed tree species, the proportion of biotically dispersed trees decreased with forest age (Figure 5.5). The proportion of anemochorous trees increased slightly over succession.

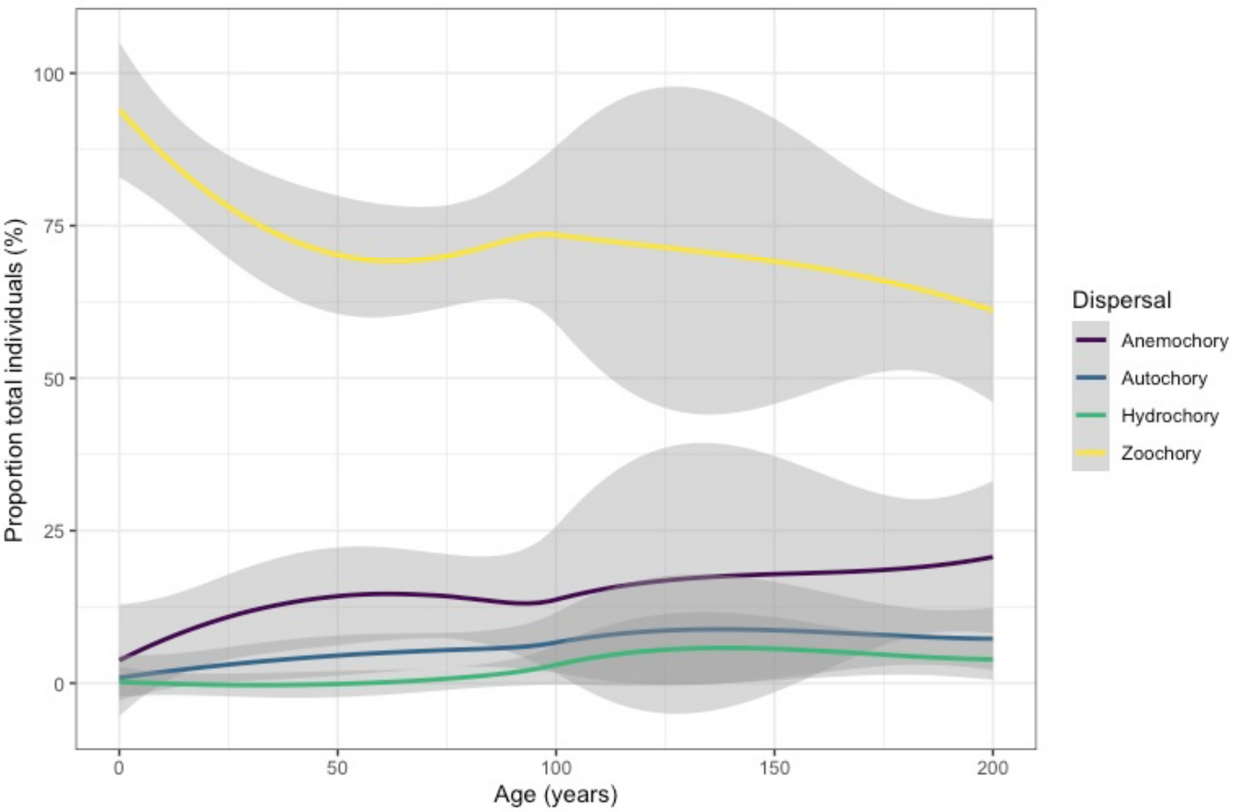


Figure 5.5 Loess lines representing the relative proportion of anemochorous (purple), autochorous (blue), hydrochorous (green) and zoochorous (yellow) trees with forest age with confidence intervals shown in grey.

Loess regressions were further used to assess changes in the dominant colour of flowers within tree assemblages. The proportion of trees with white flowers was higher in active cacao agroforests and young secondary forests (Figure 5.6), while older forests had more trees with red, pink, and green flowers compared to the young forests. Yellow flowers were common in young secondary forests and primary forests.

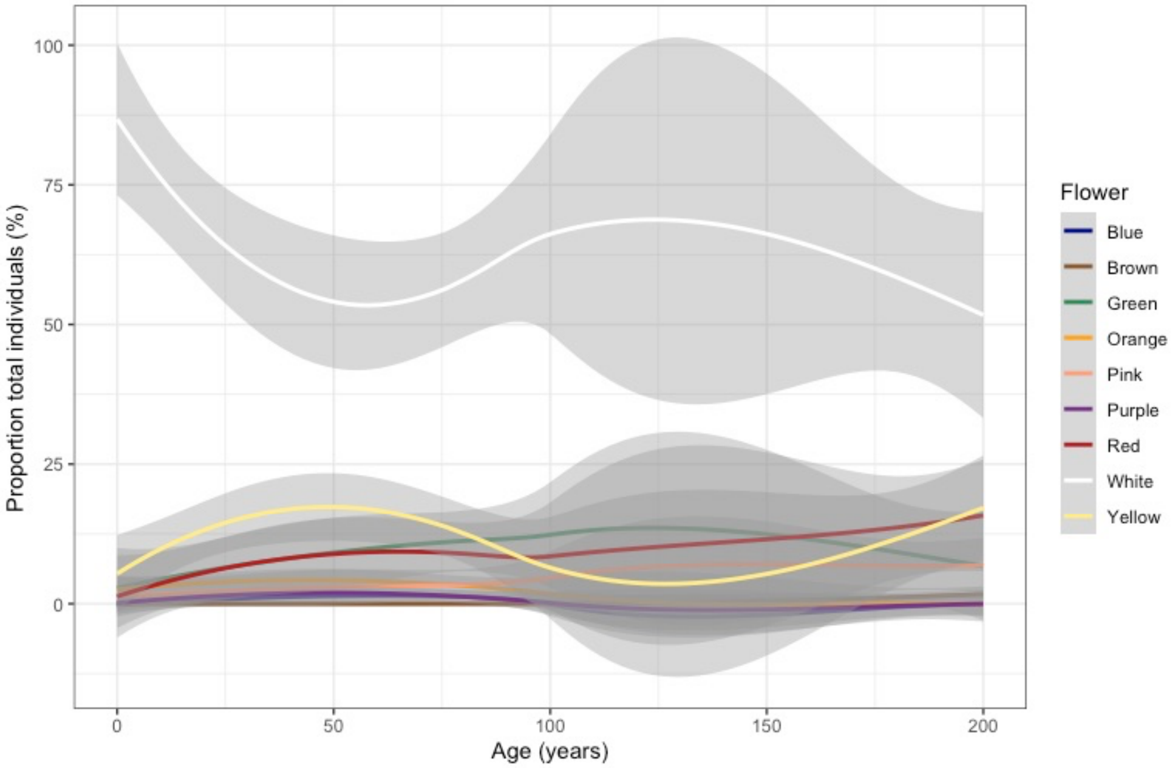


Figure 5.6 Tree dominant flower colour with forest age. The loess lines represent the proportion of individual trees which have flowers of a given colour (lines are coloured according to flower colour) with confidence intervals shown in grey.

Ground vegetation

As with trees, the proportions of anemochorous, autochorous, hydrochorous, and zoochorous ground plants were illustrated using loess regrerssions (Figure 5.7). In line with the results from tree assemblages, the proportion of biotically dispersed ground plants decreased with forest age while the proportion of wind dispersed ground plants increased. There was little change in the proportion of hydrochorous or autochorous ground plants over succession.

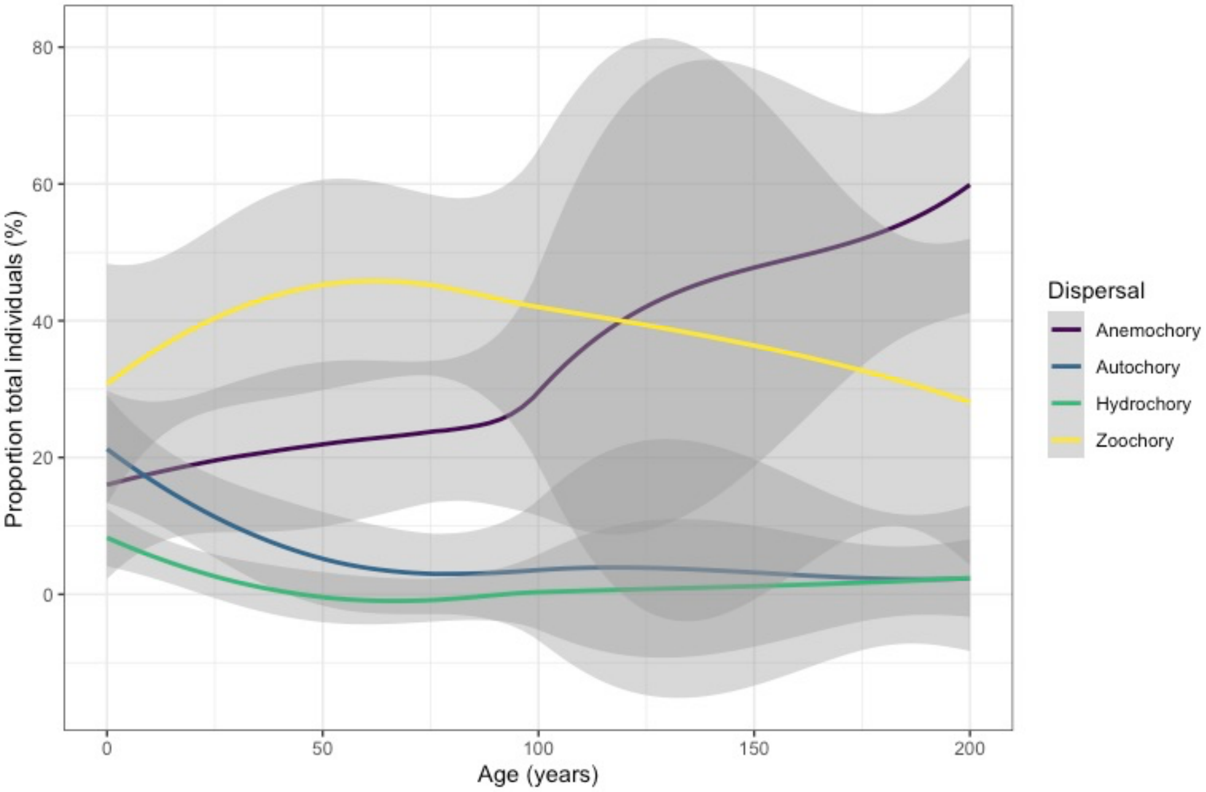


Figure 5.7 Loess lines represent the proportion of anemochorous (purple), autochorous (blue), hydrochorous (green) and zoochorous (yellow) ground plants with forest age with confidence intervals shown in grey.

Unlike the trees, there was a high proportion of red-flowered plants in young secondary forests (Figure 5.8). The proportion of ground plants with white flowers was highest in actively managed agroforests and old secondary forests. There was also a higher proportion of green-flowered plants in active agroforests. The proportion of flowerless plants increased with forest age.

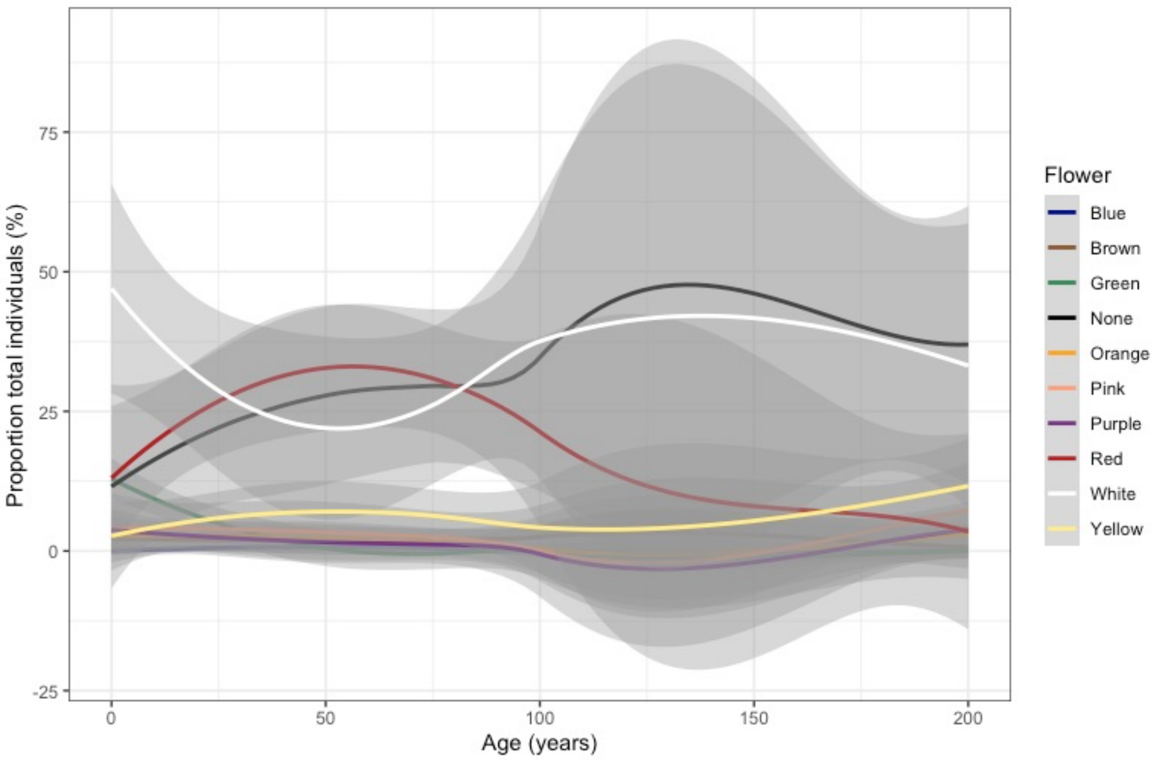


Figure 5.8 Ground vegetation dominant flower colour with forest age. The loess lines represent the proportion of individual trees which have flowers of a given colour (lines are coloured according to flower colour) with confidence intervals shown in grey. Flowerless plants are shown in black.

Birds

Linear regressions were used to test for changes in the proportion of bird trophic guilds over succession: granivores (seeds, nuts, and dry fruits), insectivores (invertebrates), omnivores (generalist diet including animal and plant foods), predators and scavengers (meat and carrion), and pollinators and seed dispersers (fruits and nectar; information from Acevedo-Charry & Aide, 2019; Wilman et al., 2014). For these analyses, the proportional abundance of each trophic guild was calculated as the percentage of the number of bird species in a given guild out of the total bird population for each site. The results showed that there was a significant decrease in the proportion of omnivorous birds (p=0.02), and a significant increase in the proportion of insectivorous birds with forest age (p=0.01; Figure 5.9; Table 5.3). There was no significant change in the proportion of predators and scavengers, pollinators and dispersers, or granivorous birds over succession (Table 5.3).

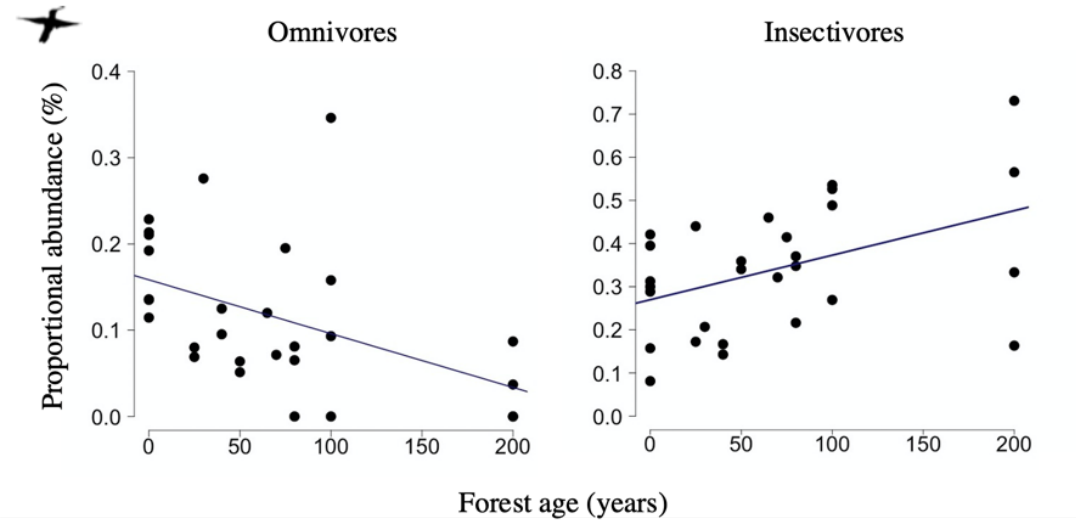


Figure 5.9 Change in the relative abundance of bird trophic guilds over time. Figures show the proportional abundance of all species in a given trophic group (individuals summed) out of the total number of individuals surveyed for each site. Blue lines indicate a significant trend.

Table 5.3 GLM regression results for the proportion of birds assigned to different trophic guilds with forest age.

Model	df	adj R^2	F value	P value
Insectivores (%) ~ Forest age	1 on 26	0.19	7.30	0.01
Omnivores (%) ~ Forest age	1 on 26	0.17	6.46	0.02
Predators & scavengers (%) ~ Forest age	1 on 26	-0.04	0.02	0.89
Pollinators & dispersers (%) ~ Forest age	1 on 26	-0.02	0.46	0.5
Granivores (%) ~ Forest age	1 on 26	-0.02	0.46	0.5

Lastly, GLMs were further used to test for changes in the proportion of birds with high, medium, and low forest dependence using trait information from BirdLife International (BirdLife International, 2020). The results from these regressions showed that there was a significant increase in the proportion of highly forest dependant birds with forest age ($p<0.01$; Figure 5.10; Table 5.4). There was no significant change, however, in the proportion of birds with medium and low forest dependence (Table 5.4). Further analyses on changes in individual bird traits are listed in Appendix 5.2.

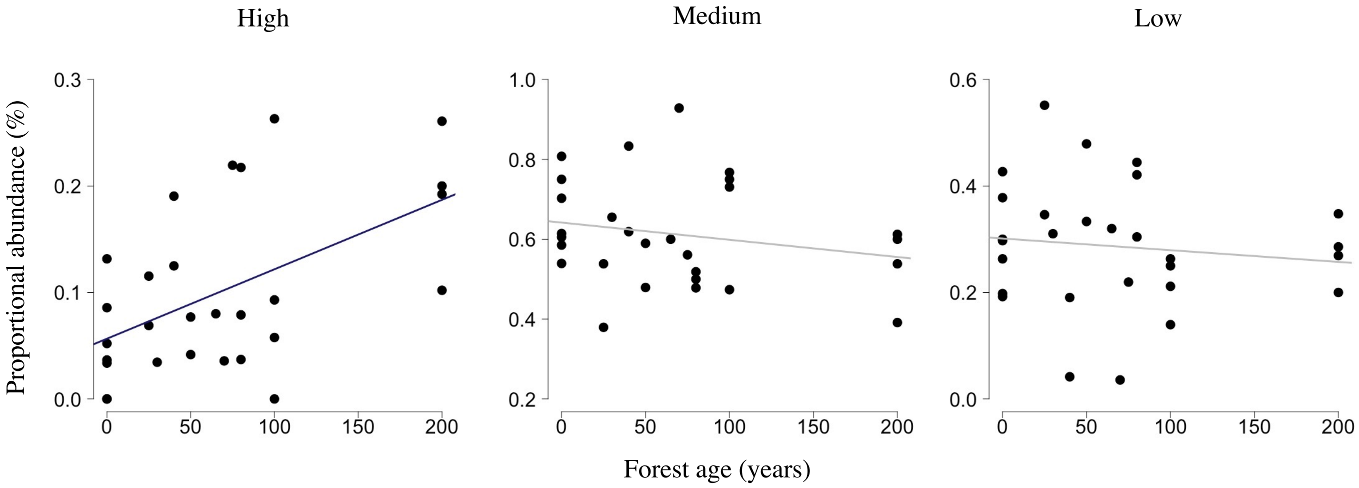


Figure 5.10 Change in the proportion of birds with high, medium, and low forest dependence over time. Figures show the proportional abundance of all forest-dependent species (individuals summed) out of the total number of individuals surveyed for each site. Blue lines indicate a significant trend.

Table 5.4 GLM regression results for the proportion of birds with high, medium, and low forest dependence with forest age.

Model	df	adj R^2	F value	P value
High dependence (%) ~ Forest age	1 on 26	0.26	10.39	<0.001
Medium dependence (%) ~ Forest age	1 on 26	0.01	1.23	0.28
Low dependence (%) ~ Forest age	1 on 26	-0.02	0.38	0.54

5.5 Discussion

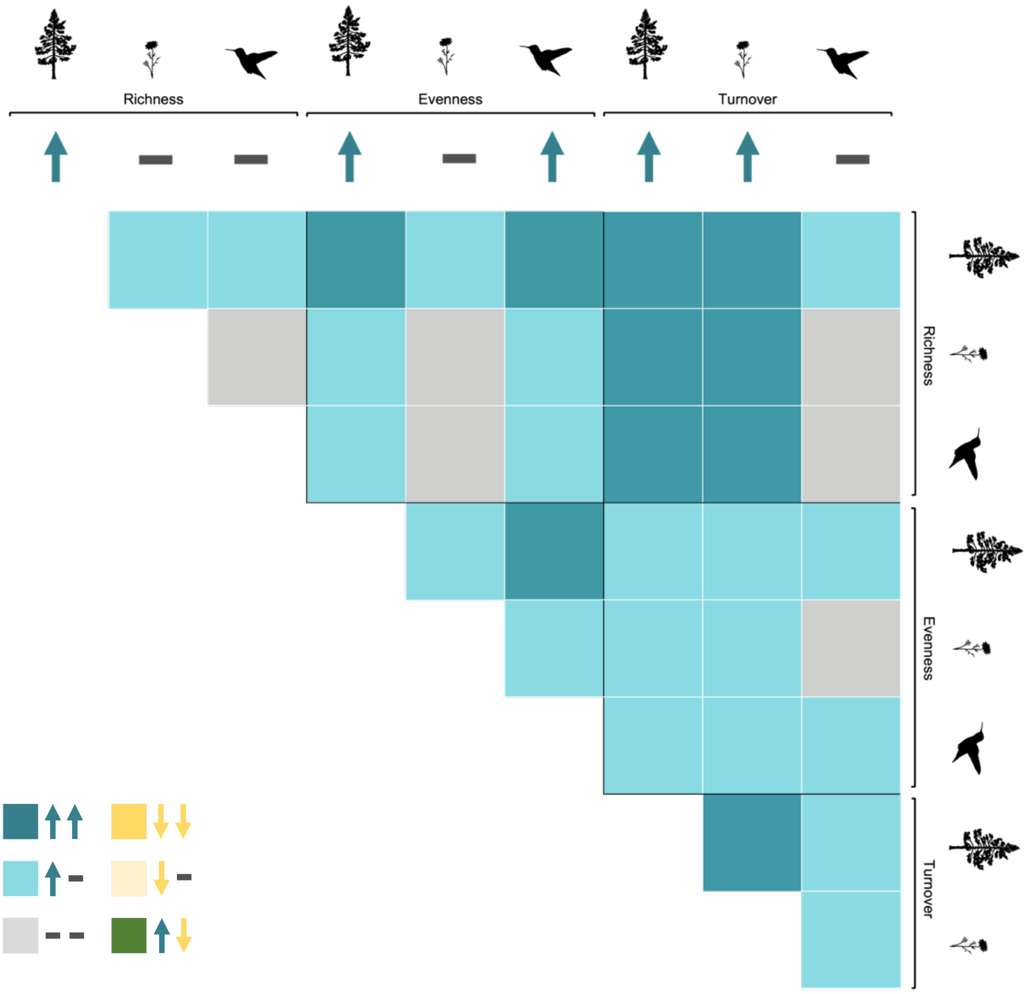


Figure 5.12 Summary figure of the functional diversity results. Upward arrows (dark blue) indicate a positive trend with forest age. Grey dashes indicate no significant change in the diversity measure over succession. The coloured grid indicates the relationship between different taxa and aspects of biodiversity. Dark blue indicates a strong positive relationship. Light blue squares indicate conflicting trends with one of the pair increasing and one showing no change. Grey squares indicate that the taxon and aspects of biodiversity being compared both did not change over succession.

There was a significant increase in tree functional alpha-diversity, and in bird functional evenness with forest age. Tree functional divergence primarily increased within the first 30 years of succession. There was no significant change, however in bird functional richness or divergence, nor in ground vegetation alpha-diversity over time.

As for beta-diversity, there was significant turnover in tree and ground vegetation functional trait composition with increasing age difference and environmental distance between sites. The proportion of zoochorous plants decreased over succession in both the tree and ground vegetation assemblages. The proportion of anemochorous individuals increased in the ground-vegetation layer. Most of the trees surveyed in actively cultivated agroforests and young secondary forests had white flowers while the distribution of flower colours was more even in secondary and primary forest. The proportion of flowerless plants in the ground vegetation layer was higher in secondary and primary forests compared to active cacao agroforests.

In contrast, there was no significant change in bird functional trait composition with either age difference or environmental distance between sites. There was a significant decrease in omnivorous birds, and a significant increase in insectivorous birds with forest age. There was also a significant increase in the proportion of highly forest dependant birds. There was overall little change in bird body mass, eggs per clutch or generation time with forest age, however.

Trees and ground vegetation

The significant increase in tree functional alpha-diversity with forest age was generally in line with expectations based on succession theory and empirical research (Chapter 2). Firstly, succession theory suggests that taxonomic and functional diversity should be positively linked, depending on the degree of functional redundancy within an assemblage (Chapter 2.2). It is thought that the more species there are in an assemblage, the more likely there are to be species with complementary traits (Huston, 1997; Mayfield *et al.*, 2010), and that greater functional complementarity within an assemblage facilitates greater coexistence between species (Brown and Lugo, 1990b; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Lohbeck *et al.*, 2012; Chazdon, 2014).

Results from taxonomic diversity analyses in Chapter 4 found that tree species richness and evenness increased significantly over time, especially early on in succession. Functional alpha-diversity increased with forest age as well, with functional divergence increasing mostly withing the first 30 years of succession. While results from other research have yielded mixed results (eg. Böhnke *et al.*, 2014), some studies have also found that species and functional alpha-diversity change similarly over time (eg. Craven *et al.*, 2018; Chapter 2.3).

The increase in functional alpha-diversity over succession also supports the concept of temporal shifts in the relative strength of deterministic processes. These results support a model of succession where environmental filtering may limit functional diversity early on, while increasing pressure from competition may promote greater functional diversity over time (Letcher, 2010; Lohbeck, Poorter, Lebrija-Trejos, *et al.*, 2013; Blanchard *et al.*, 2021).

In contrast, there was no significant change ground vegetation functional alpha-diversity with forest age, despite there being a significant decrease in taxonomic alpha-diversity (Chapter 4). This can occur when there is sufficient functional redundancy (species with similar traits) within an assemblage to buffer against declines in taxonomic diversity, where functions can be supported even without all the species in an assemblage present (Guariguata and Ostertag, 2001; Liu *et al.*, 2017).

The decrease in ground vegetation taxonomic alpha-diversity and increase in shade-tolerant species abundances over succession suggests that there is strong pressure from environmental filtering later in more mature forests due to limited light availability (Chapter 4; Laska, 1997; Lebrija-Trejos *et al.*, 2010; dos Santos-Junior *et al.*, 2017). Contrary to this, however, the results from the ground vegetation functional diversity analyses are more in line with the tree assemblage in supporting a theoretical model of succession where environmental filtering declines and competition increases though time (Letcher, 2010; Lohbeck, Poorter, Lebrija-Trejos, *et al.*, 2013; Blanchard *et al.*, 2021). There may be greater pressure from competition later in succession for ground vegetation as well if declines are occurring primarily among functionally redundant species and there is comparatively greater functional complementarity in older forests.

Furthermore, there was significant turnover in tree and ground vegetation composition over time and over environmental distance. This suggests that plant functional trait composition is a product of both successional processes and the local environment. PCoA plots illustrated that primary forest sites had more unique functional trait compositions across taxa compared to the agroforest and secondary forest sites. These results indicate that, like species composition, functional trait composition can take over a century to converge with that of primary forest. Other studies have similarly found that plant functional trait composition changes throughout succession (Lohbeck *et al.*, 2012; Böhnke *et al.*, 2014; Muscarella *et al.*, 2016; Sanaphre-Villanueva *et al.*, 2016; Craven *et al.*, 2018).

The proportion of zoochorous plants declined over succession while the proportion of anemochorous plants increased, especially in the ground vegetation layer. This is contrary to expectation as zoochorous plants tend to be more specialist and sensitive species common to older forests compared to abiotically-dispersed plants, which are usually early colonisers (Chapter 2; Guariguata and Ostertag, 2001; Sanaphre-Villanueva *et al.*, 2017). Other studies have found that animals are important seed dispersers that can facilitate secondary succession and that the proportion of zoochorous species increases over time (Parrotta, 1995; Guariguata and Ostertag, 2001; Muñiz-Castro, Williams-Linera and Martínez-Ramos, 2012; Sanaphre-Villanueva *et al.*, 2017).

This result could be because the trees planted in cacao agroforests are usually fruiting trees with biotic dispersal syndromes (Chapter 4). The sapling composition in the understory vegetation was similar to the tree composition of the surrounding forest in this study, and other studies show that standing trees act as direct seed sources (Lambin *et al.*, 2001; Mora *et al.*, 2015). Thus, since the tree assemblage included more abiotically dispersed species in older forests, the sapling community likely included more abiotically dispersed individuals as well. Furthermore, abiotically dispersed species such as ferns and mosses dominated the understory of older forests which could further drive the patterns of understory vegetation dispersal modes found in this study (Chapter 4).

These patterns of compositional change could also explain patterns of floral diversity and composition in the plant assemblages. Cacao trees have predominantly white flowers, as do some of the other crop trees found in cacao agroforests such as *Citrus sinensis* and *C. paradisi*. Therefore, the high proportion of trees with white flowers is likely due to there being a high proportion of these crop trees in cacao agroforests. As tree composition changes, flower colour diversity increases.

Likewise, secondary forests appeared to have greater ground vegetation floral diversity compared to active agroforests and primary forests. The ground vegetation was actively suppressed in the agroforests surveyed for this research, which likely contributed to these patterns. The increase in flowerless plants, including ferns and bryophytes, over succession is also reflected in these results (Chapter 4).

Birds

Apart from functional evenness, bird functional alpha and beta-diversity changed little with forest age. This is counter to expectation from theory, which predicts that bird functional diversity should increase with plant diversity (Chapter 2). Plants, and especially trees, provide habitat, food, and resources for other animals (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Weiher, 2011). Greater plant diversity is thought to increase the diversity of these resources (Hooper *et al.*, 2000; Waldrop *et al.*, 2006; Sobek *et al.*, 2009; Haddad *et al.*, 2011; Tedersoo *et al.*, 2016; Brockerhoff *et al.*, 2017), and thus should facilitate greater species and functional diversity in other taxa. Bird diversity should also positively affect plant diversity, for example, as a more varied array of seed dispersers may increase seed rain diversity (Gallagher, 2013; Schleuning, Fründ and García, 2014; Tedersoo *et al.*, 2016; Rolo, Olivier and van Aarde, 2017; Gardner *et al.*, 2019). Environmental filtering may also play a role in limiting the types of birds can which move through and utilise harsher early-successional habitats.

While other research on bird functional diversity over succession has produced varied results, some have similarly found that bird functional alpha-diversity remains consistent over succession (Sayer, Bullock and Martin, 2017; Rocha *et al.*, 2019; Lee *et al.*, 2020; Borges *et al.*, 2021; Jarrett *et al.*, 2021). Other studies have found that bird diversity and composition are able to recover more quickly as they are highly mobile animals (Barlow et al., 2007; Chazdon, 2014; Dunn, 2004b), and that they are more strongly influenced by habitat connectivity and condition at larger spatial scales (Lehmkuhl and Ruggiero, 1991; Brotons and Herrando, 2001; Rey-Benayas, Galván and Carrascal, 2010). All the sites were situated within a forested matrix in this study, and the lack of change in bird diversity could therefore be due to the landscape-level forest cover and habitat connectivity in the Northern Range.

Furthermore, the lack of change in bird functional alpha-diversity could again be due to the role of starting point. Unlike other forms of land disturbance, cacao agroforests maintain many characteristics of older forests such as complex three-dimensional structure and an abundant and diverse array of food and resources (Calvo and Blake, 1998; Buechley *et al*., 2015; Arroyo-Rodríguez *et al*., 2017). Some studies even concluded that cacao agroforests can act as wildlife corridors for birds between larger tracts of forest (Clough *et al*., 2009; Cabral, Faria and Morante-Filho, 2021b).

The result that bird functional composition did not change over time was also unexpected. Theory predicts that species and trait composition should change alongside shifts in environmental conditions and resource availability over succession (Fox, 1982; Dewalt, Schnitzer and Denslow, 2000; Bowen *et al*., 2007). In line with theory, other studies commonly found that bird functional composition changes through time (Jarrett et al., 2021; Oksuz et al., 2021; Sayer et al., 2017; Waltert et al., 2005). As with alpha-diversity, it could be that bird assemblages are more affected by larger landscape-level change, and that cacao agroforests maintain a sufficient degree of natural forest characteristics to support the same kinds of bird species as older forests.

There was a significant decrease in omnivorous birds, and a significant increase in the proportion of insectivorous birds, however. This is in line with expectation, as omnivorous birds are more generalist species while insectivorous birds are commonly specialist species (Sherry *et al*., 2020). Other studies have similarly found that there are more specialist species in older forests (Jarrett et al., 2021; Oksuz et al., 2021; Sayer et al., 2017; Waltert et al., 2005). Furthermore, the proportion of highly forest dependent species significantly increased over succession which further highlights the importance of older forests in sustaining sensitive and specialist species.

Overall, the results of these analyses suggest that bird functional diversity and composition remain relatively stable despite changes in species composition over succession. Other studies have also found that functional diversity and composition are more stable than taxonomic composition over time (eg. Böhnke et al., 2013; Blanco et al., 2021). This could be the result of a higher degree of functional redundancy in bird assemblages or species being replaced with similar species as composition changes (Guariguata and Ostertag, 2001; Liu *et* *al*., 2017). It is encouraging that bird functional diversity remains consistent despite changes in species composition over succession, and it suggests that cacao agroforests and young secondary forest can provide some of the same resources as older forests. The independent responses of taxonomic and functional diversity over succession, however, further highlights the need to integrate multiple aspects of biodiversity in ecological assessments.

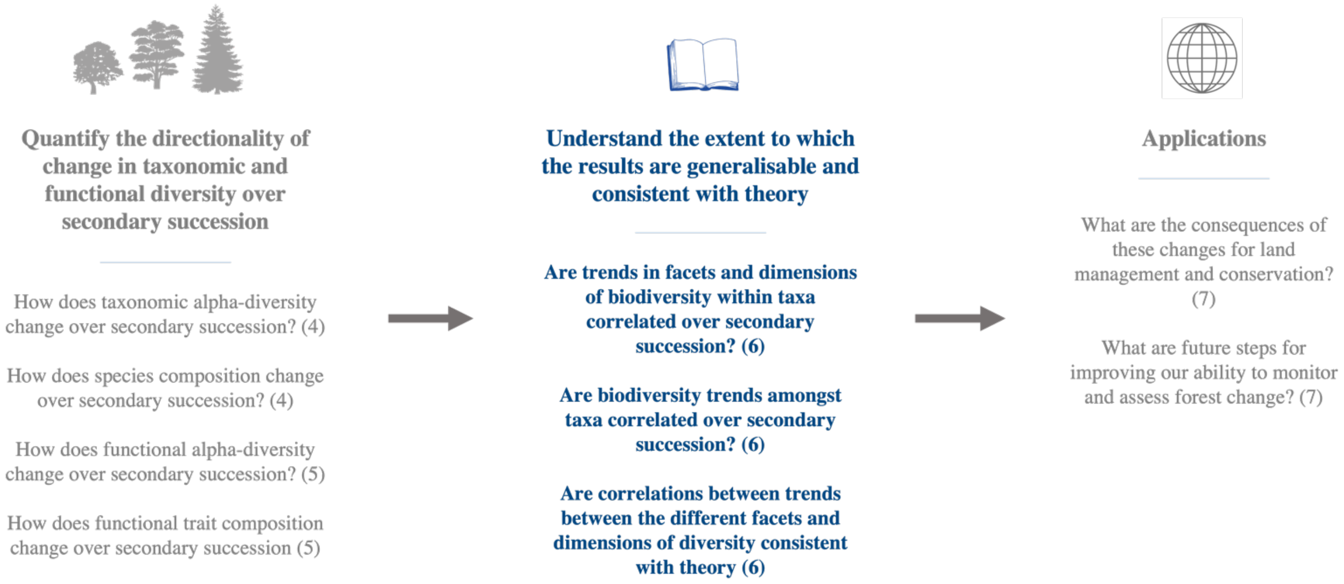
Conclusion

The results of this study reveal heterogenous responses over succession, which reinforces the need to assess multiple taxa and aspects of biodiversity to obtain a fuller understanding of how ecosystems change over time. As with taxonomic diversity, agroforests and secondary forests maintained a high degree of functional alpha-diversity, especially within the ground vegetation and bird assemblages. Agroforests and secondary forests can therefore be important biodiversity reservoirs for both taxonomic and functional diversity across taxa. The functional composition of the plant assemblages changed over time as the community shifted from agricultural to natural forest species and a shade-tolerant ground vegetation layer. Plant functional composition in secondary forests remained different from that of primary forests after c. 100 years of succession, and older forests supported more forest dependant and insectivorous birds. These findings highlight the importance of primary forests in supporting different types of species and in maintaining certain ecosystem functions.

Chapter 6

Synthesis of biodiversity change in abandoned cacao agroforests in Trinidad

6.1 Introduction



Quantify the directionality of change in taxonomic and functional diversity over secondary succession

How does taxonomic alpha-diversity change over secondary succession? (4)

How does species composition change over secondary succession? (4)

How does functional alpha-diversity change over secondary succession? (5)

How does functional trait composition change over secondary succession (5)

Understand the extent to which the results are generalisable and consistent with theory

Are trends in facets and dimensions of biodiversity within taxa correlated over secondary succession? (6)

Are biodiversity trends amongst taxa correlated over secondary succession? (6)

Are correlations between trends between the different facets and dimensions of diversity consistent with theory (6)

Applications

What are the consequences of these changes for land management and conservation? (7)

What are future steps for improving our ability to monitor and assess forest change? (7)

Figure 6.1. Schematic of questions being addressed in this thesis. Questions highlighted in blue are the focus of this chapter.

Our understanding of succession processes plays a central role in many conservation policies and initiatives, such as in making environmental impact assessments, in the expansion renewable resources, and in mitigating the effects of climate change and habitat loss (West, Shugart and Botkin, 1981). Despite the longstanding history of research into succession, an overarching theory of it has been illusive and studies have yielded divergent results even within the same ecosystem (Chapter 2; West, Shugart and Botkin, 1981; Westoby, Walker and Noy-Meir, 1989; Tilman, 1990; Vandermeer *et al*., 2004; Breugel, Martínez-Ramos and Bongers, 2006; Chazdon *et al*., 2007; Feldpausch *et al*., 2007; Lebrija-Trejos *et al*., 2010; Norden *et al*., 2015). The degree to which successional changes are consistent across taxa and facets of biodiversity also remains unclear. Further research is needed to test how generalisable patterns of succession are and to improve our ability to predict how ecosystems will change following disturbance, especially in rapidly changing tropical regions.

This chapter will examine the observed correlations in biodiversity change over succession between different taxa (trees, ground vegetation, epiphytes, and birds), and between taxonomic and functional diversity within each taxon following cacao agroforest abandonment in Trinidad (Figure 6.1). To do this, I ask how the results of this chapter and those of Chapters 4 and 5 fit within our existing understanding of succession (Chapter 2). The predictions regarding abandoned agroforests in Trinidad and succession explored in this chapter are based on more contemporary views of community assembly (Chang and HilleRisLambers, 2016) and succession driven by a combination of successional mechanisms including biotic interactions, species' traits, and environmental conditions, as well as empirical research (Chapter 2).

While the relative importance and effect of different successional mechanisms is debated, most theoretical models of succession indicate that plant taxonomic alpha-diversity should increase over time, especially early on in succession with the initial wave of colonising species post-disturbance (eg. Clements, 1916; Connell and Slatyer, 1977; Egler, 1953; Schoonmaker and McKee, 1988; and others). Plant functional alpha-diversity is also hypothesised to increase over time, given the assumption that environmental filtering is stronger in early successional stages while competition is stronger later in succession (Letcher, 2010; Lohbeck, Poorter, Lebrija-Trejos, *et al.*, 2013; Blanchard *et al.*, 2021).

Furthermore, plant taxonomic and functional composition is also expected to change throughout succession as changing environmental and competitive regimes shift the relative fitness of species based on species' traits (Connell and Slatyer, 1977; Uhl and Jordan, 1984; Brown and Lugo, 1990; Guariguata and Ostertag, 2001; Garnier *et al.*, 2004; Chazdon *et al.*, 2010; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Lohbeck *et al.*, 2012; Chazdon, 2014). Within this, the concept that the types of species which make up plant assemblages shift from being dominated by pioneer-type species to being dominated by climax-type species is shared among multiple theoretical frameworks (Finegan, 1996; Guariguata and Ostertag, 2001; DeWalt, Maliakal and Denslow, 2003; Garnier *et al.*, 2004; Dent, DeWalt and Denslow, 2013; Lasky *et al.*, 2014; Sanaphre-Villanueva *et al.*, 2017; Craven *et al.*, 2018). The relative abundance of specialist species is expected to increase over succession as well (Brown and Lugo, 1990a; Lebrija-Trejos, Pérez-García, *et al.*, 2010; Lohbeck *et al.*, 2012).

While most succession theory has revolved around plant dynamics, it is expected that changes in biodiversity will be correlated across taxa as species interact with and shape their environment (van der Heijden *et al.*, 1998; Vogelsang, Reynolds and Bever, 2006; Hiiesalu *et* *al*., 2014; Pellissier *et al*., 2014; Rolo, Olivier and van Aarde, 2017; Catterall, 2018; Gardner *et al*., 2019; Díaz-García *et al*., 2020). This especially the case for the relationships between plant and non-plant taxa (eg. Fox, 1982), due to the ability of trees and other plants to provide habitat and resources, and to regulate local environmental conditions (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Weiher, 2011). Thus, a diverse plant community should provide more varied resources for other organisms to exploit, and so support a more diverse biotic assemblage overall (Hooper *et al*., 2000; Waldrop *et al*., 2006; Sobek *et al*., 2009; Haddad *et al*., 2011; Tedersoo *et al*., 2016; Brockerhoff *et al*., 2017). Moreover, change in plant community composition should facilitate change in other taxa as the types of habitat and resources provided by plants change (DeWalt, Maliakal and Denslow, 2003; Bowen *et al*., 2007; Chazdon, 2014). There are other important feedbacks between taxa as well, such as the role of some animal species as seed dispersers, where a greater diversity of seed dispersers may increase the diversity of seed rain (Gallagher, 2013; Schleuning, Fründ and García, 2014; Fraser *et al*., 2015; Tedersoo *et al*., 2016; Rolo, Olivier and van Aarde, 2017; García, Donoso and Rodríguez-Pérez, 2018; Gardner *et al*., 2019).

Overall, trends in taxonomic and functional diversity change are expected to be correlated as well. It is hypothesised that greater trait complementary between species facilitates coexistence (Brown and Lugo, 1990a; Lebrija-Trejos, Pérez-García, *et al*., 2010; Lohbeck *et al*., 2012; Chazdon, 2014), and there are likely to be more functionally unique species when the species pool is larger (Huston, 1997; Mayfield and Levine, 2010). Therefore, taxonomic and functional diversity should change in parallel, though with possibly reduced change in functional diversity due to some functional redundancy in the assemblages (Diaz and Cabido, 2001).

Results from previous research have varied greatly, however, illustrating the difficulty in making predictions based on these theoretical expectations. Field-based research of succession in tropical forests largely agrees that core functions, such as canopy cover and forest structure, and plant species richness can recover quickly, within the first 50 years of succession (Chapter 2; Lebrija-Trejos *et al*., 2008; Derroire *et al*., 2016; Martin, Newton and Bullock, 2013). Plant species composition and complex traits such as soil properties take longer to develop, however, and it is often centuries before secondary forests recover these old-growth characteristics (Martin, Newton and Bullock, 2013; Derroire *et al*., 2016).

Though the literature reports mixed results, many studies have found relatively little change in bird alpha-diversity over succession (eg. Waltert *et al.*, 2005; Borges, 2007; Sayer, Bullock and Martin, 2017; Rocha *et al.*, 2019; Lee *et al.*, 2020; Borges *et al.*, 2021; Jarrett *et al.*, 2021). Studies have found that both taxonomic and functional composition change over succession both in plants and in other taxa such as birds (Finegan, 1996; Guariguata and Ostertag, 2001; Peña-Claros, 2003; Garnier *et al.*, 2004; Waltert *et al.*, 2005; Sanaphre-Villanueva *et al.*, 2017; Sayer, Bullock and Martin, 2017; Jarrett *et al.*, 2021; Oksuz, Palmeirim and Correia, 2021). Overall, while there is some evidence of ecological links between taxa (eg. Jüriado, Paal and Liira, 2003; Kapusta, Szarek-Łukaszewska and Kiszka, 2004), patterns of biodiversity change over succession vary widely across taxa (eg. Barlow *et al.*, 2007; Winter *et al.*, 2015; Tinya *et al.*, 2021).

Similarly, research comparing taxonomic and functional diversity over succession is relatively limited and results differ. Some sources have found similar patterns in both (eg. Whitfeld *et al.*, 2014; Craven *et al.*, 2018), while others have found comparatively little change in functional diversity over succession (Böhnke *et al.*, 2014).

Overall, while some generalities are apparent, there is disagreement over theoretical frameworks of succession and incongruence in results from empirical research. More research is needed across taxa and facets of biodiversity, especially in tropical regions, to improve our understanding of succession and our ability to predict how ecosystems will change following disturbance. The aim of this chapter is to evaluate the results reported in Chapters 4 and 5 to assess correlation in biodiversity change between taxa and between facets of biodiversity over succession as revealed by my study of this Trinidadian system. The chapter will also synthesise the results from previous chapters within the context of succession theory and empirical research using the expectations outlined above (discussed in detail in Chapter 2).

6.2 Methods

Spearman tests were used to examine whether tree, ground vegetation, epiphyte and bird assemblages exhibited correlated trends in taxonomic and functional alpha-diversity (GGally package in R; Revelle, 2015; Schloerke, 2021). Next, tanglegrams were used to assess the degree of concordance in beta-diversity change between taxa, and between taxonomic and functional diversity within each taxon. A cluster analysis was performed for each of the four assemblages, and a tanglegram was used to explore the congruence between dendrograms in order to understand the extent of agreement in species composition change.

To conduct the tanglegram analyses, dendrograms were created for each taxonomic group based on Chao-Jaccard and functional turnover values between sites using agglomerative nesting, hierarchical clustering, the agnes function of the cluster package in R (Maechler *et al*., 2019), and the Ward method. Different untangling methods within dendextend (untangle function) were applied in order to optimise the alignment between dendrogram pairs. The Side2Step method was chosen as it provided the lowest entanglement values and thus was the best untangling method for all the tanglegrams in this study. The degree of alignment between dendrogram pairs was expressed using the entanglement metric, where zero signifies complete alignment and one is complete entanglement. A cophenetic correlation coefficient was used to further assess the degree of agreement between dendrograms (cor_cophenetic function R; Spearman). The cophenetic correlation coefficient measures the correlation between the cophenetic distance matrices of the two dendrograms being compared. The cophenetic corelation coefficient is bound between -1 and 1, where values closer to zero signify there is no significant correlation between the dendrogram pairs.

A null model was used to test if the alignment of each dendrogram pair differed from what would be expected by chance. In this model, the site names for one of the two assemblages in a comparison were randomly reshuffled to produce a new dendrogram; the cophenetic correlation between this and the dendrogram produced by the other, unshuffled assemblage was then computed. This process was repeated 200 times to generate a null distribution of the cophenetic correlation coefficients against which the observed alignment value could be compared (Gotelli and Entsminger, 2003; Galili, 2015). Given that there are multiple comparisons involved, these statistics are included to provide intuitive information of the correlations within and between taxa, rather than in a classical hypothesis-testing context.

6.3 Results

Correlations between alpha-diversity indices

Comparisons were conducted between taxa, and between facets of biodiversity. Results from Spearman's correlation analyses found that species richness, Shannon and Simpson diversity (i.e. taxonomic alpha-diversity) were significantly positively correlated within each taxonomic group (Figure 6.2-4).

Trees

In tree assemblages, all the functional alpha-diversity indices were also strongly positively correlated (p<0.05), except for functional richness and functional divergence which were only weakly correlated (p=0.15; Figure 6.2). Taxonomic and functional diversity indices were strongly positively correlated within tree assemblages.

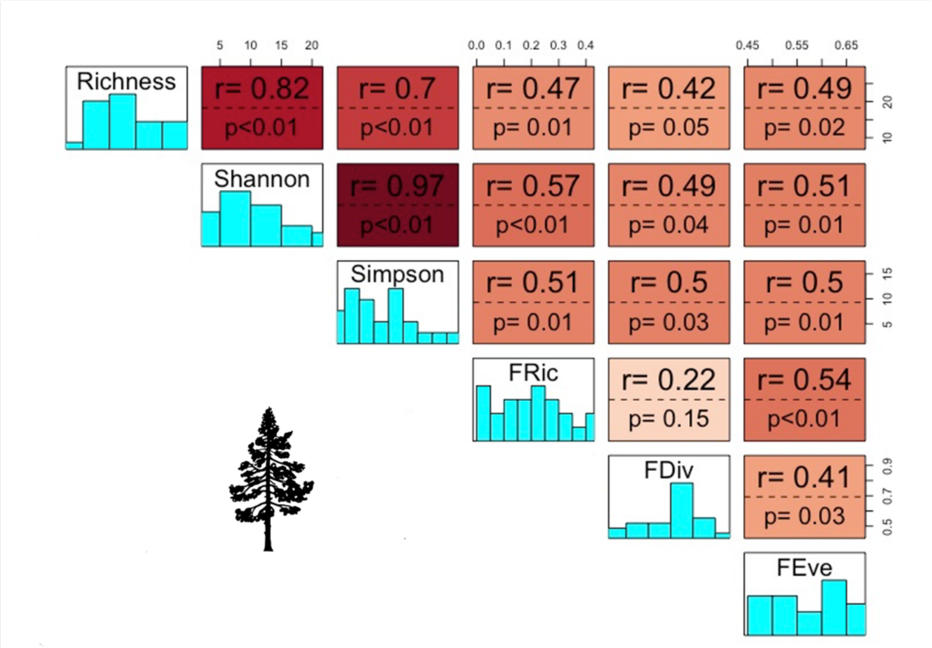


Figure 6.2 Correlation matrix testing for correlated trends in taxonomic and functional alpha-diversity indices for trees. The upper right side of the matrix displays Spearman correlation coefficients and correlation p values. The colour gradient indicates the direction of the correlation (red for positive correlations, blue for negative correlations and white for no correlation). Density plots are shown diagonally across the centre of the matrix.

Ground vegetation

For the ground vegetation assemblages, the functional alpha-diversity indices were only weakly correlated (Figure 6.3). Functional richness was strongly positively correlated with species richness, Shannon and Simpson diversity ($p<0.05$). There were no strong correlations between functional divergence or functional evenness with any of the taxonomic alpha-diversity indices.

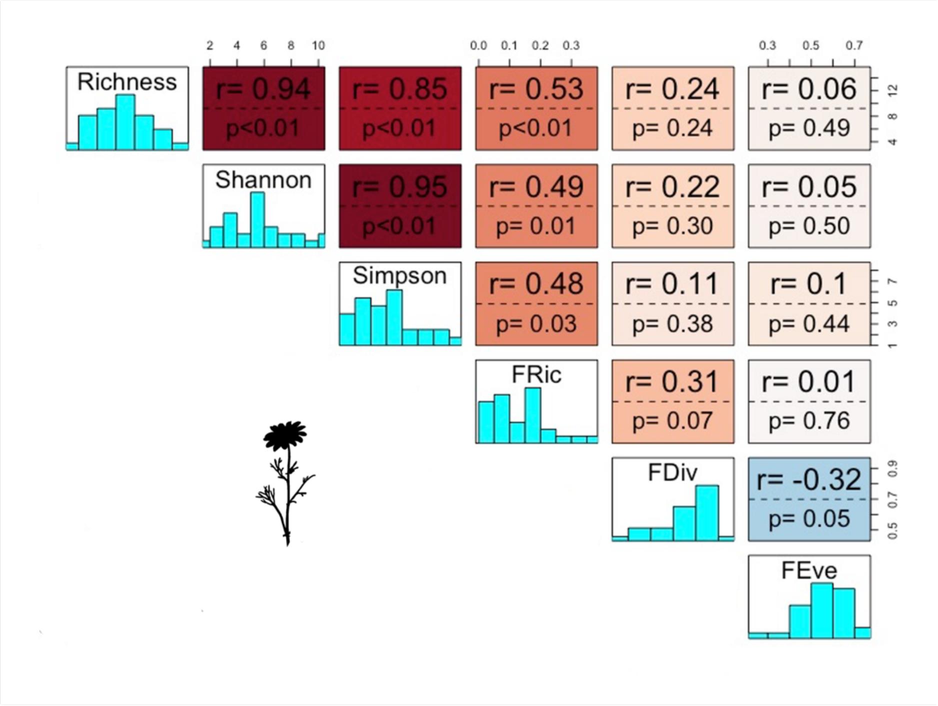


Figure 6.3 Correlation matrix testing for correlated trends in taxonomic and functional alpha-diversity indices for ground vegetation. The upper right side of the matrix displays Spearman correlation coefficients and correlation p values. The colour gradient indicates the direction of the correlation (red for positive correlations, blue for negative correlations and white for no correlation). Density plots are shown diagonally across the centre of the matrix.

Birds

For birds, functional alpha-diversity indices were weakly correlated (Figure 6.4). Functional richness was weakly negatively correlated with functional divergence and functional evenness, while functional divergence and functional evenness were weakly positively correlated. Functional richness was strongly positively correlated with species richness, Shannon, and Simpson diversity ($p<0.05$). Functional divergence was strongly negatively correlated with Shannon and Simpson diversity ($p<0.05$). Functional evenness was only weakly correlated with the taxonomic alpha-diversity indices.

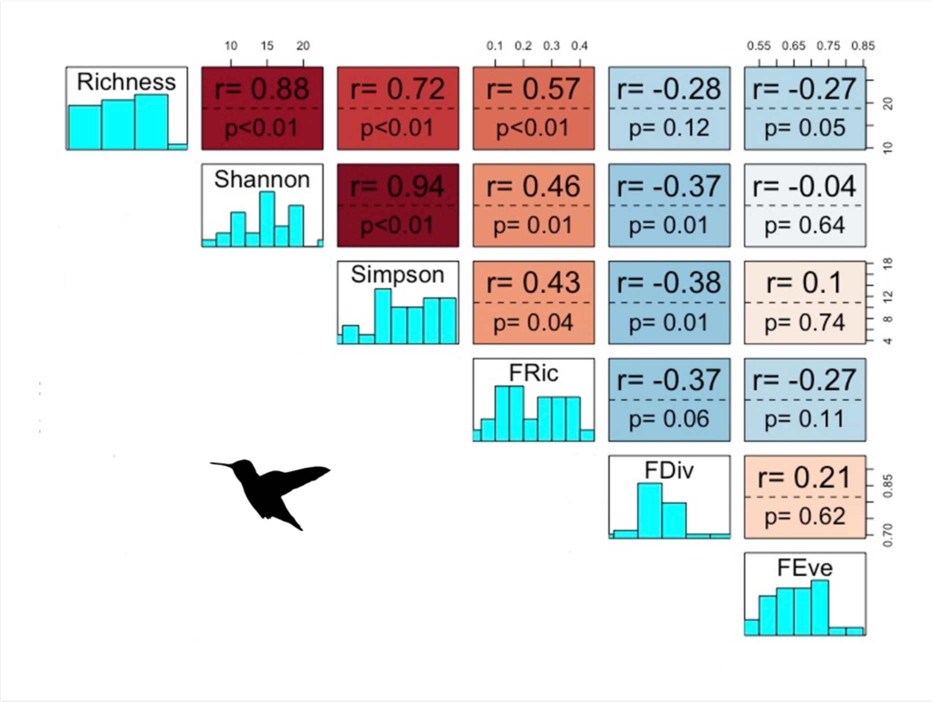


Figure 6.4 Correlation matrix testing for correlated trends in taxonomic and functional alpha-diversity indices for birds. The upper right side of the matrix displays Spearman correlation coefficients and correlation p values. The colour gradient indicates the direction of the correlation (red for positive correlations, blue for negative correlations and white for no correlation). Density plots are shown diagonally across the centre of the matrix.

Correlations in alpha-diversity between taxa

Taxonomic alpha-diversity

There were no strong correlations in taxonomic alpha-diversity indices between taxonomic groups (Figure 6.5). Tree and ground vegetation taxonomic alpha-diversity indices were weakly negatively correlated. Epiphyte taxonomic alpha-diversity was weakly positively correlated with tree and ground vegetation species richness, Shannon, and Simpson diversity. Bird species richness was weakly negatively correlated with tree and epiphyte species richness, but weakly positively correlated with tree and epiphyte Shannon and Simpson

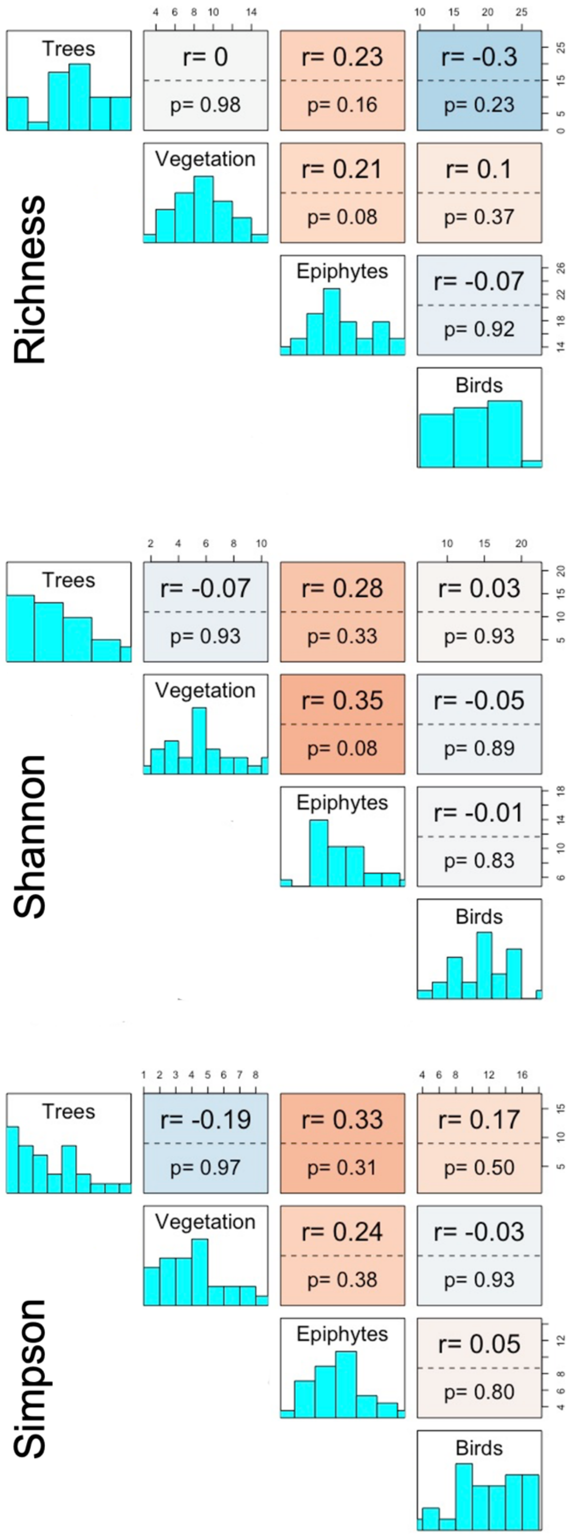


Figure 6.5 Correlation matrix testing for correlated trends in taxonomic alpha-diversity indices between taxa. The upper triangle of the matrix displays Spearman correlation coefficients and correlation p values. The colour gradient indicates the direction of the correlation (red for positive correlations, blue for negative correlations, and white for no correlation). Density plots are shown diagonally across the centre of the matrix.

diversity. Conversely, bird species richness was weakly positively correlated with ground vegetation species richness, but weakly negatively correlated with ground vegetation species evenness.

Functional alpha-diversity

There were likewise no significantly correlated trends in functional alpha-diversity between taxa (Figure 6.6). Tree functional richness was weakly positively correlated with ground vegetation functional richness. Tree and bird functional alpha-diversity indices were weakly negatively correlated. Bird and ground vegetation functional richness and evenness were weakly positively correlated, but functional divergence between these taxa was weakly negatively correlated.

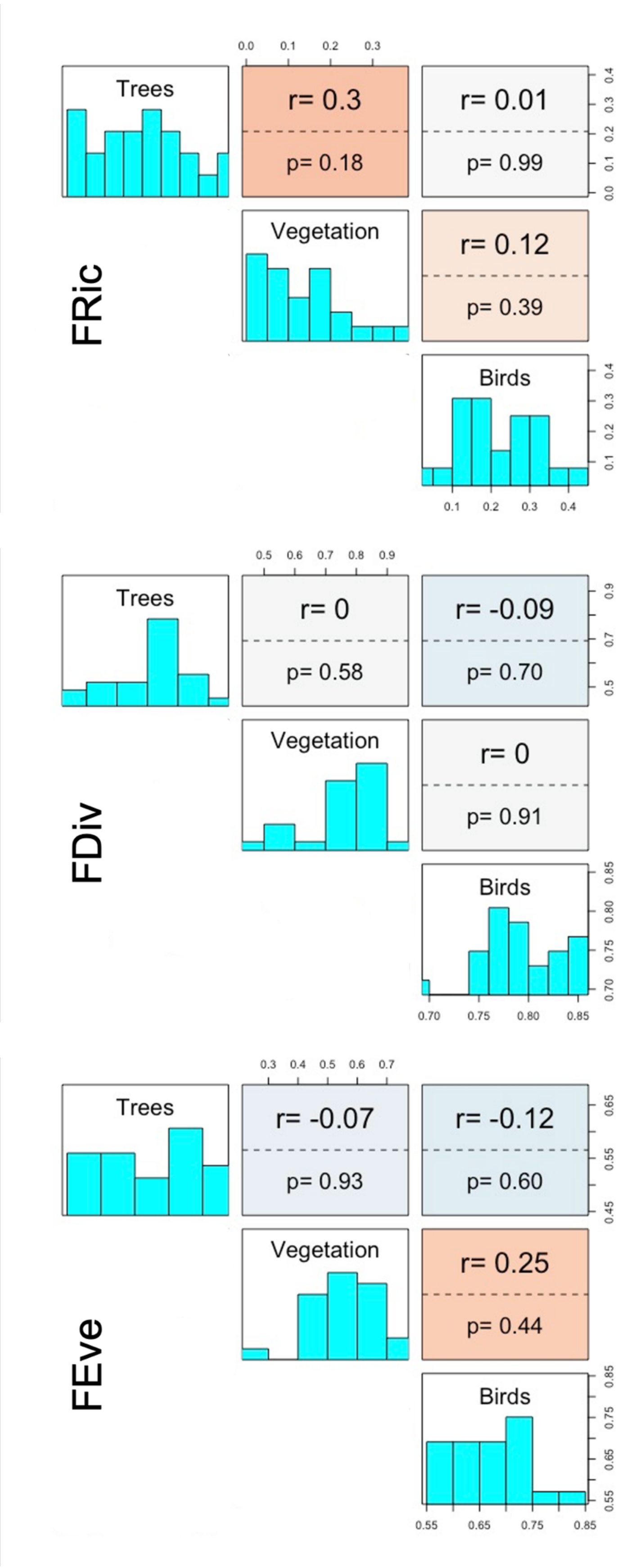


Figure 6.6. Correlation matrix testing for correlated trends in functional alpha-diversity indices between taxa. The upper right side of the matrix displays Spearman correlation coefficients and correlation p values. The colour gradient indicates the direction of the correlation (red for positive correlations, blue for negative correlations, and white for no correlation). Density plots are shown diagonally across the centre of the matrix.

Correlations in taxonomic and functional beta-diversity

Next, tanglegrams were used to compare taxonomic and functional composition within each taxonomic group (Figure 6.7). The entanglement value between the tree taxonomic and functional composition dendrograms was 0.141, the entanglement coefficient was 0.199 for ground vegetation, and was 0.283 for birds. A null model revealed that turnover in tree taxonomic and functional composition was more correlated than would be expected by chance (Appendix 6.1). There was no equivalent correlation between taxonomic and functional trait composition for ground vegetation or for birds.

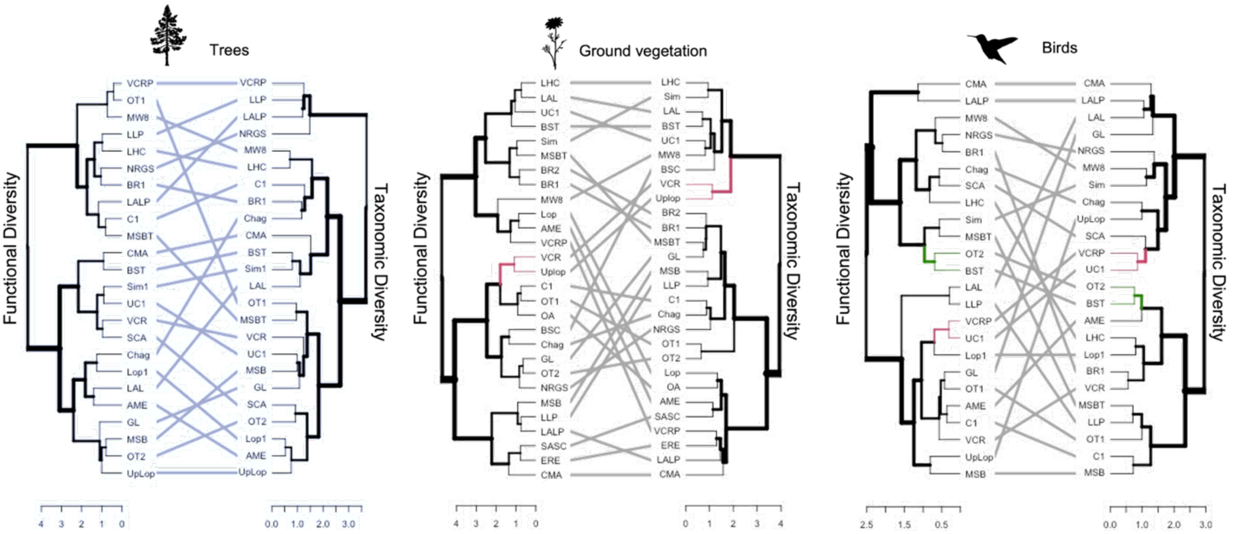


Figure 6.7. Tanglegrams comparing the hierarchical clustering of sites based on tree, ground vegetation, and bird species and functional trait composition. Red and green branches indicate common groupings between the two dendrograms. The horizontal axes represent the distance between sites or clusters of sites. Blue indicates that taxonomic and functional diversity are more correlated than would be expected by chance.

Tanglegrams were further used to test for correlations in compositional turnover between taxonomic groups (Figure 6.7). The entanglement metric between trees and ground vegetation was 0.198, entanglement was 0.245 between trees and epiphytes, and 0.183 between trees and birds. The entanglement metric between ground vegetation and epiphytes was 0.179, and between vegetation and birds was 0.158. Lastly the entanglement coefficient between birds and epiphytes was 0.213.

The cophenetic correlation null model found that the observed cophenetic correlation coefficient between trees and epiphytes lies outside of the confidence limits of the null distribution and so is greater than would be expected by chance (Appendix 6.1). The cophenetic correlation coefficient between trees and birds was also greater than would be expected by chance. All other comparisons between taxa were no more correlated than would be expected at random.

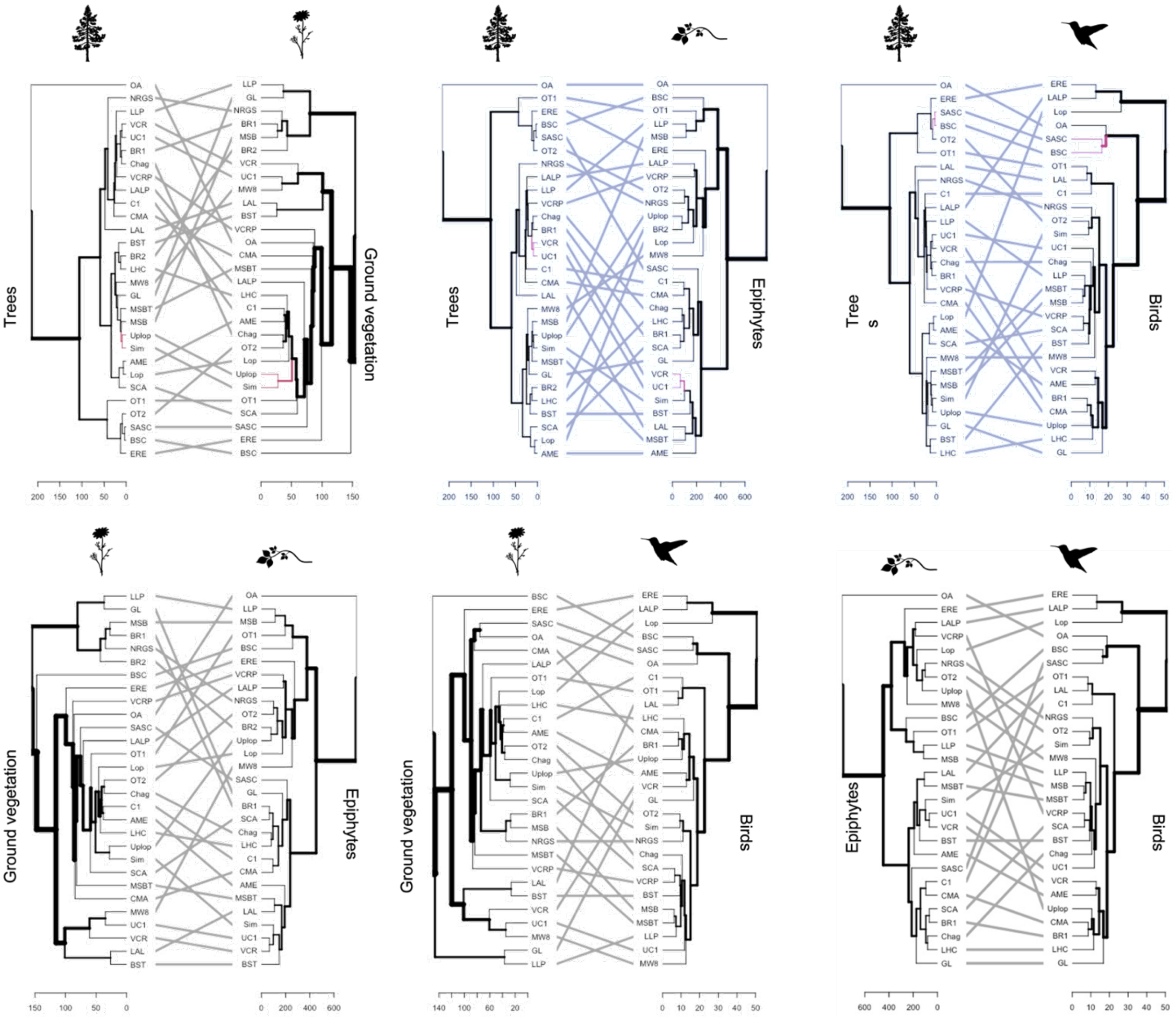


Figure 6.6. Tanglegrams comparing the hierarchical clustering of sites based on tree, ground vegetation, epiphyte, and bird composition. Red lines indicate common branches between the two dendrograms. The horizontal axes represent the distance between sites or clusters of sites. Blue indicates that the taxa being compared are more correlated than would be expected by chance.

6.4 Synthesis of results from Chapters 4-6

Forest structure

Chapters 4 and 5 assessed how forest structural characteristics, taxonomic diversity and functional diversity changed over secondary succession following cacao agroforest abandonment in Trinidad's Northern Range. Forest canopy height and DBH became increasingly bimodal over succession suggesting the formation of multiple canopy layers and strata within the forest, though canopy closure occurred quickly following cacao agroforest abandonment. This is in line with expectation from theory and research, where the forest became more structurally complex over succession (Guariguata and Ostertag, 2001; Lebrija-Trejos *et al*., 2008; Derroire *et al*., 2016).

Trees

Tree species richness increased significantly in the first 25 years of succession, and species evenness increased throughout succession. Tree functional alpha-diversity also increased over succession, and functional divergence increased mostly within the first 30 years of succession. Species and functional trait composition also changed significantly with forest age, and the secondary forests had not recovered old-growth characteristics even after c. 100 years of succession in this study.

Of all the taxa, tree assemblages showed the clearest directional change in taxonomic and functional diversity with forest age and aligned most closely with predictions based on theory and other research (Chapter 2; Toky and Ramakrishnan, 1983; Lebrija-Trejos *et al*., 2008; Lebrija-Trejos *et al*., 2010; Martin, Newton and Bullock, 2013; Derroire *et al*., 2016). Succession research has primarily focused on tree dynamics and there is a clearer understanding of how and why tree assemblages change over succession compared to other taxa (Chapter 2).

Most theoretical frameworks suggest that tree alpha-diversity should increase over succession as more species colonise the area following disturbance, and changes in the relative strength of deterministic processes, such as a decrease in environmental filtering and an increase in competitive pressure over time, are generally expected to facilitate greater taxonomic and functional alpha-diversity in later successional stages (Chapter 2; Letcher, 2010; Lohbeck *et al.*, 2013; Blanchard *et al.*, 2021).

Research further supports the idea that species richness recovers early in succession, while species composition can remain altered for centuries (Riswan, Kenworthy and Kartawinata, 1985; García-Montiel and Scatena, 1994; Finegan, 1996; Lebrija-Trejos *et al.*, 2008; Chazdon *et al.*, 2010; Derroire *et al.*, 2016). Expectations for functional diversity change over succession based on existing research are uncertain as there are relatively few studies and inconsistent results (Chapter 2). Most studies agree, however, that functional beta-diversity changes substantially over succession (Lohbeck *et al.*, 2012; Böhnke *et al.*, 2014; Muscarella *et al.*, 2016; Sanaphre-Villanueva *et al.*, 2016; Craven *et al.*, 2018).

Though functional diversity changed over succession, results from trait analyses suggest that there is a decrease in zoochorous and an increase in anemochorous species with forest age (Chapter 5). This result is incongruous with the idea that the tree community shifts from pioneer-type species to climax-type species, as abiotic dispersal syndromes are more commonly associated with early colonising plants (Guariguata and Ostertag, 2001; Sanaphre-Villanueva *et al.*, 2017)

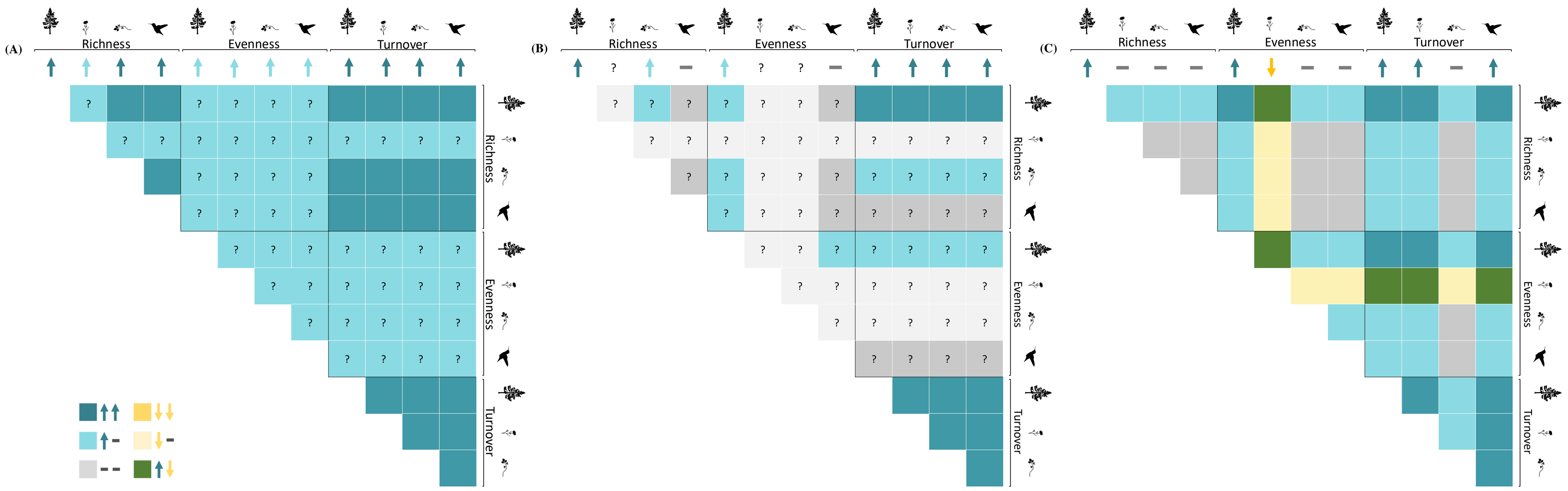


Figure 6.14 Summary figure of the taxonomic diversity theory (A), expectations from published research (B), and the results of this study (C). Upward arrows (dark blue) indicate a positive trend with forest age. Grey dashes indicate no significant change in the diversity measure over succession. The coloured grid indicates the relationship between different taxa and aspects of biodiversity. Dark blue indicates a strong positive relationship. Light blue squares indicate conflicting trends with one of the pair increasing and one showing no change. Grey squares indicate that the taxa and aspects of biodiversity being compared both did not change over succession.

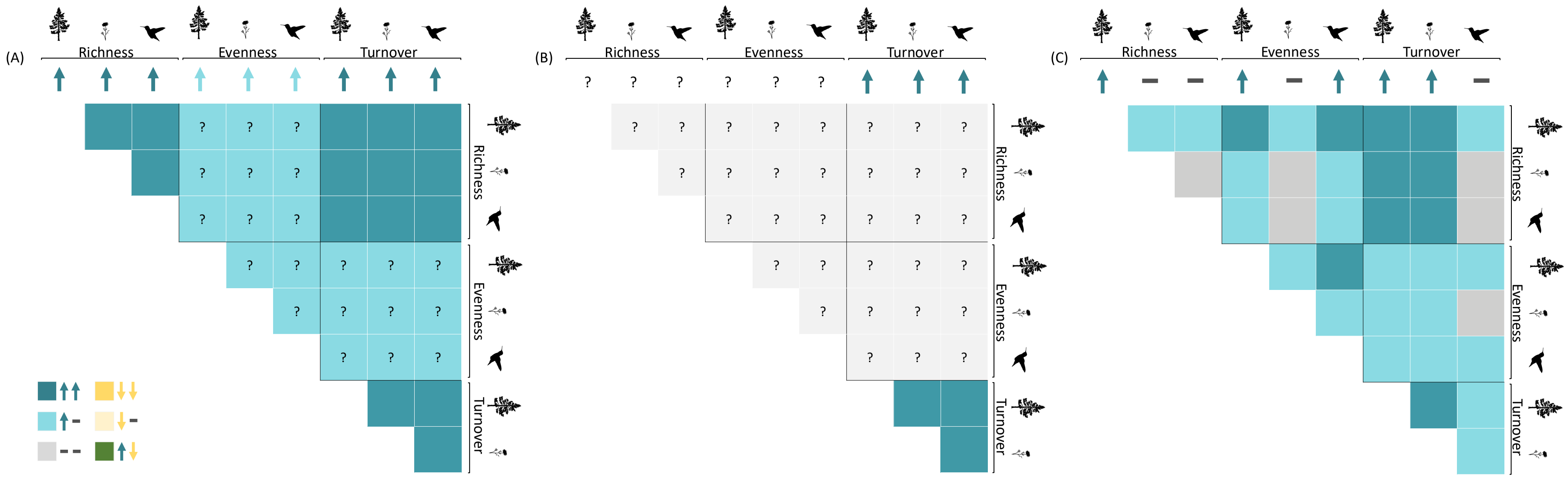


Figure 6.15 Summary figure of the functional diversity theory (A), expectations from published research (B), and the results of this study (C). Upward arrows (dark blue) indicate a positive trend with forest age. Grey dashes indicate no significant change in the diversity measure over succession. The coloured grid indicates the relationship between different taxa and aspects of biodiversity. Dark blue indicates a strong positive relationship. Light blue squares indicate conflicting trends with one of the pair increasing and one showing no change. Grey squares indicate that the taxa and aspects of biodiversity being compared both did not change over succession.

Ground vegetation

Contrary to expectations from theory and research, there was no significant change in ground vegetation species richness, and species evenness decreased significantly over succession. As with trees, ground vegetation was expected to increase following disturbance with an influx of new colonisers and changing deterministic regimes (Letcher, 2010; Lohbeck *et al.*, 2013; Blanchard *et al.*, 2021). This suggests that ground plants may experience greater environmental filtering later in succession due to limited light levels (Laska, 1997; Lebrija-Trejos, Meave, *et al.*, 2010; dos Santos-Junior *et al.*, 2017) and other studies have reported similar findings (Laska, 1997; Rasingam and Parthasarathy, 2009; dos Santos-Junior *et al.*, 2017). This concept is further supported by the significant change in functional composition (Chapter 5), the increase in flowerless and abiotically-dispersed plants (Chapter 5), and the increase in shade-tolerant plants such as ferns and bryophytes in older forests (Chapter 4).

Epiphytes

The lack of change in epiphyte species alpha or beta-diversity over succession is also divergent from expectation. Epiphytes were expected to increase over time as new species colonise disturbed areas, and greater tree diversity provides more varied microhabitats for different epiphyte species to exploit (Jüriado, Paal and Liira, 2003; Kapusta, Szarek-Łukaszewska and Kiszka, 2004). Many epiphytes, especially cryptogamic species, are also sensitive to light, humidity, pollution levels, and other environmental factors (Kantvilas and Minchin, 1989; Kuusinen, 1994; Gustafsson and Eriksson, 1995; Campbell and Fredeen, 2004; Belinchón *et al.*, 2007; Fritz, Brunet and Caldiz, 2009; Moning *et al.*, 2009; Leppik, Jüriado and Liira, 2011). Thus, species composition was expected to change with shifting environmental conditions over time. The lack of change in epiphyte diversity suggests that cacao agroforests and young secondary forests were able to maintain suitable structural characteristics and environmental conditions to support a diverse epiphyte assemblage like those of local primary forests.

Functional diversity analyses were not conducted for the epiphyte assemblages as epiphytes incorporated multiple taxonomic groups (plants and fungi), and lichens were categorised as morphospecies (Appendix 3.2).

Birds

There was likewise no significant change in bird taxonomic or functional alpha-diversity, though functional evenness increased significantly over time. While theory predicts that bird alpha diversity increases through succession with changing environmental conditions and faciliatory interactions with plant assemblages, other studies have similarly found that bird diversity changes little over succession (Waltert *et al.*, 2005; Borges, 2007; Sayer, Bullock and Martin, 2017; Rocha *et al.*, 2019; Lee *et al.*, 2020; Borges *et al.*, 2021; Jarrett *et al.*, 2021). Research on bird assemblages has yielded widely varying results, however, and thus making predictions is challenging (Robert R Dunn, 2004; J. Barlow *et al.*, 2007; Chazdon, 2014).

There was significant turnover in bird species composition, but there was no significant change in functional trait composition over time. Both theory and research suggest that bird taxonomic and functional beta-diversity change substantially over succession as environmental conditions, resource availability, and deterministic regimes change (Jarrett et al., 2021; Oksuz et al., 2021; Sayer et al., 2017; Waltert et al., 2005). The maintenance of functional composition despite changes in species composition suggests that cacao agroforests and secondary forests are able to maintain structural characteristics and provide similar resources to older forests, and so support the same types of species.

The increase in highly forest-dependant and insectivorous birds, and the decrease in omnivorous birds are in line with predictions from theory and empirical research, where the proportion of sensitive and specialist birds is expected to increase over succession (Chapter 2; Lennox *et al.*, 2018). This result emphasises that, while agroforests and secondary forests can provide valuable habitat for many species, they are not able to support all the same species as older forests including those of particular conservation concern.

6.5 Comparisons across taxa and facets of biodiversity

Results from this chapter found that the taxonomic alpha-diversity indices were significantly positively correlated within each taxonomic group (Figure 6.2). Correlations between the functional alpha-diversity indices were more complex and taxon-dependant. Overall taxonomic and functional diversity were positively correlated across taxa. In tree assemblages, all the taxonomic and functional diversity indices were strongly positively correlated. For the ground vegetation and birds, functional richness was strongly positively correlated with the taxonomic alpha-diversity indices. Also in birds, functional divergence was strongly negatively correlated with Shannon and Simpson diversity, while functional evenness was only weakly correlated with taxonomic alpha-diversity. There were no significantly correlated trends in taxonomic alpha-diversity indices or in functional alpha-diversity indices between taxonomic groups (Figure 6.3).

Turnover in tree taxonomic and functional composition was more correlated than would be expected by chance. There was no correlation between taxonomic and functional trait composition for ground vegetation or for birds. Tree and bird, and tree and epiphyte species compositional change were both more aligned than would be expected at random as well. All other comparisons between taxa were no more correlated than would be expected by chance.

Comparisons across taxa

There were no strong correlations in taxonomic or functional alpha-diversity indices between taxa, and there was only significant correlation in compositional change between trees and epiphytes, and between trees and birds. Overall, there was little agreement between the taxonomic groups and patterns of successional change varied widely. Based on theory, it was expected that biodiversity change over succession would be correlated between taxa. For example, a more taxonomically and functionally diverse tree assemblage could provide more resource and habitat heterogeneity for other taxa such as birds, ground vegetation, and epiphytes to exploit (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Waldrop *et al.*, 2006; Hooper, 2008; Sobek *et al.*, 2009; Haddad *et al.*, 2011; Vockenhuber *et al.*, 2011; Weiher, 2011; Tedersoo *et al.*, 2016; Brockerhoff *et al.*, 2017). It could be, however, that the relative strength of successional mechanisms varies between taxa, or that taxa respond to successional processes at different temporal and spatial scales (Chapter 2).

While there was no significant correlation between tree and ground vegetation alpha or beta-diversity in this study, some studies indicate that diversity in tree and understory communities should be positively correlated (Nadrowski, Wirth and Scherer-Lorenzen, 2010; Vockenhuber *et al.*, 2011; Chamagne *et al.*, 2016). For example, tree diversity can increase heterogeneity in soil conditions and in crown light transmittance which promotes greater ground vegetation diversity (Augusto, Dupouey and Ranger, 2003; Lassau *et al.*, 2005; Barbier, Gosselin and Balandier, 2008; Sobek *et al.*, 2009; Vockenhuber *et al.*, 2011). Conversely, studies such as research by Vockenhuber and colleagues (2011) have found that understory diversity is negatively affected by increased canopy cover which can lead to conflicting results as light becomes increasingly limited over succession (Kirby, 1988; Jennings, Brown and Sheil, 1999; Hofmeister *et al.*, 2009). It could therefore be that, in the secondary forest of Trinidad's Northern Range, vegetation diversity is more strongly affected by light transmittance. This is supported by the result that the ground vegetation assemblages became increasingly dominated by shade-tolerant ferns and bryophytes. Therefore, the lack of correlation between tree and ground vegetation diversity could be because cacao agroforests are densely forested and canopy cover remained largely consistent throughout succession in these forest stands.

There was also no correlation between tree and epiphyte alpha-diversity, which is counter to expectation. It is hypothesised that greater tree diversity provides more niche variation for epiphyte species to exploit (eg Ellis, 2012). Cryptogenic epiphytes (lichens, mosses, liverworts, and algae), for example, have varied tolerances and responses to bark chemistry, texture, and stability, and so are influenced by tree composition and diversity (Ihlen, Gjerde and Sætersdal, 2001; Cleavitt, Dibble and Werier, 2009; Ellis, 2012). Though research on epiphytes is limited, other studies have found that epiphyte diversity increases with tree diversity (Jüriado, Paal and Liira, 2003; Kapusta, Szarek-Łukaszewska and Kiszka, 2004; Ellis, 2012) and with forest age (Neitlich and McCune, 1997; Brunialti *et al.*, 2010). Research has also highlighted that epiphytes are strongly influenced by humidity and shading (Kantvilas and Minchin, 1989; Kuusinen, 1994, 1994; Gustafsson and Eriksson, 1995; Uliczka and Angelstam, 1999; Sillett *et al.*, 2000; Campbell and Fredeen, 2004; Löbel, Snäll and Rydin, 2006; Belinchón *et al*., 2007; Fritz, Brunet and Caldiz, 2009; Moning *et al*., 2009; Leppik, Jüriado and Liira, 2011). As with ground vegetation, it could be that epiphyte alpha-diversity was more strongly affected by forest structure and canopy cover, which remained relatively consistent over succession following cacao farming in this study. There was a significant correlation between tree and epiphyte compositional change, however, which suggests that tree composition did influence epiphyte composition.

Trends in bird and tree alpha-diversity were not correlated. There is some evidence in the literature that temporal trends in bird and tree assemblages are linked, though studies also highlight the complexity in these relationships (Hansen *et al*., 1994; Laiolo, 2002; Zhang *et al*., 2013; Muiruri, Rainio and Koricheva, 2016). For example, Muiruri, Rainio, and Koricheva (2016) found that the relationship between bird predation rates and tree species richness depended on spatial scale in forest stands in Finland (Muiruri, Rainio and Koricheva, 2016). Other studies have similarly noted the effect of spatial scale on patterns of bird diversity (Lehmkuhl and Ruggiero, 1991). Factors such as distance to urban centres, forest patch size and isolation, and matrix habitat conditions can also influence bird assemblages (Brotons and Herrando, 2001; Rey-Benayas, Galván and Carrascal, 2010), although these were largely controlled for in this study.

Many studies indicate that birds are particularly affected by the structural characteristics of a forest (Cody, 1985; Laiolo, 2002; Díaz *et al*., 2005; Shahabuddin and Kumar, 2006; Campos-Silva and Piratelli, 2021). Greater structural complexity can provide more varied habitat and niches, and so increase faunal diversity (James, 1971; Urban and Smith, 1989). Some studies have also found that bird diversity increases with forest age (eg. Lack and Lack, 1951; Moss, 1978; Laiolo, 2002; Zhang *et al*., 2013), and the abundance and diversity of mature trees in older forests. Older trees tend to have greater bark structural complexity and surface area which provides more habitat for invertebrates, and more foraging opportunities for insectivorous birds (Nilsson, 1979; Schieck, Nietfeid and Stelfox, 1995). Laiolo (2002) found that the responses of different types of birds (eg. hole nesters, trunk feeders, ground feeders etc) to forest age, diversity, and structural characteristics vary widely, however. For example, hole nesting birds tend to be confined to mature forests, since older trees tend to have more crevices which the birds can utilise (Laiolo, 2002). The complexity in responses of different bird guilds to changes in tree diversity and composition over succession could confound correlations between the taxa.

It could also be that birds are more affected by larger-scale landscape changes (Robert R Dunn, 2004; J. Barlow *et al.*, 2007; Chazdon, 2014). In this study, the stand size was relatively small due to the small size of cacao agroforests, and all sites were situated within a forested matrix. Another possibility is that birds were more affected by forest structure (Robert R Dunn, 2004; J. Barlow *et al.*, 2007; Chazdon, 2014), and thus the maintenance of many structural elements through succession following cacao farming buffered against changes in tree diversity.

Despite this complexity, there was a significant correlation between tree and bird compositional change over succession. This is in line with expectation, and other studies have similarly found that tree composition can affect habitat quality and bird composition (Fuller *et al.*, 1995). Furthermore, birds can affect plant communities through pollination and seed dispersal (Gallagher, 2013; Schleuning, Fründ and García, 2014; Fraser *et al.*, 2015; Tedersoo *et al.*, 2016; Rolo, Olivier and van Aarde, 2017; García, Donoso and Rodríguez-Pérez, 2018; Gardner *et al.*, 2019).

As with trees, there was no correlation between trends in bird and epiphyte diversity, or between bird and ground vegetation diversity. It is also hypothesised that ground vegetation and epiphytes can affect patterns of bird diversity and composition, and vice versa. Ground vegetation can provide food and habitat for birds, and other studies have found correlations in biodiversity between the two taxa (eg. McShea and Rappole, 2000; Laiolo, 2002; Díaz *et al.*, 2005; Vogeler *et al.*, 2014; Dagan and Izhaki, 2019). Some epiphytes such as bromeliads can be sources of nectar and fruit, and even cryptogamic epiphytes can provide nesting materials and be sources of insects for birds (Nadkarni and Matelson, 1989; Hayward and Rosentreter, 1994; Nadkarni, 1994; Ellis, 2012; Gotsch, Nadkarni and Amici, 2016). Conversely, epiphytes such as vines and lianas can impede trunk-feeding birds from foraging (Laiolo, 2002). Birds can act as pollinators, dispersers, and defenders against herbivory for ground vegetation and epiphytic plants, and subsequently influence patterns of biodiversity in those assemblages (Nadkarni and Matelson, 1989; Mondragón, Valverde and Hernández-Apolinar, 2015; Bleiweiss *et al.*, 2019; Spicer and Woods, 2022). The mismatch between the results and expectation could be because bird, epiphyte, and ground vegetation diversity and composition are more strongly influenced by forest structure than by biotic interactions in this study, as well as because of the inherent complexity in these interactions and feedbacks as each taxon simultaneously inhibits and facilitates the colonisation and diversity in others.

Trends in taxonomic and functional alpha-diversity were generally positively correlated, especially between taxonomic alpha-diversity measures and functional richness in plant assemblages. This follows the expectation that, the more species there are, the more likely there are to be different functional traits represented within the community, and that complementary traits support species coexistence (Chapter 2; Huston, 1997; Mayfield *et al.*, 2010). The only significant correlation observed was between taxonomic and functional composition change in tree assembles, however, while taxonomic and functional composition changed independently in bird and ground vegetation assemblages. It could therefore be that some functional traits are conserved in bird and ground vegetation assemblages throughout succession despite changes in species composition.

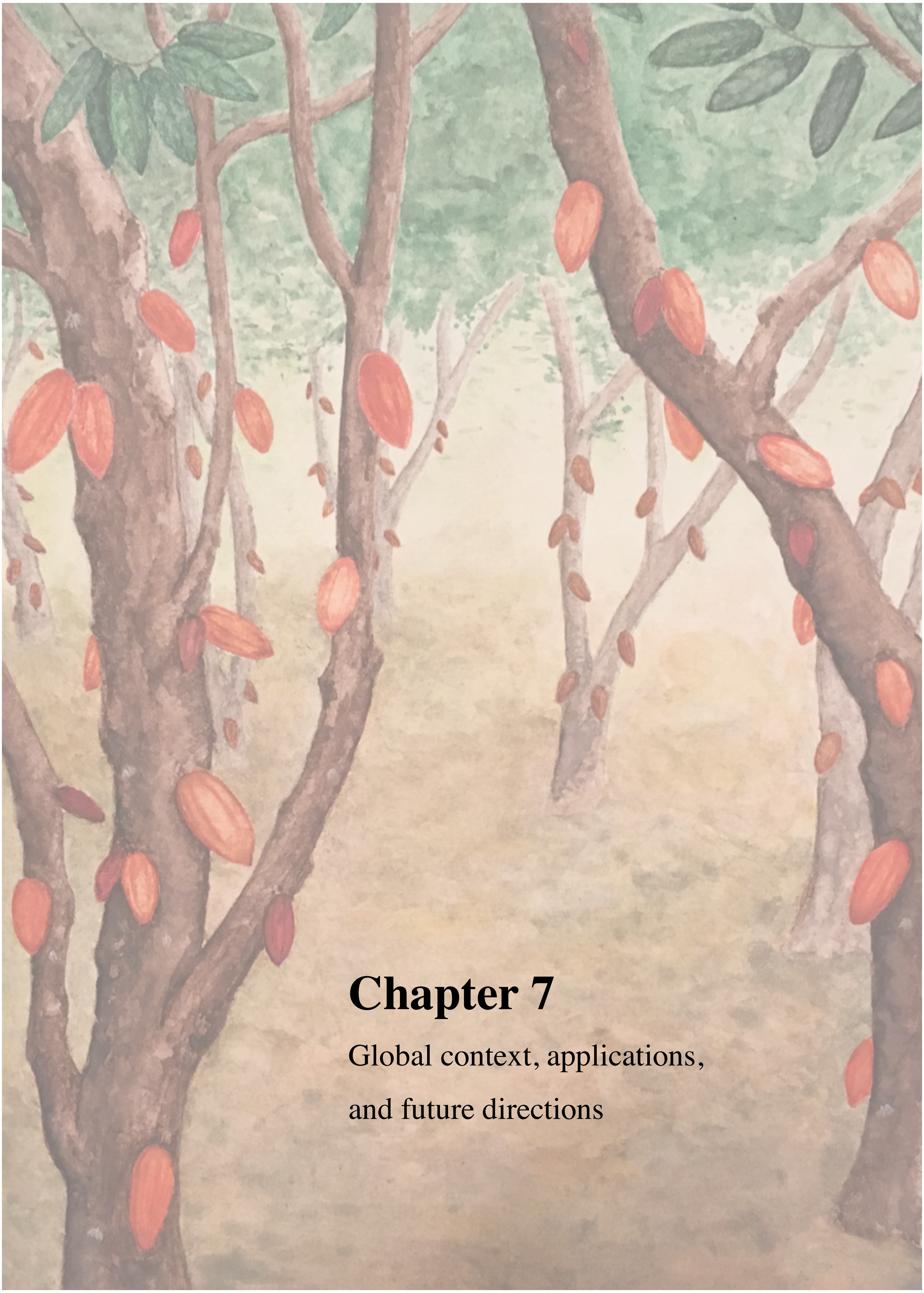
The divergent patterns of biodiversity across taxa and facets of diversity in this study highlight how focusing on one taxonomic group, or using one measure of biodiversity alone, may not be sufficient to assess the wellbeing and conservation value of habitats. Other studies have shown that spatial biodiversity patterns can be uncorrelated across different taxa (Pärt and Söderström, 1999; Wolters, Bengtsson and Zaitsev, 2006; Mandl *et al.*, 2010), with the conclusion that one taxon cannot necessarily be used as a surrogate of others when comparing biodiversity between sites. This research supports the idea that this is also true for temporal biodiversity patterns (Magurran *et al.*, 2018), and illustrates that not all taxa will respond similarly to environmental changes.

Overall correspondence with succession theory and a priori expectations

As with previous research, the results of this study largely deviated from expectations. This is likely due to the starting point of succession being cacao agroforests. Other studies have found that agroforests maintain high levels of biodiversity and some of the ecosystem functions of older forests (dos Santos *et al.*, 2021), and may recover more rapidly as a result.

For example, many studies have found that shade agroforests and systems which mimic natural forest can support diverse animal assemblages, similar structural characteristics, and maintain some ecosystem functions (Calvo and Blake, 1998; Buechley *et al.*, 2015; Rajab *et al.*, 2016; Arroyo-Rodríguez *et al.*, 2017; dos Santos *et al.*, 2021; Schuler *et al.*, 2022). If crop trees are planted in an existing secondary forest, or if native trees are used as shade trees, then species composition could recover more rapidly as well, for example as a direct seed source and by attracting seed dispersers. The maintenance of biodiversity and ecosystem functioning could similarly facilitate regeneration if a more abundant and diverse array of seed dispersers are attracted to the agroforests post abandonment.

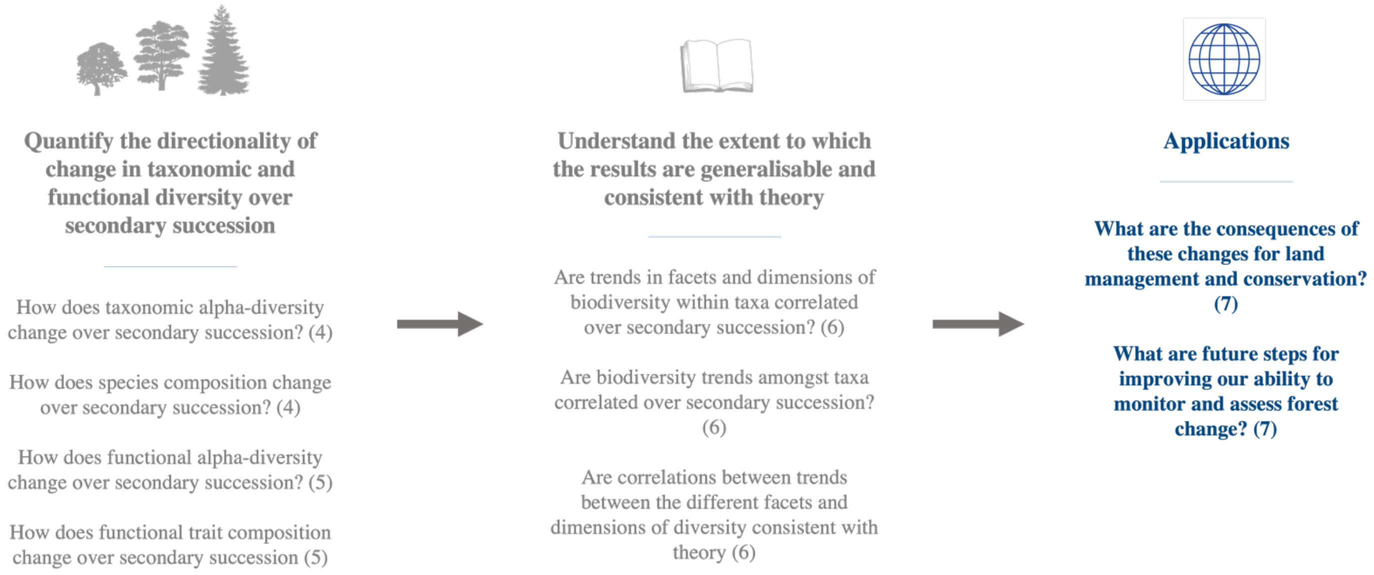
Overall, the lack of congruence between succession theory and the results of this and other research emphasises the gaps in our understanding of successional processes. This is especially true for tropical regions where there are many species and complex ecological interactions, which makes predicting how biodiversity will change following disturbance across taxa all the more challenging. Moving forward, theoretical models of succession will need to account for more of the complexity in these systems, and particularly the role of starting point, spatial and temporal scale, and changes in primary drivers of succession over space and time.



Chapter 7

Global context, applications, and future directions

7.1 Introduction



Quantify the directionality of change in taxonomic and functional diversity over secondary succession

How does taxonomic alpha-diversity change over secondary succession? (4)

How does species composition change over secondary succession? (4)

How does functional alpha-diversity change over secondary succession? (5)

How does functional trait composition change over secondary succession (5)

Understand the extent to which the results are generalisable and consistent with theory

Are trends in facets and dimensions of biodiversity within taxa correlated over secondary succession? (6)

Are biodiversity trends amongst taxa correlated over secondary succession? (6)

Are correlations between trends between the different facets and dimensions of diversity consistent with theory (6)

Applications

What are the consequences of these changes for land management and conservation? (7)

What are future steps for improving our ability to monitor and assess forest change? (7)

Figure 7.1. Schematic of questions being addressed in this thesis. Questions highlighted in blue are the focus of this chapter.

Anthropogenic pressures on ecosystems are growing, and global biodiversity is under unprecedented threat (Chapter 1; Blowes et al., 2019; Isbell et al., 2017; Magurran & Dornelas, 2010). Landscape transformation, including the appropriation natural habitat for crop use, is viewed as a major contributor to this ongoing biodiversity crisis (Ehrlich & Pringle, 2008; Semper-Pascual et al., 2019). This thesis has quantified biodiversity in active and abandoned cacao agroforests and primary forests, and has explored how these forests recover through secondary succession in Trinidad. The results presented in chapters 4-6 showed that tree taxonomic and functional alpha-diversity increased significantly over time, especially within the first 30 years of succession. While this was in line with expectations from theory and research, the other taxa studied showed heterogeneous responses. There was significant change in species and functional trait composition across taxa with forest age, however, even after c. 100 years of succession. The following chapter will place these results into the wider context of biodiversity and land cover change, and explore future directions for research and conservation (Figure 7.1). Section 7.2 will address the value of secondary forests and cacao agroforests to conservation, and how agroforestry systems can work within a people and nature framework to support local livelihoods and biodiversity. Section 7.3 will investigate current knowledge gaps and possibilities for how we can better monitor changes in forest cover and biodiversity moving forward.

7.2 People and nature

Secondary forest

The results presented in chapters 4-6 illustrate that young secondary forests and actively managed cacao agroforests can be valuable for sustaining biodiversity. While tree taxonomic and functional alpha-diversity increased significantly with forest age, the active cacao agroforests and young secondary forests sustained high levels of diversity across taxa overall. Other studies similarly have found that species richness often recovers early in succession across taxa (Chapter 2; Lebrija-Trejos *et al*., 2008; Martin, Newton and Bullock, 2013; Chazdon, 2014; Derroire et al., 2016). Vegetation diversity increases primarily within the first 50 years (Lebrija-Trejos *et al*., 2008; Martin, Newton and Bullock, 2013; Derroire *et al*., 2016), and bird diversity often recovers within the first 30 years (Blake and Loiselle, 2001; Borges, 2007; Karthik et al., 2009; Sberze et al., 2010). Other studies have likewise found that secondary forests provide many other important functions and services such as sequestering carbon and water cycling (Batterman et al., 2013; Davidson et al., 2007; Hassler et al., 2011; Martin, Newton, & Bullock, 2013; Neumann-Cosel et al., 2011; Ogden et al., 2013; Poorter et al., 2016; Zimmermann et al., 2013; Craven et al., 2017). These results emphasise the potential role of secondary forests as biodiversity reservoirs in a rapidly changing world (Chapter 1).

The early recovery of taxonomic and functional alpha-diversity over succession also supports the utility passive restoration programs. Many conservation initiatives involve actively restoring disturbed land, which can be costly and labour-intensive (Díaz-Garcia et al., 2020). Passive restoration, which consists of leaving an area of disturbed land to recover naturally without active management, offers a more cost-effective alternative, though not all disturbed ecosystems will recover without intervention ("arrested succession"; Chazdon, 2003; Arroyo-Rodríguez et al., 2017). Field studies have found contrasting results on the relative effectiveness of passive and active restoration. Some have found that passive restoration is a viable option in many situations (Meli et al., 2017; Crouzeilles et al., 2017), while others disagree (Reid, Fagan and Zahawi, 2018).

Generally, passive restoration is most effective where disturbance has been minimal and brief leaving the soil properties and the soil seed bank largely intact (Guariguata and Ostertag, 2001; Lawrence, 2005; Sovu *et al*., 2009; Derroire *et al*., 2016), where there is remnant vegetation or existing three-dimensional structure such as dead trees (Franklin et al., 2002; Chazdon, 2003; Sandor and Chazdon, 2014), and in areas which are situated within a forested matrix or near mature forest (Chapter 2; Cubiña and Aide, 2001; Hooper, Legendre and Condit, 2004; Derroire et al., 2016, Rolim, Machado and Pillar, 2017). These conditions facilitate regeneration and can increase the rate of forest recovery.

Cacao agroforests often incorporate native remnant vegetation for shade, maintain complex three-dimensional structure, and provide food resources which attract seed dispersers. The sites in this study were all situated near larger tracts of mature forest as well. Abandoned cacao agroforests in Trinidad and similar systems may therefore be good candidates for passive restoration, which can be applied in conjunction with active conservation projects.

Furthermore, the habitat heterogeneity generated from the long history of cacao farming in Trinidad can increase the collective landscape-level diversity (gamma-diversity) when habitat patches support different species (Fischer & Lindenmayer, 2005; Peintinger et al., 2003; Socolar et al., 2016; Tscharntke et al., 2002, 2012). The results presented in Chapter 5 show that there is considerable turnover in species and functional trait composition between forest patches at different stages of succession for multiple taxa. Other studies have similarly shown that forests at different stages of regeneration provide different types of habitat and resources (Dewalt et al., 2003; Bowen et al., 2007). Thus, the patchwork mosaic of forest types making up the Northern Range is contributing to the overall richness of the species pool and maintenance of gamma-diversity.

Conservation has historically focused on preserving pristine natural areas and protecting charismatic species (Barlow et al., 2007; Barnosky et al., 2017; Chazdon, Harvey, et al., 2009; Gardner et al., 2009). However, the proportion of secondary forests and transformed landscapes is growing relative to old-growth forests and unaltered environments globally, and Trinidad is no exception (Chapter 1; Arroyo-Rodríguez et al., 2017; Derroire et al., 2016; Lebrija-Trejos et al., 2008; Martin et al., 2013). Thus, understanding the dynamics and recognising the potential value of altered ecosystems is increasingly important to maximise conservation efforts (Chazdon, 2014; Chazdon, Harvey, et al., 2009; Chazdon, Peres, et al., 2009; DeClerck et al., 2010). Such knowledge can inform key decisions faced in managing biodiversity, including which areas to conserve, when and how to implement restoration initiatives, how populations or ecosystems are likely to respond to perturbation, and how to measure ecosystem health.

Cacao farming

Taken together, the results of this thesis highlight that cacao agroforests can contribute to biodiversity conservation. Research has found that cacao and similarly managed coffee and vanilla agroforests can be remarkably biodiverse, though the ability of these systems to support wildlife depends on how they are managed (Cassano et al., 2011; Schroth et al., 2011; Arroyo-Rodríguez et al., 2017; Buechley et al., 2015; Calvo & Blake, 1998).

Agricultural trees can be either be planted in single-species plantations or in mixed agroforests with multiple different tree species. For example, cacao, coffee, and vanilla are naturally found in the lower canopy layers of a forest and can grow in varying light levels. They can thus be grown either as a monoculture with full sun exposure in “sun plantations,” or in the shade of other trees in “shade agroforests” (Ruf and Schroth, 2004; Waldron *et al.*, 2012; Jezeer *et al.*, 2017; Araújo *et al.*, 2021). Shade agroforests more closely resemble natural forest with a mix of different agricultural trees and taller “shade trees” which provide shade for the shade-tolerant crop trees (Alvim and Nair, 1986; Ruf and Schroth, 2004; Waldron *et al.*, 2012; Rajab et al., 2016; Jezeer *et al.*, 2017; Araújo *et al.*, 2021).

Furthermore, agroforestry systems such as forest gardens, multifunctional agriculture, and successional, dynamic, syntropic, and regenerative analogue agroforestry intentionally mimic natural forests (Young, 2017; dos Santos *et al.*, 2021; Brodbeck, Hapla and Mitloehner, 2022; Schuler *et al.*, 2022). These systems utilise a functionally diverse array of herbaceous and woody crop plants to maintain biodiversity and ecosystem functioning including key services such as improving soil quality, weed suppression, and pest management. As a result, land management is often less intensive and damaging in these systems compared to conventional agricultural practices (Young, 2017; dos Santos *et al.*, 2021; Brodbeck, Hapla and Mitloehner, 2022; Schuler *et al.*, 2022). Traditional, polyculture shade agroforestry systems offer multiple canopy layers and a diverse array of flowering and fruiting plants, and so can provide valuable habitat for wildlife despite being human-managed and dominated by agricultural trees.

There are ongoing debates over the best farming methods for cacao which could lead to the expansion of more intensive sun plantations, however (Waldron et al., 2012). All but one of the active cacao agroforests surveyed in this study were traditionally managed shade-cocoa agroforests. Sun plantations can seem attractive economically in the short-term as the cacao trees may mature more rapidly and produce higher yields. Cacao trees in shade-cocoa systems, however, commonly live longer, may be less susceptible to pests (Ruf & Schroth, 2004; Andres et al., 2016; Jezeer et al., 2017), and are more protected against the effects of climate change depending on the shade trees used (Lin, 2007; Padovan et al., 2015; Schroth, Läderach, Martinez-Valle, Bunn et al., 2016; Schwendenmann et al., 2010; Tscharntke et al., 2011; Vaast and Somarriba, 2014; Abdulai et al., 2017). Shade trees also increase the structural complexity of the agroforests and can contribute towards supporting greater biodiversity across taxa (Araújo-Santos et al., 2021; Jezeer et al., 2017; Waldron et al., 2012). Furthermore, due to the growing market for ethical and environmentally responsible products (Poelmans & Rousseau, 2016), traditional shade-cacao can be more profitable despite lower yields as the cacao can be sold for higher prices (Jezeer et al., 2017). Shade and other crop plants such as mango, orange, avocado, guava, banana, and coconut can provide additional income and greater financial stability for farmers as well.

Further research is needed on the optimal land management strategies for cacao and similar farming systems to maximising benefits both to the farmers and to nature conservation. For example, there may be scope for maintaining native shade tree species, to utilise nitrogen-fixing plants instead of chemical fertilisers, or to implement integrated pest management systems. Some cacao farms in Trinidad also grew epiphytic plants such as dragon fruit (*Hylocereus undatus*) on shade trees, and ornamental *Anthurium* species under cacao trees, which can generate further income for farmers and provide additional habitat for wildlife (personal communication with local farmers). The location of agroforests affects their biodiversity value as well, where cocoa farms close to larger tracts of forest or those situated within a forested matrix are commonly more biodiverse (Chazdon, 2014).

Despite the potential benefits of cacao agroforestry to nature in supporting biodiversity and important ecosystem functions, it is a major driver of tropical deforestation (Chapter 1; Dixon et al., 2001; Vaast and Somarriba, 2014; Borda *et al*., 2021). While cacao farms are commonly expanded at the expense of natural forests, there are more sustainable avenues for development.

For example, successional agroforestry systems (SAFS) and similar systems aim to mimic successional processes, where crops with different tolerances and which provide different functions are planted over time, ultimately forming a diverse polyculture shade agroforest (Young, 2016). The initial planting stage may also include annual and perennial crops and native plants which can tolerate early successional conditions and improve the soil (eg. leguminous species), including shade trees and plants such as *Inga* and *Musa* species. As the system develops, crops such as cacao, coffee and vanilla can be planted in the understory. In this way, each cycle contributes to the land and allows for agroforests to be started in formerly deforested and degraded areas. Moreover, faster-growing crop species planted early on can provide income while slower-growing agroforest crops such as cacao mature. The succession of different crops thus helps offset the initial investment required for starting an environmentally responsible agroforest (Young, 2018).

Additionally, instead of clearing a forest entirely before planting crop trees, some farmers ‘thin’ existing secondary forests and plant shade-tolerant crops such as cacao in the understory, thus keeping much of the natural canopy cover which can include endemic and threatened plant species (Tadesse, Zavaleta and Shennan, 2014; Asigbaase *et al*., 2019). A successful example of this from Trinidad can be seen in the village of Brasso Seco, where the community is reclaiming former cacao agroforests by harvesting cacao pods from abandoned land using low intensity management methods. In this way, no natural forests are being compromised and income is created for local people through the tree-to-bar chocolate products produced (*The Brasso Seco Chocolate Company*, 2022).

Furthermore, unlike annual herbaceous crops, forestry and agricultural systems that include woody vegetation have the potential to expedite regeneration post abandonment. Standing trees can provide microclimates and structural features similar to older forests which can attract animals, increase seed rain, protect against wind and storms, contribute to soil formation, enhance water percolation and stabilise the soil, and create suitable conditions for plant germination (Lambin *et al*., 2001; Franklin *et al*., 2002; Chazdon, 2003; Mora *et al*., 2015; Derroire *et al*., 2016). For example, Parrotta, Turnbull, and Jones (1997) propose that tree plantations can catalyse succession by modifying environmental conditions such as temperature and soil moisture, and by altering animal behaviour such as attracting seed dispersers (Parrotta, Turnbull and Jones, 1997; Rolim *et al*., 2017). In another study, Ferguson et al. (2003) found that successional processes, such as basal-area accumulation and species recruitment, were significantly faster following agroforest abandonment than following pasture abandonment (Ferguson *et al*., 2003).

Though research is limited, 'agro-successional restoration', which integrates forest restoration and agriculture, is being considered as an approach to support reforestation initiatives in tropical regions (Vieira, Holl and Peneireiro, 2009; Jagoret *et al*., 2012). Agro-successional restoration uses successional or polyculture shade agroforests as an initial stage of forest restoration, to reduce the costs of reforestation projects and generate local income while catalysing succession. There is also some evidence that cacao agroforests could be used as wildlife corridors in deforested landscapes (Clough *et al*., 2009; Cabral, Faria and Morante-Filho, 2021).

Finding agricultural systems, such as cacao, that can support biodiversity, has utility in reconciling our need to generate local income and meet demands for food and other goods, with our need to protect biodiversity and important ecosystem functions (Mace, 2014). Cacao, vanilla, coffee, and similar agroforestry systems have the potential to be conservation solutions which support both livelihoods and wildlife in the tropics.

Conclusions

In this study, primary forests had unique combinations of species and functional trait composition, even compared to the oldest secondary forest sites across taxa. This is in line with other studies which suggest that it can take centuries for the species and functional composition of secondary forests to converge with that of old-growth forests (Derroire et al., 2016; Finegan, 1996; Rozendaal et al., 2019). It is clearly important to protect primary forests due to their slow recovery. However, these findings emphasise the potential value of agroforests and secondary forests in sustaining biodiverse assemblages. These habitats are becoming increasingly important reservoirs of biodiversity as the proportion of planted and secondary forests continues to rise relative to primary forest (Ellis, Antill and Kreft, 2012; Martin, Newton and Bullock, 2013). Agroforests and secondary forests not only play an important role in enriching regional biodiversity, but can also provide conservation solutions that support both people and nature.

7.3 Future directions

The results of this study showed considerable mismatches with expectations based on succession theory (Chapter 6). Other empirical research has also yielded mixed results in how ecosystems change over time following disturbance (West, Shugart & Botkin, 1981; Westoby et al., 1989; Tilman, 1990). These inconsistencies may be explained by differences in the starting point of succession, and the spatial and temporal scale at which succession is viewed (West, Shugart & Botkin, 1981; Chapter 2). Despite inconsistent support, succession theory plays a key role in many environmental policies and conservation initiatives including in environmental impact assessments and in mitigating the effects of climate change and habitat loss (West, Shugart & Botkin, 1981). While finding generalities in successional change has been challenging due to the inherent complexity in ecosystems, deepening our understanding of successional patterns and processes helps to improve conservation efforts (Chapters 1 and 6). Further research is needed to better understand and predict successional processes, and to identify generalities across systems and biomes (Chapter 6).

Also contrary to expectation, patterns in biodiversity change varied widely across taxa and facets of biodiversity in this study. This underscores that focusing on one taxonomic group or measuring one aspect of biodiversity may not be sufficient to assess the condition and conservation value of habitats. Other research has shown that spatial biodiversity patterns can be uncorrelated across taxa (Mandl et al., 2010; Pärt & Söderström, 1999; Wolters et al., 2006), with the result that one taxon cannot necessarily be used as a surrogate of others. This study has shown that this is also true for temporal biodiversity patterns (see also: Magurran et al., 2018), and illustrates that not all taxa will respond similarly to disturbance and environmental changes.

Taxonomic and functional diversity were largely uncorrelated in this study. The independent variation in the different facets and aspects of biodiversity stresses the need for taking a multifaceted approach and assessing biodiversity change from multiple angles. Changes in taxonomic composition, functional composition, and ecosystem functioning over time, and the interconnectivity between them, are especially important to consider as they are often the most affected by disturbance and the slowest to recover (Finegan, 1996; Díaz and Cabido, 2001; Chazdon, 2014; Derroire et al., 2016; Rozendaal et al., 2019). Research on functional diversity has grown in popularity, though differences in the traits and analysis methods used make comparisons across studies difficult (Mouchet et al., 2010) and further research on functional diversity change over succession is needed. Major gaps in functional trait information also remain, especially for tropical plant species. The traits used for the functional diversity analyses in this research were restricted to those where information on a sufficient number of species could be obtained, and imputation was required to fill remaining data gaps (Chapter 5; Box 7.1).

Further ecological research in tropical regions is crucial as well. Though tropical forests are exceptionally biodiverse and complex ecosystems, they are less well studied than temperate forests. BioTIME is the largest biodiversity time series database with over 12 million records and 42,000 species from multiple biomes (Dornelas et al., 2018). Despite the extensive coverage of the BioTIME database and ongoing efforts to incorporate new data from around the world, there is regional patchiness in the data available. For example, while there are 64 datasets for terrestrial plants in temperate regions, there are only 20 for tropical regions. Box 7.1 analyses some of these datasets to quantify change in taxonomic and functional diversity with forest age. It reveals clear discrepancies in patterns of taxonomic alpha-diversity change between the temperate and tropical datasets; functional diversity could only be measured for the temperate datasets due to lack of functional trait data for the tropical plant species. The case study presented in Box 7.1 also highlights the potential utility of meta-analyses in assessing the effects of starting point and biome on the rate and trajectory of successional processes. Overall, the comparative dearth of data for tropical regions highlights a major knowledge gap in our understanding of how tropical forests change over time.

Box 7.1 BioTIME temperate and tropical forest change over time

BioTIME is the largest biodiversity time series database with over 12 million records and 42,000 species from around the world (Dornelas et al., 2018). Twenty-four forest timeseries datasets from the BioTIME database were used as an example to compare patterns of tree diversity over time in temperate and tropical forests.

Methods

Species richness, PIE, and Berger-Parker indices were used to quantify temporal change in species α-diversity. Species richness was quantified using extrapolated rarefaction curves, and the diversity values of each assemblage at 400 individuals were plotted over time (Hseih, Ma & Chao, 2016). A positive slope indicates that species richness increased over time. Changes in species evenness (PIE) and dominance (Berger-Parker) over time were also assessed. A positive slope for the PIE analyses indicates that species evenness increased over time, while a positive slope in the Berger-Parker analysis indicates that species dominance increased over time.

Change in species composition over time was quantified using the Jaccard dissimilarity index for each dataset. The rate of change in species composition was measured as the change in Jaccard between each sample in the time series relative to the first sampling time (Jaccard slope). A greater Jaccard slope indicates rapid change in species composition. Linear models were used to further test for overall changes in each diversity index with time. Firstly, GLMs of each diversity index value as a factor of time and dataset were used to assess changes in each diversity metric over time for all data, while controlling for variation between datasets. Further GLMs assessing the interaction between forest type and year were used to test if changes in the diversity metrics over time differed between temperate and tropical forests.

Functional diversity analyses were conducted on the 19 temperate datasets. Tree functional traits used for these analyses were tree maximum height at maturity, longevity, growth form, the presence of armature (eg. spines or thorns), the number of leaves per node, leaf type (eg. broadleaf or needle), whether leaves were compound and leaflet formation, leaf length, leaf morphology and venation pattern, leaf arrangement along the branch, whether the tree produced flowers (angiosperm), and seed type. Trait information was compiled and checked across multiple databases and resources (Hunt, 1984; Collins, 2007; Gilman & Watson, 2014; Russell et al., 2014; Press, 2016; New England Wildflower Society, 2018; ConiferBase, 2022; Keele University Arboretum, 2022; Encyclopedia of Life, 2022). If a tree was only identified to genus level, the most common or average traits for the genus were used. The functional diversity metrics were tested for changes over time using GLMs as the variation in each functional diversity metric with time and survey.

Functional α-diversity was measured using the functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) indices (Villéger, Mason & Mouillot, 2008). The functional diversity metrics were plotted over time, where a positive slope in FRic, FEve, or FDiv values indicates an increase in functional richness, evenness, and divergence respectively (Chapter 3). Functional trait compositional change was measured using the Villegar *et al*. (2008) β-diversity Jaccard-like metric of functional dissimilarity where identical assemblages are zero, and completely unique assemblages are one. The slope of functional β-diversity over time (each time point relative to the first time point) was then measured for each dataset.

Continued

Box 7.1 BioTIME temperate and tropical forest change over time (continued)

Taxonomic diversity

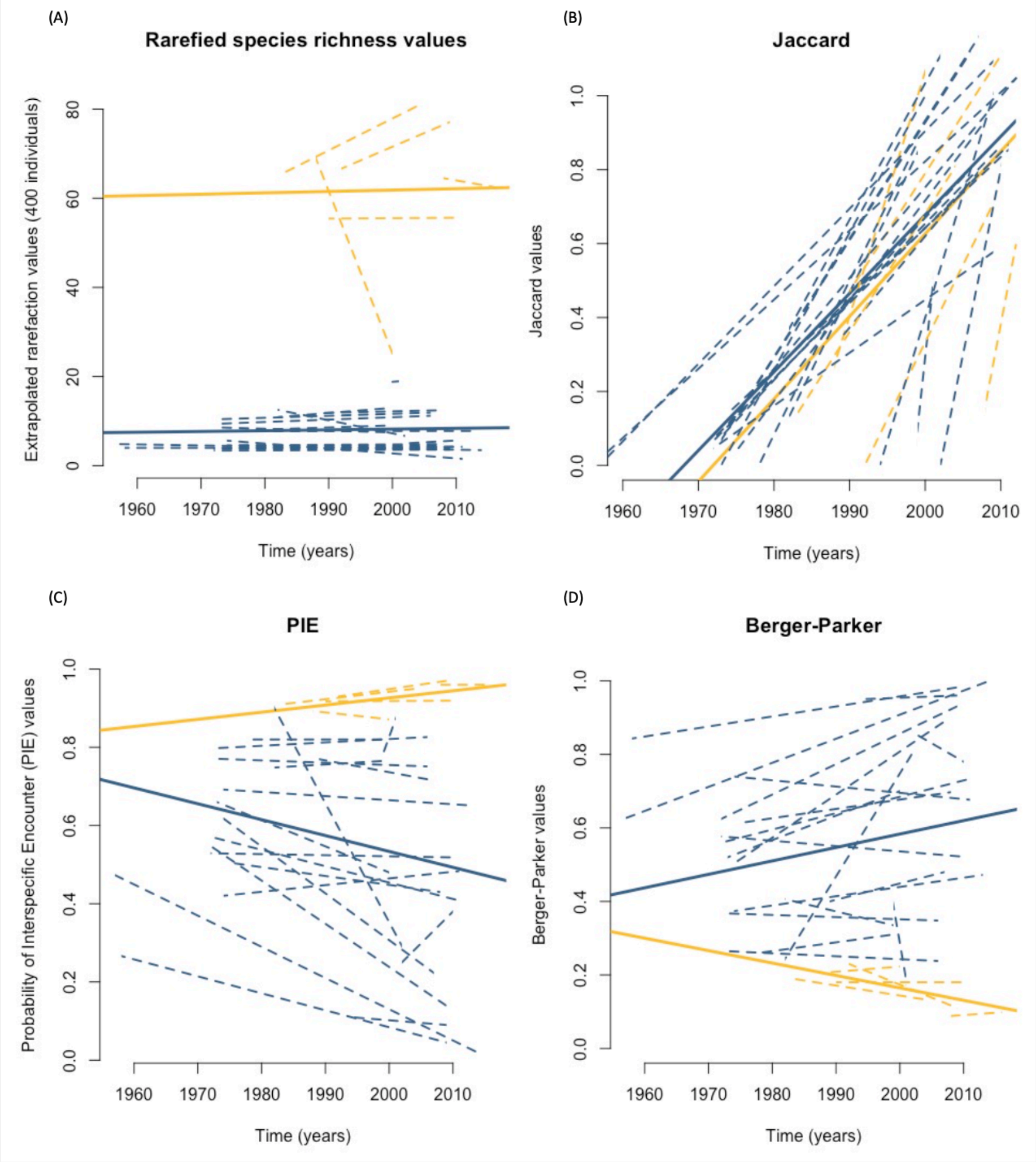


Figure 7.2 Tree species diversity change over time (n=24 datasets). (A) is the species richness (rarefied values to 400 individuals), (B) is the Jaccard beta-diversity index for compositional dissimilarity, (C) is the PIE measure for species evenness, (D) is the Berger-Parker dominance measure. The slope of each diversity metric for each study is shown with a dotted line. Blue represents temperate forest studies and yellow represents tropical forest studies. The overall slope of each diversity metric is shown with a solid line (yellow fitted to all tropical data (n=5 datasets) and blue is fitted to temperate data (n=19 datasets).

Continued

Box 7.1 BioTIME temperate and tropical forest change over time (continued)

There was no significant overall change in species richness over time ($t_{(1,56)}$= -1.5, p=0.13). Forest type likewise did not have a significant effect on species richness change over time ($t_{(1,77)}$= 0.2, p=0.84). There was a significant difference in species richness between tropical and temperate forests across all years, however, with over 5 times more species in tropical assemblages compared to temperate assemblages ($t_{(1,78)}$= 14.08, p<0.001).

Species evenness significantly decreased over time overall ($t_{(1,56)}$= 3.88, p<0.001). There was no significant difference in the change in evenness over time between temperate and tropical forests ($t_{(1,77)}$= 0.97, p=0.33). However, evenness decreased significantly over time in temperate forests and increased over time in tropical forests.

Species dominance significantly increased over time by 0.004 Berger-Parker values per year overall ($t_{(1,56)}$= -4.38, p<0.001). There was no significant difference in the change in dominance over time between temperate and tropical forests ($t_{(1,77)}$= -1.25, p=0.21). conversely with evenness, though, dominance increased significantly over time in temperate forests and decreased over time in tropical forests.

Species dissimilarity (Jaccard) increased significantly over time overall ($t_{(1,56)}$= 10.31, p<0.001). There was no significant difference in how species composition changed over time between temperate and tropical forests ($t_{(1,77)}$= 0.136, p=0.89). Species dissimilarity increased in both temperate and tropical forests.

Functional diversity

In temperate forests, there was no significant change in FRic ($t_{(1,43)}$= 1.78, p=0.8) or in FDiv over time ($t_{(1,77)}$= 0.97, p=0.33). There was a significant decrease in the functional evenness over time, however ($t_{(1,43)}$= -2.47, p=0.02). Functional β-diversity values were generally low (mean = 0.2), though there was a significant increase in β-diversity over time overall ($t_{(1,43)}$= 3.44, p=0.001).

Continued

Box 7.1 BioTIME temperate and tropical forest change over time (continued)

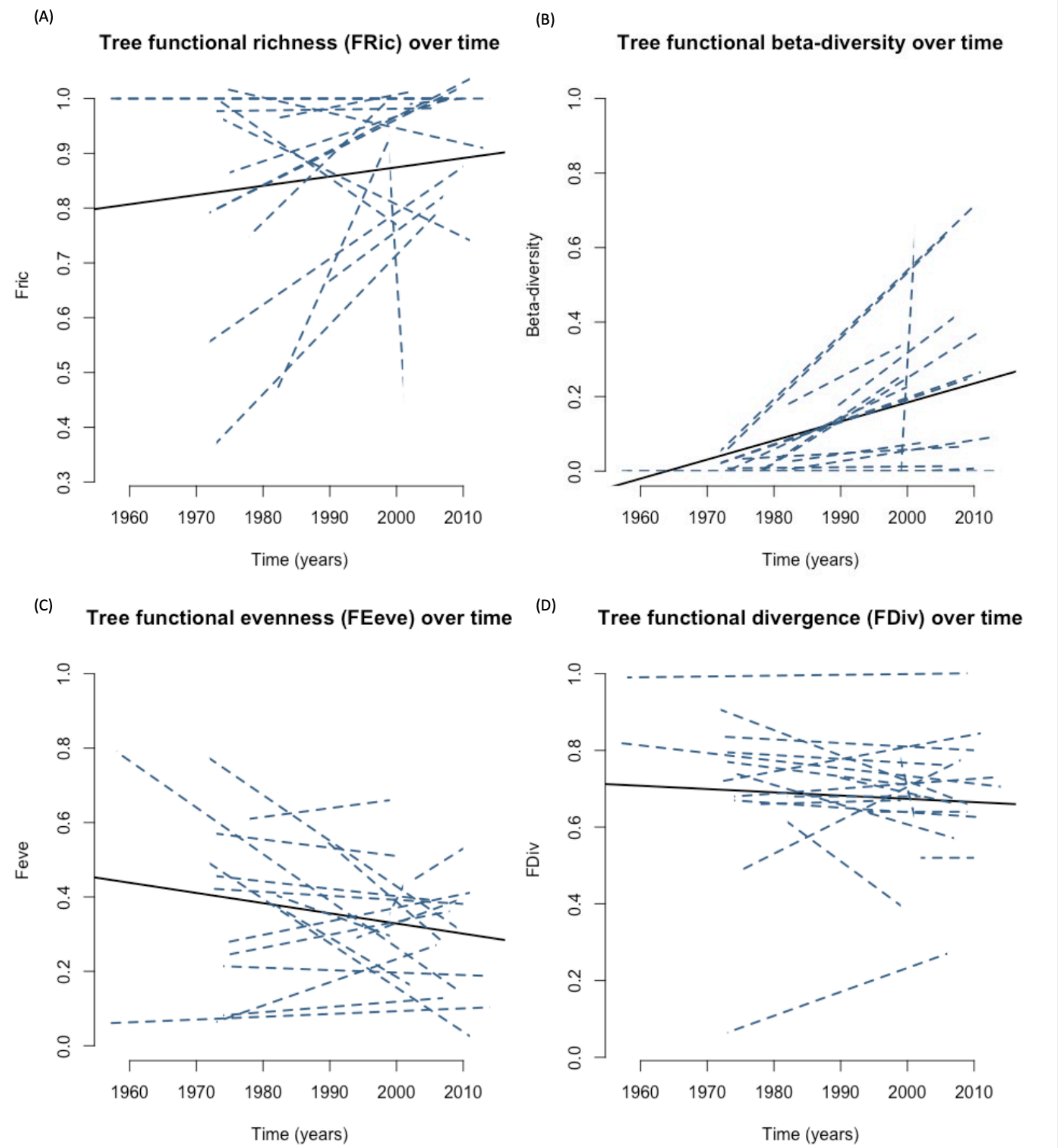


Figure 7.3 Tree functional trait diversity change over time (n=19 temperate datasets). Dotted blue lines represent the slopes of a functional diversity metric over time for individual datasets while the overall slope of all data is shown with a solid black line. (A) is tree functional trait richness (FRic), (B) is tree functional trait dissimilarity (functional beta-diversity), (C) is functional trait evenness (FEve), and (D) is functional trait divergence (FDiv).

Continued

Box 7.1 BioTIME temperate and tropical forest change over time (continued)

Conclusions

Overall, the analysis of these BioTIME datasets found that there was no significant change in species or functional richness over time. Both species and functional evenness decreased significantly, while compositional dissimilarity increased significantly over time. Although there was no statistically significant difference in how the species diversity indices changed over time between temperate and tropical forests, they do appear to have different trends. Tropical forests were generally more species rich, and increased in evenness and decreased in dominance over time. Temperate forests had the opposite trends.

There was also a high degree of variation between datasets within temperate and tropical biomes. These datasets incorporate multiple forest types beyond tropical and temperate (dry and wet forests, and different conditions at the starting point of these time series) which may affect how biodiversity changes over time (Chapter 2). Further accounting for these differences may improve the detectability of trends in forest biodiversity change

Overall, these analyses indicate that temperate and tropical forests change differently over time. More research is needed to better understand successional dynamics in tropical ecosystems. Furthermore, functional diversity analyses were not conducted on the tropical forest assemblages due to a lack of functional trait data for many of the species. This further demonstrates the exigency of research on tropical species and ecosystems.

Lastly, while field research can help provide a nuanced understanding of these ecosystems, it is spatially limited, laborious, and costly to conduct (Levrel et al., 2010). Tropical ecosystems can be especially challenging to study as they are often less accessible, the terrain is more difficult to navigate, and infrastructure is commonly limited. Remote sensing (RS) is gaining momentum as a means of studying spatial and temporal changes in vegetation diversity and land cover at regional and global scales (Box 7.2; Malatu et al., 2017; Anderson, 2018; Hansen et al., 2013; Luque et al., 2018). However, there are some limits in using RS to monitor biodiversity and landcover change. For example, RS only provides information on the top-most layer of vegetation, uses spectral species which may not align perfectly with patterns of species diversity, and relies heavily on the quality of the satellite images (Rocchini et al., 2016; Malatu et al., 2017; Anderson, 2018; Luque et al., 2018; Wang et al., 2019; Rocchini et al., 2021). This is illustrated in Box 7.2 where taxonomic diversity generated using field data presented in this thesis (Chapter 3) and diversity estimates generated using RS techniques for the same sites in Trinidad are compared. Results from the case study showed that, unlike the field data, the remote sensing data did not detect a significant change in alpha-diversity with forest age. However, RS shows promise in extrapolating on ground data to map vegetation diversity and habitat condition similar to the work presented in the RS case study, which would be especially useful in tropical regions where field research can be difficult.

Box 7.2 Remote sensing

Biodiversity is often monitored using field-based approaches (Rozendaal et al., 2019) which can be difficult, slow, and costly (Levrel et al., 2010). These challenges can be especially acute in tropical regions where sites are often less accessible, the terrain more difficult to navigate, and infrastructure may be limited. Surveying biodiversity and land cover at large spatial scales is essential for efficient monitoring and informed policymaking (Schiller et al., 2001). Scaling up field-based research has proved challenging (Barton et al., 2013; Cardinale et al., 2018), however, and new strategies are needed (Proença et al., 2017).

Remote sensing (RS) presents a solution for monitoring large-scale changes in vegetation cover and biodiversity (Rocchini et al., 2016; Malatu et al., 2017; Anderson, 2018; Luque et al., 2018; Wang et al., 2019; Rocchini et al., 2021). Studies have shown that remote sensing can be used for species identification (Clark et al., 2005; Féret et al., 2013; Baldeck et al., 2015), species diversity assessment and community mapping (Vaglio et al., 2016; Draper et al., 2019), and for research on plant functional diversity (Asner et al., 2017; Schneider et al., 2017; Duran et al., 2019). The following case study compares changes in vegetation biodiversity over c. 100 years of secondary succession following cacao agroforest abandonment, as detected by RS data compared to the field research presented in Chapters 3 and 4. Further information on this case study can be found in Chraibi et al. (2021).

Methods

19 of the 29 forest sites in Trinidad (see Chapter 3.2) were analysed using both field and remote sensing techniques. The sites included five of the active cacao agroforests, five of the 25-50 year old, and seven of the 60-100 year old secondary forests regrowing following cacao agroforest abandonment. Two of the primary forests sites were used for comparison. Site choice was limited due to persistent cloud cover which prevented remote sensing analyses. Field surveys were conducted in accordance with the methods outlined in Chapter 3.

The RS data presented here were compiled by Chraibi, Féret, and Luque using the methods detailed in Chraibi et al. (2021). The RS analyses were based on multispectral images obtained from the Sentinel-2 (S2) satellites (Copernicus open access hub, 2020). The S2 image (tile T20PPS of the S2 tiling grid) taken on February 13 2019 was used as it corresponded with the timing of the field data collection, included the most plots, and had <50% cloud cover.

Continued

Box 7.2 Remote sensing (continued)

Diversity indices were quantified for the remote sensing data using the R package BiodivMapR (Féret and Boissieu, 2020) developed by Féret and Asner (Féret and Asner, 2014; Chraibi et al., 2021). This method extracts information on the diversity of spectral signals in a given area, and aims to assign a "spectral species" to each pixel. Diversity indices can then be quantified for the spectral species assemblage similarly to the tree assemblage data from field surveys.

Shannon diversity (Chapter 3.1) was used to measure tree alpha-diversity, and Bray Curtis dissimilarity (BC; Bray and Curtis, 1957; Magurran, 2004) was used to measure beta-diversity. BC is bound between 0 and 1 where higher values indicate greater compositional dissimilarity and lower values indicate greater compositional similarity between sites. Spearman correlations were used to assess change in Shannon diversity with forest age and between field and RS-derived data. 0.5 quantile regressions were used to assess changes in BC with age difference between site pairs (Chapter 3.1; Koenker, 2013). A tanglegram was used to compare field tree species composition and RS vegetation spectral species composition (BC change between sites; Chapters 3.1 and 6.2; Maechler et al., 2022).

Results

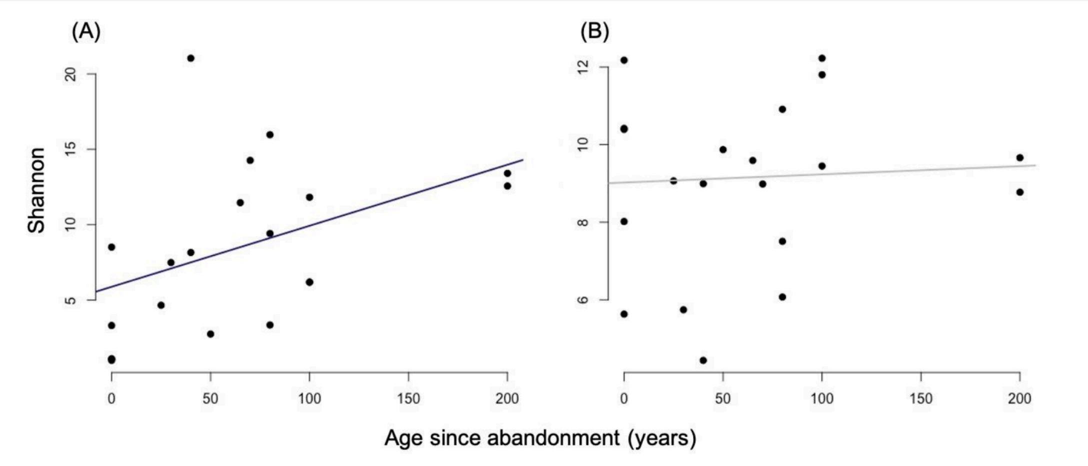


Figure 7.4 Shannon diversity with forest age using field data (A) and RS data (B). Primary forests are given a conservative age estimate of 200 years old. Blue lines indicate a significant correlation between Shannon diversity and forest age.

There was a significant correlation between Shannon diversity and forest age using field data ($r_s = 0.50$, $p = 0.03$), but not using RS data (Figure 7.4; $r_s = 0.05$, $p = 0.85$). There was also no correlation between the two datasets ($r_s = -0.37$, $p = 0.21$). Quantile regressions showed that there was a significant increase in compositional dissimilarity with increasing age difference between sites for both field ($t_{(169,\,171)} = 6.70$, $p < 0.001$) and RS data (Figure 7.5; $t_{(169,\,171)} = 5.18$, $p < 0.001$).

Continued

Box 7.2 Remote sensing (continued)

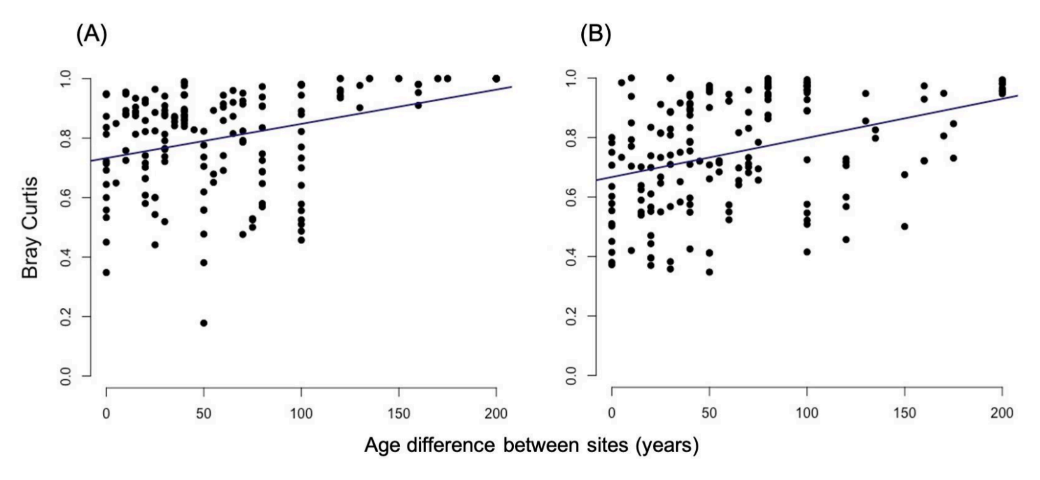


Figure 7.5 Quantile regression of Bray Curtis dissimilarity with age difference between site pairs using field data (A) and RS data (B). Primary forests are given a conservative age estimate of 200 years old. Blue lines indicate a significant correlation between Shannon diversity and forest age.

While a tanglegram found that the two dendrograms of Bray Curtis dissimilarity between sites using field data and RS data aligned well (entanglement =0.15; side2step method), there was no significant correlation between the topologies of the field and RS dendrograms (Figure 7.6; cophenetic correlation coefficient = 0.08).

Continued

Box 7.2 Remote sensing (continued)

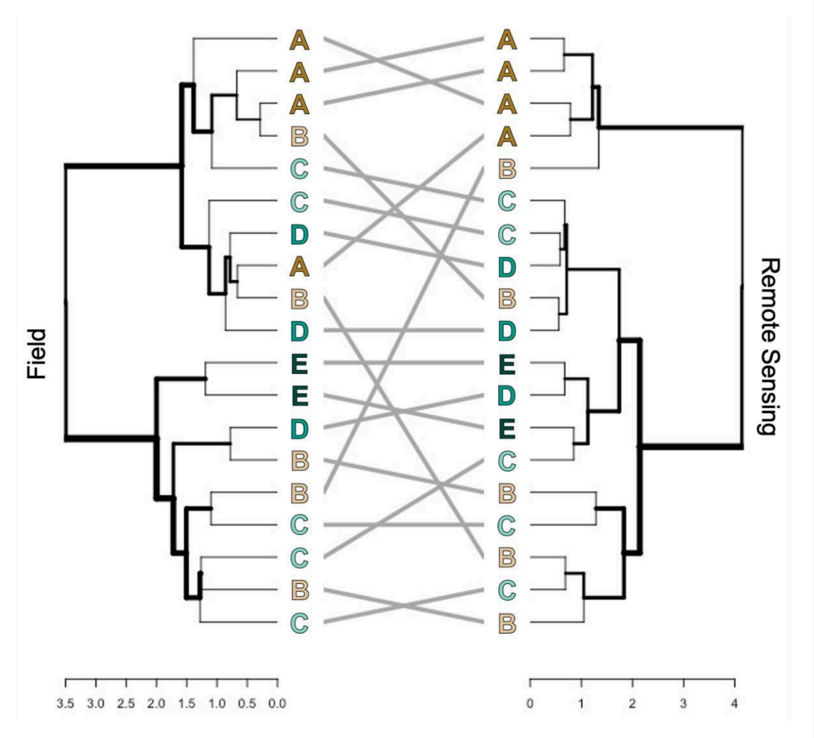


Figure 7.6 Tanglegram comparing Bray Curtis dissimilarity between field ad RS data. Dendrograms for field data (left) and RS data (right) are based on the degree of compositional dissimilarity between sites using hierarchical clustering. Grey lines connect corresponding sites. Sites are labelled according to age category: active agroforests (A), 25-50yo secondary forests (B), 60-80yo secondary forests (C), >100yo secondary forests (D) and primary forests (E).

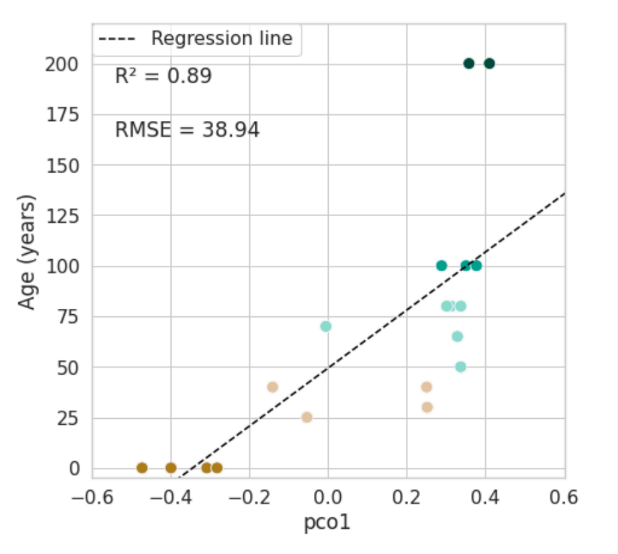


Figure 7.7 Linear regression of the first component of a PCoA analysis using BC dissimilarity and forest age for RS data.

Continued

Box 7.2 Remote sensing (continued)

The first component of the PCoA using RS Bray Curtis information was strongly correlated with forest age (Figure 7.7; R2=0.89). The linear relationship between pco1 and BC was then used to extrapolate on existing data and estimate forest age over the entire S2 image (Figure 7.8). There was high overlap between 100 year old secondary forests and primary forests at around 0.4, however, which limited the maximum age estimates to 120 years.

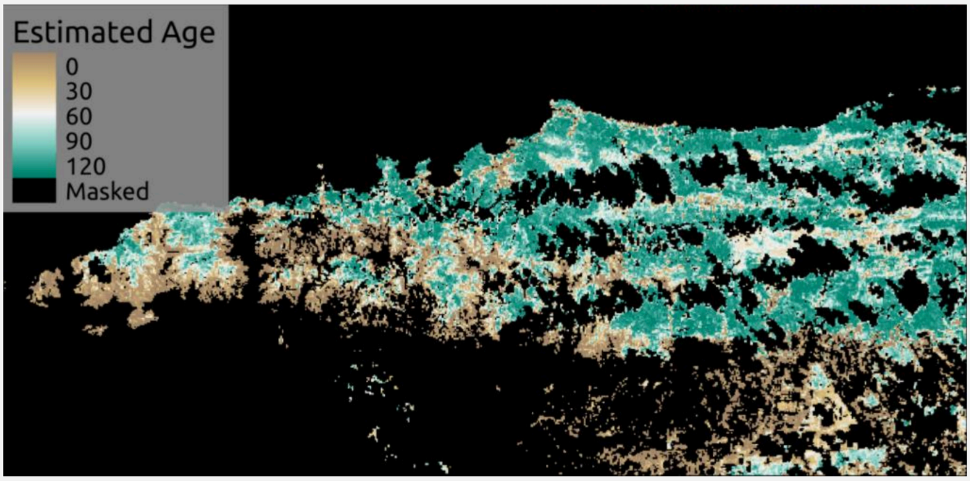


Figure 7.8 Map of forest age estimates

The map of forest age estimates indicated that more than 20% of tiles consisted of young forests (<10y abandoned), primarily in the southwest of Trinidad's Northern Range. Most of the Northern Range mountains had older forest cover, however, especially in the North-West of the region.

Conclusions

Overall, there was little congruence in patterns of biodiversity change between RS and field data. This is likely because RS cannot penetrate to the lower strata of forests and so primarily detects spectral signals from the canopy-layer. The field surveys included relatively small saplings and understory trees (>3m in height and 6cm DBH) in order to ensure cacao trees, which tend to be small multi-stemmed trees, were incorporated. Furthermore, RS analyses are based on spectral species. Different species may have similar spectral signals and so be lumped together as the same spectral species which could inhibit the ability of RS methods to detect changes in biodiversity when compared to taxonomic diversity (Wallis et al., 2017). It could therefore be that RS more closely aligns with functional diversity, especially using photosynthetic traits and forest structure, than with taxonomic diversity (Schneider et al., 2017; Ma et al., 2019; Aguirre-Gutiérrez, 2021). Other studies have had success in using RS methods to estimate alpha-diversity (Schäfer et al., 2016), and thus it could be that incorporating more sites and larger sites in the analyses would yield more comparable results between the field and RS data (Wang et al., 2018).

Continued

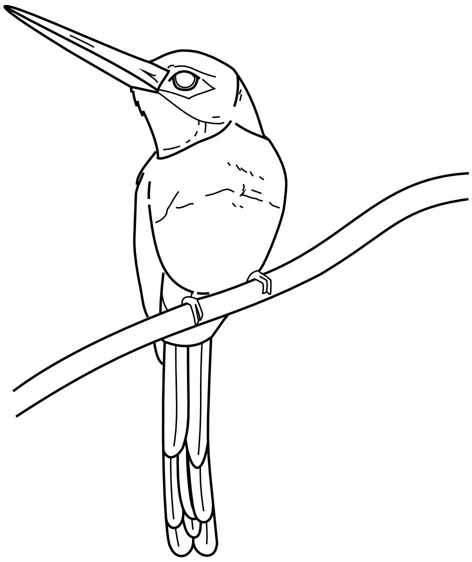
Box 7.2 Remote sensing (continued)

RS was able to detect distinct compositional change with forest age, however. This allowed RS to be used to scale-up field surveys and generate a map of forest successional age for the region despite the limited data. The results of this map are in line with expectations of forest age for the Northern Range. Forests in the southwest are more densely populated and easier to access (Helmer et al., 2012), and so have experienced greater anthropogenic disturbance and modification. Conversely, forests in the northeast of the region and those at higher altitudes are more remote with fewer roads and settlements and likely older. Understanding patterns of forest cover can provide important insight into both local and landscape-level ecological processes and patterns of biodiversity. For instance, the matrix surrounding an agroforest can mediate its habitat value, as well as the rate and trajectory of succession (Cebral et al., 2021). Maps of forest age can also deepen our understanding of habitat connectivity and regional gamma diversity as forests at different stages of succession provide different amounts and types of habitat and resources (DeWalt et al., 2003; Bowen et al., 2007; Chazdon, 2014). RS therefore provides valuable complementary information to field studies, and there is scope for its further use in monitoring large-scale changes in biodiversity and land cover.

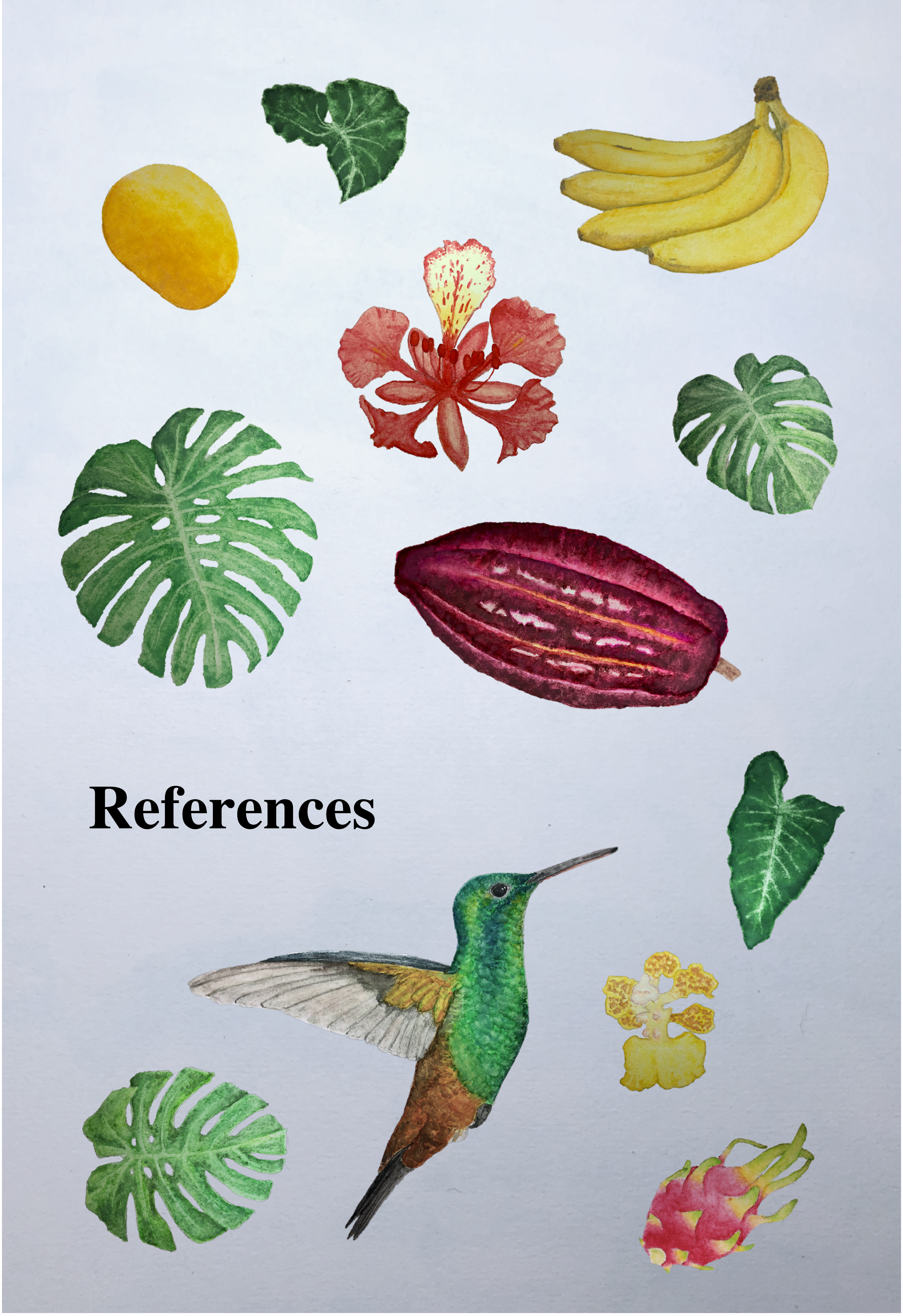
Overall, this thesis has highlighted gaps in succession theory and our understanding of biodiversity change over succession across taxa, especially in biodiverse tropical regions. Further studies that consider multiple facets and aspects of biodiversity, and which assess change in multiple taxa would help fill gaps in our understanding of successional processes. Biodiversity time-series meta-analyses and advances in remote sensing are useful tools for uncovering generalities in successional processes and for providing a more global context of how biodiversity is changing over time and space. As land continues to be transformed for and by human use, it is crucial that we monitor and understand what these changes mean for biodiversity conservation and how ecosystems respond at multiple levels to disturbance.

Table 7.1 Principal conclusions

Preserving primary forests is important as the recovery of species and functional composition over secondary succession can take centuries.
Secondary forests are becoming increasingly important biodiversity reservoirs, and patchwork landscapes can contribute to regional gamma-diversity.
Cacao agroforests and similar systems can be conservation solutions which support both people and nature. Traditional farming methods are more beneficial than intensive sun plantations to wildlife and may ultimately provide a more lucrative and stable source of income.
Species and functional alpha-diversity recover quickly, highlighting the potential utility of passive habitat restoration, SAFS, agro-successional restoration, and similar systems to supplement ongoing conservation initiatives.
There is a need for better succession theory to improve conservation policy and actions which incorporates more of the variability in succession processes, especially regarding the role of starting point, temporal and spatial scale and the idea of a climax state.
There are major ecological data gaps in biodiverse, yet under-studied, tropical regions limiting our understanding of these systems.
Future research should take a more multifaceted approach by surveying multiple aspects and facets of biodiversity change across multiple taxa.
Meta-analyses and remote sensing offer opportunities to monitor changes in biodiversity and land cover at large spatial and temporal scales, and to uncover generalities in responses to disturbance.



References



References

Abbas, S. *et al.* (2019) 'The accumulation of species and recovery of species composition along a 70 year succession in a tropical secondary forest', *Ecological Indicators*, 106, p. 105524. doi:10.1016/j.ecolind.2019.105524.

Acevedo-Charry, O. and Aide, T.M. (2019) 'Recovery of amphibian, reptile, bird and mammal diversity during secondary forest succession in the tropics', *Oikos*, 128(8), pp. 1065–1078. doi:10.1111/oik.06252.

Adams, C.C. (1908) 'The Ecological Succession of Birds', *The Auk*, 25(2), pp. 109–153. doi:10.2307/4070690.

Aerts, R. and Honnay, O. (2011) 'Forest restoration, biodiversity and ecosystem functioning', *BMC Ecology*, 11(1), p. 29. doi:10.1186/1472-6785-11-29.

Alho, C.J.R. (2008) 'The value of biodiversity', *Brazilian Journal of Biology*, 68, pp. 1115–1118. doi:10.1590/S1519-69842008000500018.

Álvarez-Yépiz, J.C. *et al.* (2008) 'Variation in vegetation structure and soil properties related to land use history of old-growth and secondary tropical dry forests in northwestern Mexico', *Forest Ecology and Management*, 256(3), pp. 355–366. doi:10.1016/j.foreco.2008.04.049.

Anderson, W.R. (1990) 'Notes on Neotropical Malpighiaceae-III', 17, p. 15.

Araújo-Santos, I. *et al.* (2021) 'Seed rain in cocoa agroforests is induced by effects of forest loss on frugivorous birds and management intensity', *Agriculture, Ecosystems & Environment*, 313, p. 107380. doi:10.1016/j.agee.2021.107380.

Arroyo-Rodríguez, V. *et al.* (2017) 'Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research', *Biological Reviews*, 92(1), pp. 326–340. doi:https://doi.org/10.1111/brv.12231.

Asigbaase, M. *et al.* (2019) 'Tree diversity and its ecological importance value in organic and conventional cocoa agroforests in Ghana', *PLOS ONE*, 14(1), p. e0210557. doi:10.1371/journal.pone.0210557.

Augusto, L., Dupouey, J.-L. and Ranger, J. (2003) 'Effects of tree species on understory vegetation and environmental conditions in temperate forests', *Annals of Forest Science*, 60(8), pp. 823–831. doi:10.1051/forest:2003077.

Aximoff, I., Soares, H. and Bernadello, G. (2020) 'Acnistus arborescens (Solanaceae): an important food resource for birds in an Atlantic Forest site, Southeastern Brazil', *Rodriguésia*, 71. doi:10.1590/2175-7860202071030.

Bai, Y. *et al.* (2004) 'Ecosystem stability and compensatory effects in the Inner Mongolia grassland', *Nature*, 431(7005), pp. 181–184. doi:10.1038/nature02850.

Barber, C.B., Dobkin, D.P. and Huhdanpaa, H. (1996) ‘The quickhull algorithm for convex hulls’, *ACM Transactions on Mathematical Software*, 22(4), pp. 469–483. doi:10.1145/235815.235821.

Barbier, S., Gosselin, F. and Balandier, P. (2008) ‘Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests’, *Forest Ecology and Management*, 254(1), pp. 1–15. doi:10.1016/j.foreco.2007.09.038.

Barlow, J. *et al.* (2007) ‘Quantifying the biodiversity value of tropical primary, secondary, and plantation forests’, *Proceedings of the National Academy of Sciences of the United States of America*, 104(47), pp. 18555–18560. doi:10.1073/pnas.0703333104.

Barlow, Jos *et al.* (2007) ‘The value of primary, secondary and plantation forests for Amazonian birds’, *Biological Conservation*, 136(2), pp. 212–231. doi:10.1016/j.biocon.2006.11.021.

Barnagaud, J.-Y. *et al.* (2017) ‘Temporal changes in bird functional diversity across the United States’, *Oecologia*, 185(4), pp. 737–748. doi:10.1007/s00442-017-3967-4.

Barnosky, A.D. *et al.* (2011) ‘Has the Earth’s sixth mass extinction already arrived?’, *Nature*, 471(7336), pp. 51–57. doi:10.1038/nature09678.

Barnosky, A.D. *et al.* (2017) ‘Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems’, *Science*, 355(6325), p. eaah4787.

Batkhuu, N. and Udval, B. (2013) ‘Seed and Cone Characteristics of Scots pine (Pinus sylvestris L.) from Diverse Seed Sources in Northern Mongolia’, *Eurasian Journal of Forest Research*, 16, pp. 57–62.

Baxter, T. (2018) ‘Birch identification’, p. 11.

Bazzaz, F.A. (1991) ‘Habitat Selection in Plants’, *The American Naturalist*, 137, pp. S116–S130.

Bekele, F. (2004) *The History of Cocoa Production in Trinidad and Tobago*. APASTT.

Bekele, F.L. (2004) ‘The history of cocoa production in Trinidad and Tobago’.

Belinchón, R. *et al.* (2007) ‘Edge effects on epiphytic communities in a Mediterranean Quercus pyrenaica forest’, *Journal of Vegetation Science*, 18(1), pp. 81–90. doi:10.1111/j.1654-1103.2007.tb02518.x.

Benton, T.G. *et al.* (2021) ‘Food system impacts on biodiversity loss’, p. 75.

Benzing, D.H. (1998) ‘Vulnerabilities of Tropical Forests to Climate Change: The Significance of Resident Epiphytes’, in Markham, A. (ed.) *Potential Impacts of Climate Change on Tropical Forest Ecosystems*. Dordrecht: Springer Netherlands, pp. 379–400. doi:10.1007/978-94-017-2730-3_19.

Betts, M. *et al.* (2017) ‘Global forest loss disproportionately erodes biodiversity in intact landscapes’, *Nature* [Preprint]. doi:10.1038/nature23285.

Bhaskar, R., Dawson, T.E. and Balvanera, P. (2014) 'Community assembly and functional diversity along succession post-management', *Functional Ecology*, 28(5), pp. 1256–1265. doi:10.1111/1365-2435.12257.

Bihn, J.H., Gebauer, G. and Brandl, R. (2010) 'Loss of functional diversity of ant assemblages in secondary tropical forests', *Ecology*, 91(3), pp. 782–792. doi:10.1890/08-1276.1.

BirdLife International (2020) *Birdlife International: Data Zone*. Available at: http://datazone.birdlife.org/home.

Blake, J.G. and Loiselle, B.A. (2001) 'Bird Assemblages in Second-Growth and Old-Growth Forests, Costa Rica: Perspectives From Mist Nets and Point Counts', *The Auk*, 118(2), pp. 304–326. doi:10.1093/auk/118.2.304.

Blanchard, G. *et al*. (2021) 'Drivers of tree community assembly during tropical forest post-fire succession in anthropogenic savannas', *Perspectives in Plant Ecology, Evolution and Systematics*, 52, p. 125630. doi:10.1016/j.ppees.2021.125630.

Blanco, F. *et al*. (2021) 'Punctuated ecological equilibrium in mammal communities over evolutionary time scales', *Science*, 372(6539), pp. 300–303. doi:10.1126/science.abd5110.

Bleiweiss, R. *et al*. (2019) 'Bird visitation to a high Andean Anthurium (Araceae) in Eastern Ecuador', *Flora*, 255, pp. 80–85. doi:10.1016/j.flora.2019.02.010.

Blowes, S.A. *et al*. (2019) 'The geography of biodiversity change in marine and terrestrial assemblages', *Science*, 366(6463), pp. 339–345. doi:10.1126/science.aaw1620.

Böhnke, M. *et al*. (2014) 'Maintenance of constant functional diversity during secondary succession of a subtropical forest in China', *Journal of Vegetation Science*, 25(3), pp. 897–911. doi:10.1111/jvs.12114.

Borda, A. *et al*. (2021) 'Addressing Sustainable Rural Development with Shared Value: A Peruvian Model from the Cacao Industry', *Sustainability*, 13(14), p. 8028. doi:10.3390/su13148028.

Borges, S.H. (2007) 'Bird assemblages in secondary forests developing after slash-and-burn agriculture in the Brazilian Amazon', *Journal of Tropical Ecology*, 23(4), pp. 469–477. doi:10.1017/S0266467407004105.

Borges, S.H. *et al*. (2021) 'Sucessional trajetories of bird assemblages in amazonian secondary forests: Perspectives from complementary biodiversity dimensions', *Forest Ecology and Management*, 483, p. 118731. doi:10.1016/j.foreco.2020.118731.

Bosselman, F.P. and Tarlock, A.D. (1994) 'The Influence of Ecological Science on American Law: An Introduction', 69, p. 29.

Boukili, V.K. and Chazdon, R.L. (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, pp. 37–47. doi:10.1016/j.ppees.2016.11.003.

Bowen, M.E. *et al*. (2007) 'Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna', *Biological Conservation*, 140(3), pp. 273–296. doi:10.1016/j.biocon.2007.08.012.

Bowman, A. and Azzalini, A. (2021) *sm: Smoothing Methods for Nonparametric Regression and Density Estimation*. Available at: https://CRAN.R-project.org/package=sm (Accessed: 24 May 2022).

Bradshaw, C.J., Sodhi, N.S. and Brook, B.W. (2009) 'Tropical turmoil: a biodiversity tragedy in progress', *Frontiers in Ecology and the Environment*, 7(2), pp. 79–87. doi:https://doi.org/10.1890/070193.

Brancalion, P.H.S. *et al*. (2019) 'Global restoration opportunities in tropical rainforest landscapes', *Science Advances*, 5(7), p. eaav3223. doi:10.1126/sciadv.aav3223.

Breugel, M. van, Martínez-Ramos, M. and Bongers, F. (2006) 'Community dynamics during early secondary succession in Mexican tropical rain forests', *Journal of Tropical Ecology*, 22(6), pp. 663–674. doi:10.1017/S0266467406003452.

Brockerhoff, E.G. *et al*. (2017) 'Forest biodiversity, ecosystem functioning and the provision of ecosystem services', *Biodiversity and Conservation*, 26(13), pp. 3005–3035. doi:10.1007/s10531-017-1453-2.

Brodbeck, F., Hapla, F. and Mitloehner, R. (2022) 'Traditional forest gardens as "safety net" for rural households in Central Sulawesi, Indonesia'.

Brotons, L. and Herrando, S. (2001) 'Factors affecting bird communities in fragments ofsecondary pine forests in the north-western Mediterranean basin', *Acta Oecologica*, 22(1), pp. 21–31.

Brown, J.H. *et al*. (2001) 'Regulation of diversity: maintenance of species richness in changing environments', *Oecologia*, 126(3), pp. 321–332. doi:10.1007/s004420000536.

Brown, S. and Lugo, A.E. (1990) 'Effects of forest clearing and succession on the carbon and nitrogen content of soils in Puerto Rico and US Virgin Islands', *Plant and Soil*, 124(1), pp. 53–64. doi:10.1007/BF00010931.

Brunialti, G. *et al*. (2010) 'Lichens and bryophytes as indicators of old-growth features in Mediterranean forests', *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, 144(1), pp. 221–233. doi:10.1080/11263500903560959.

Buckland, S.T., Marsden, S.J. and Green, R.E. (2008) 'Estimating bird abundance: making methods work', *Bird Conservation International*, 18(S1), pp. S91–S108. doi:10.1017/S0959270908000294.

Buechley, E.R. *et al*. (2015) 'Importance of Ethiopian shade coffee farms for forest bird conservation', *Biological Conservation*, 188, pp. 50–60.

CABI (2021) *Invasive Species Compendium*, *CAB International*. Available at: https://www.cabi.org/isc/.

Cabral, J.P., Faria, D. and Morante-Filho, J.C. (2021) 'Landscape composition is more important than local vegetation structure for understory birds in cocoa agroforestry systems', *Forest Ecology and Management*, 481, p. 118704. doi:10.1016/j.foreco.2020.118704.

Cade, B.S. and Noon, B.R. (2003) 'A gentle introduction to quantile regression for ecologists', *Frontiers in Ecology and the Environment*, 1(8), pp. 412–420. doi:https://doi.org/10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2.

Cadotte, M.W. (2017) 'Functional traits explain ecosystem function through opposing mechanisms', *Ecology Letters*, 20(8), pp. 989–996. doi:10.1111/ele.12796.

Cadotte, M.W., Carscadden, K. and Mirotchnick, N. (2011) 'Beyond species: functional diversity and the maintenance of ecological processes and services', *Journal of Applied Ecology*, 48(5), pp. 1079–1087. doi:10.1111/j.1365-2664.2011.02048.x.

Calvo, L. and Blake, J. (1998) 'Bird diversity and abundance on two different shade coffee plantations in Guatemala', *Bird Conservation International*, 8(3), pp. 297–308.

Campbell, J. and Fredeen, A.L. (2004) 'Lobaria pulmonaria abundance as an indicator of macrolichen diversity in Interior Cedar Hemlock forests of east-central British Columbia', *Canadian Journal of Botany*, 82(7), pp. 970–982. doi:10.1139/b04-074.

Campos-Silva, L.A. and Piratelli, A.J. (2021) 'Vegetation structure drives taxonomic diversity and functional traits of birds in urban private native forest fragments', *Urban Ecosystems*, 24(2), pp. 375–390. doi:10.1007/s11252-020-01045-8.

Cardinale, B.J. *et al.* (2012) 'Biodiversity loss and its impact on humanity', *Nature*, 486(7401), pp. 59–67. doi:10.1038/nature11148.

Catterall, C.P. (2018) 'Fauna as passengers and drivers in vegetation restoration: A synthesis of processes and evidence', *Ecological Management & Restoration*, 19(S1), pp. 54–62. doi:10.1111/emr.12306.

Cequinel, A. *et al.* (2018) 'Determinism in tree turnover during the succession of a tropical forest', *Perspectives in Plant Ecology, Evolution and Systematics*, 34, pp. 120–128. doi:10.1016/j.ppees.2018.08.007.

Chamagne, J. *et al.* (2016) 'Do the rich get richer? Varying effects of tree species identity and diversity on the richness of understory taxa', *Ecology*, 97(9), pp. 2364–2373. doi:10.1002/ecy.1479.

Chang, C. and HilleRisLambers, J. (2016) 'Integrating succession and community assembly perspectives', *F1000Research*, 5, p. F1000 Faculty Rev-2294. doi:10.12688/f1000research.8973.1.

Chang, C.C. and Turner, B.L. (2019) 'Ecological succession in a changing world', *Journal of Ecology*, 107(2), pp. 503–509. doi:10.1111/1365-2745.13132.

Chao, A. *et al.* (2004) 'A new statistical approach for assessing similarity of species composition with incidence and abundance data: A new statistical approach for assessing similarity', *Ecology Letters*, 8(2), pp. 148–159. doi:10.1111/j.1461-0248.2004.00707.x.

Chao, A. *et al*. (2006) 'Abundance-Based Similarity Indices and Their Estimation When There Are Unseen Species in Samples', *Biometrics*, 62(2), pp. 361–371. doi:10.1111/j.1541-0420.2005.00489.x.

Chao, A. *et al*. (2014) 'Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies', *Ecological Monographs*, 84(1), pp. 45–67. doi:https://doi.org/10.1890/13-0133.1.

Chapin, F.S. *et al*. (1998) 'Ecosystem Consequences of Changing Biodiversity', *BioScience*, 48(1), pp. 45–52. doi:10.2307/1313227.

Chazdon, R. (2008) *Chance and Determinism in Tropical Forest Succession*. Available at: https://www.semanticscholar.org/paper/Chance-and-Determinism-in-Tropical-Forest-Chazdon/0c17f62c05f7813c9948b0b01dc118822427f766 (Accessed: 28 January 2022).

Chazdon, R.L. (2003) 'Tropical forest recovery: legacies of human impact and natural disturbances', *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1), pp. 51–71. doi:10.1078/1433-8319-00042.

Chazdon, R.L. *et al*. (2007) 'Rates of change in tree communities of secondary Neotropical forests following major disturbances', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1478), pp. 273–289. doi:10.1098/rstb.2006.1990.

Chazdon, R.L. *et al*. (2010) 'Composition and Dynamics of Functional Groups of Trees During Tropical Forest Succession in Northeastern Costa Rica', *Biotropica*, 42(1), pp. 31–40. doi:10.1111/j.1744-7429.2009.00566.x.

Chazdon, R.L. (2014) *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*. University of Chicago Press. doi:10.7208/chicago/9780226118109.001.0001.

Chesson, P. (2000) 'Mechanisms of Maintenance of Species Diversity', *Annual Review of Ecology and Systematics*, 31(1), pp. 343–366. doi:10.1146/annurev.ecolsys.31.1.343.

Chraibi, E., Arnold, H., Luque, S., Deacon, A., Magurran, A.E. and Féret, J.B. (2021), 'A remote sensing approach to understanding patterns of secondary succession in tropical forest', *Remote Sensing*, 13(11), pp. 2148.

Chu, C.-J. *et al*. (2007) 'On the Balance between Niche and Neutral Processes as Drivers of Community Structure along a Successional Gradient: Insights from Alpine and Sub-alpine Meadow Communities', *Annals of Botany*, 100(4), pp. 807–812. doi:10.1093/aob/mcm166.

Clavero, M., Brotons, L. and Herrando, S. (2011) 'Bird community specialization, bird conservation and disturbance: the role of wildfires', *Journal of Animal Ecology*, 80(1), pp. 128–136. doi:10.1111/j.1365-2656.2010.01748.x.

Cleavitt, N.L., Dibble, A.C. and Werier, D.A. (2009) ‘Influence of tree composition upon epiphytic macrolichens and bryophytes in old forests of Acadia National Park, Maine’, *The Bryologist*, 112(3), pp. 467–487. doi:10.1639/0007-2745-112.3.467.

Clements, F.E. (1916) *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institution of Washington.

Clements, F.E. (1928) *Plant succession and indicators*. The H. W. Wilson company. Available at: https://scholar.google.com/scholar_lookup?title=Plant+succession+and+indicators&author=Clements%2C+Frederic+E.+%28Frederic+Edward%29&publication_year=1928 (Accessed: 10 May 2022).

Clements, F.E. (1949) ‘Dynamics of Vegetation’, *Soil Science*, 68(3), p. 273.

Cleveland, W.S. and Devlin, S.J. (1988) ‘Locally Weighted Regression: An Approach to Regression Analysis by Local Fitting’, *Journal of the American Statistical Association*, 83(403), pp. 596–610. doi:10.1080/01621459.1988.10478639.

Clough, Y. *et al*. (2009) ‘Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry’, *Biological Conservation*, 142(5), pp. 1032–1041. doi:10.1016/j.biocon.2008.12.027.

Cody, M.L. (1985) *Habitat Selection in Birds*. Academic Press.

Connell, J.H. and Slatyer, R.O. (1977) ‘Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization’, *The American Naturalist*, 111(982), pp. 1119–1144.

Cooper, W.S. (1926) ‘The Fundamentals of Vegetational Change’, *Ecology*, 7(4), pp. 391–413. doi:10.2307/1931166.

COP26 (2021a) ‘COP26 IPLC forest tenure Joint Donor Statement’. UN Climate Change Conference. Available at: https://ukcop26.org/cop26-iplc-forest-tenure-joint-donor-statement/ (Accessed: 17 April 2022).

COP26 (2021b) ‘Glasgow Leaders’ Declaration on Forests and Land Use’. UN Climate Change Conference. Available at: https://ukcop26.org/glasgow-leaders-declaration-on-forests-and-land-use/ (Accessed: 17 April 2022).

COP26 (2021c) ‘The Global Forest Finance Pledge’. UN Climate Change Conference. Available at: https://ukcop26.org/the-global-forest-finance-pledge/ (Accessed: 17 April 2022).

Corbet, G.B. (1998) *The nature of Fife: wildlife and ecology*. Edinburgh: Published for the Scottish Wildlife Trust by Scottish Cultural Press.

Costa, F. and Magnusson, W. (2002) ‘Selective Logging Effects on Abundance, Diversity, and Composition of Tropical Understory Herbs’, *Ecological Applications*, 12(3), pp. 807–819. doi:10.1890/1051-0761(2002)012[0807:SLEOAD]2.0.CO;2.

Cowles, H.C. (1899) 'The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan. Part I.-Geographical Relations of the Dune Floras.', *Botanical Gazette*, 27(2), pp. 95–117. doi:10.1086/327796.

Cowles, H.C. (1901) 'The Physiographic Ecology of Chicago and Vicinity; A Study of the Origin, Development, and Classification of Plant Societies', *Botanical Gazette*, 31(2), pp. 73–108.

Cox, N. *et al*. (2022) 'A global reptile assessment highlights shared conservation needs of tetrapods', *Nature*, pp. 1–6. doi:10.1038/s41586-022-04664-7.

Craven, D. *et al*. (2015) 'Changing gears during succession: shifting functional strategies in young tropical secondary forests', *Oecologia*, 179(1), pp. 293–305. doi:10.1007/s00442-015-3339-x.

Craven, D. *et al*. (2018) 'Environmental filtering limits functional diversity during succession in a seasonally wet tropical secondary forest', *Journal of Vegetation Science*, 29(3), pp. 511–520. doi:10.1111/jvs.12632.

Crawford, C.L. (2002) *Bryophytes of native woods*. Natural Resource Consultancy for the Native Woodlands Discussion Group, Lower Plants Section. Available at: https://scholar.google.com/scholar_lookup?title=Bryophytes+of+native+woods&author=Crawford%2C+Carol+L.&publication_year=2002 (Accessed: 22 May 2022).

Cubiña, A. and Aide, T.M. (2001) 'The Effect of Distance from Forest Edge on Seed Rain and Soil Seed Bank in a Tropical Pasture', *Biotropica*, 33(2), pp. 260–267. doi:https://doi.org/10.1111/j.1744-7429.2001.tb00177.x.

Daba, M.H. and Dejene, S. (2018) 'The Role of Biodiversity and Ecosystem Services in Carbon Sequestration and its Implication for Climate Change Mitigation', 11. doi:10.19080/IJESNR.2018.10.5558.

Dagan, U. and Izhaki, I. (2019) 'Understory vegetation in planted pine forests governs bird community composition and diversity in the eastern Mediterranean region', *Forest Ecosystems*, 6(1), p. 29. doi:10.1186/s40663-019-0186-y.

Darwin, C. (1859) *Darwin, Charles. The origin of species by means of natural selection*.

De Jaegere, T., Hein, S. and Claessens, H. (2016) 'A Review of the Characteristics of Small-Leaved Lime (Tilia cordata Mill.) and Their Implications for Silviculture in a Changing Climate', *Forests*, 7(3), p. 56. doi:10.3390/f7030056.

DeGraaf, R.M., Geis, A.D. and Healy, P.A. (1991) 'Bird population and habitat surveys in urban areas', *Landscape and Urban Planning*, 21(3), pp. 181–188.

Dent, D.H., DeWalt, S.J. and Denslow, J.S. (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(3), pp. 530–542. doi:10.1111/j.1654-1103.2012.01482.x.

Derroire, G. *et al*. (2016) 'Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession', *Oikos*, 125(10), pp. 1386–1397. doi:https://doi.org/10.1111/oik.03229.

DeWalt, S.J., Maliakal, S.K. and Denslow, J.S. (2003) 'Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife', *Forest Ecology and Management*, 182(1), pp. 139–151. doi:10.1016/S0378-1127(03)00029-X.

Dewalt, S.J., Schnitzer, S.A. and Denslow, J.S. (2000) 'Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest', *Journal of Tropical Ecology*, 16(1), pp. 1–19. doi:10.1017/S0266467400001231.

Diamond, J.M. (1984) '"Normal" extinctions of isolated populations', in *Extinctions*. University of Chicago Press, pp. 191–246. Available at: https://ci.nii.ac.jp/naid/10011944049/ (Accessed: 22 February 2021).

Díaz, I.A. *et al*. (2005) 'Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile', *Biological Conservation*, 123(1), pp. 91–101. doi:10.1016/j.biocon.2004.10.011.

Díaz, I.A. *et al*. (2012) 'A field experiment links forest structure and biodiversity: epiphytes enhance canopy invertebrates in Chilean forests', *Ecosphere*, 3(1), p. art5. doi:10.1890/ES11-00168.1.

Díaz, S. *et al*. (1999) 'Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina', *Journal of Vegetation Science*, 10(5), pp. 651–660. doi:10.2307/3237080.

Díaz, S. *et al*. (2018) 'Assessing nature's contributions to people', *Science*, 359(6373), pp. 270–272. doi:10.1126/science.aap8826.

Díaz, S. and Cabido, M. (2001) 'Vive la différence: plant functional diversity matters to ecosystem processes', *Trends in Ecology & Evolution*, 16(11), pp. 646–655. doi:10.1016/S0169-5347(01)02283-2.

Díaz, S., Hector, A. and Wardle, D.A. (2009) 'Biodiversity in forest carbon sequestration initiatives: not just a side benefit', *Current Opinion in Environmental Sustainability*, 1(1), pp. 55–60. doi:10.1016/j.cosust.2009.08.001.

Díaz-García, J.M. *et al*. (2020) 'Comparing the success of active and passive restoration in a tropical cloud forest landscape: A multi-taxa fauna approach', *PLOS ONE*, 15(11), p. e0242020. doi:10.1371/journal.pone.0242020.

Dirzo, R. and Raven, P.H. (2003) 'Global State of Biodiversity and Loss', *Annual Review of Environment and Resources*, 28(1), pp. 137–167. doi:10.1146/annurev.energy.28.050302.105532.

Dobson, F. (2005a) 'A guide to common urban lichens 1'.

Dobson, F. (2005b) *Lichens: An illustrated guide to the British and Irish species*. The Richmond Publishing Co. Ltd.

Dobson, F. (2017) 'Guide to lichens of heaths and moors'. FSC.

Dobson, F.S. (2013) *A field key to lichens on trees*. Wimbledon: Intype Libra Ltd.

Dölle, M. and Schmidt, W. (2009) 'Impact of tree species on nutrient and light availability: evidence from a permanent plot study of old-field succession', *Plant Ecology*, 203(2), pp. 273–287. doi:10.1007/s11258-008-9547-2.

Dornelas, M. *et al*. (2014) 'Assemblage time series reveal biodiversity change but not systematic loss', *Science*, 344(6181), pp. 296–299. doi:10.1126/science.1248484.

Drury, W.H. and Nisbet, I.C.T. (1971) 'Inter-relations between developmental models in geomorphology, plant ecology, and animal ecology', 16, pp. 57–68.

Dunn, Robert R (2004a) 'Managing the tropical landscape: a comparison of the effects of logging and forest conversion to agriculture on ants, birds, and lepidoptera', *Forest Ecology and Management*, 191(1), pp. 215–224. doi:10.1016/j.foreco.2003.12.008.

Dunn, Robert R. (2004b) 'Recovery of Faunal Communities During Tropical Forest Regeneration', *Conservation Biology*, 18(2), pp. 302–309. doi:10.1111/j.1523-1739.2004.00151.x.

Egler, F.E. (1954) 'Vegetation Science Concepts I. Initial Floristic Composition, a Factor in Old-Field Vegetation Development', *Vegetatio*, 4(6), pp. 412–417.

Ehrlich, P.R. and Ehrlich, A.H. (1997) 'The Value of Biodiversity', in *The Economics of Transnational Commons*. Clarendon Press (World Institute for Development Economics Research).

Ehrlich, P.R. and Pringle, R.M. (2008) 'Where does biodiversity go from here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions', *Proceedings of the National Academy of Sciences*, 105(Supplement 1), pp. 11579–11586. doi:10.1073/pnas.0801911105.

Ellis, C.J. (2012) 'Lichen epiphyte diversity: A species, community and trait-based review', *Perspectives in Plant Ecology, Evolution and Systematics*, 14(2), pp. 131–152. doi:10.1016/j.ppees.2011.10.001.

Ellis, E., Antill, E. and Kreft, H. (2012) 'All Is Not Loss: Plant Biodiversity in the Anthropocene', *PloS one*, 7, p. e30535. doi:10.1371/journal.pone.0030535.

Ellison, A.M. and Gotelli, N.J. (2021) *Scaling in Ecology with a Model System*. Princeton University Press.

Emery, S.M. (2010) 'Succession: A Closer Look', 3(10), p. 7.

EOL (2021) *Encyclopedia of Life*, *National Museum of Natural History, Smithsonian*. Available at: https://eol.org/.

FAO (2015) *Global forest resources assessment 2015*. Food and Agriculture Organization of the United Nations. Available at: http://www.fao.org/3/a-i4808e.pdf (Accessed: 28 September 2021).

FAO and UNEP (2020) *The state of the world's forests 2020: forests, biodiversity and people*. doi:10.4060/ca8642en.

Feldpausch, T.R. *et al.* (2007) 'Secondary forest growth deviation from chronosequence predictions in central Amazonia', *Global Change Biology*, 13(5), pp. 967–979. doi:10.1111/j.1365-2486.2007.01344.x.

Féret, J.-B. and Asner, G.P. (2013) 'Tree Species Discrimination in Tropical Forests Using Airborne Imaging Spectroscopy', *IEEE Trans. Geosci. Remote Sens.*, 51, pp. 73–84.

Ferguson, B.G. *et al.* (2003) 'Post-Agricultural Succession in El Petén, Guatemala', *Conservation Biology*, 17(3), pp. 818–828. doi:10.1046/j.1523-1739.2003.01265.x.

Fern, K. (2021) *Useful Tropical Plants Database*. Available at: http://tropical.theferns.info (Accessed: 24 May 2022).

ffrench, R. (1973) *A Guide to the Birds of Trinidad and Tobago*. Livingston Publishing Company.

Fick, S.E. and Hijmans, R.J. (2017) 'WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas', *International Journal of Climatology*, 37(12). doi:https://doi.org/10.1002/joc.5086.

Finegan, B. (1996) 'Pattern and process in neotropical secondary rain forests: the first 100 years of succession', *Trends in Ecology & Evolution*, 11(3), pp. 119–124. doi:10.1016/0169-5347(96)81090-1.

Fischer, J. and Lindenmayer, D.B. (2005) 'Perfectly nested or significantly nested–an important difference for conservation management', *Oikos*, 109(3), pp. 485–494.

Fitter, R., Fitter, A. and Ferrer, A. (1984) *Collins Guide to the Grasses, Sedges, Rushes and Ferns of Britain and Northern Europe*. Collins.

Forbes, S.A. (1880) 'On Some Interactions of Organisms', *Illinois Natural History Survey Bulletin*, 1(3), pp. 3–18. doi:10.21900/j.inhs.v1i3.446.

Fox, B.J. (1982) 'Fire and Mammalian Secondary Succession in an Australian Coastal Heath', *Ecology*, 63(5), pp. 1332–1341. doi:10.2307/1938861.

Fox, B.J., Taylor, J.E. and Thompson, P.T. (2003) 'Experimental manipulation of habitat structure: a retrogression of the small mammal succession', *Journal of Animal Ecology*, 72(6), pp. 927–940. doi:10.1046/j.1365-2656.2003.00765.x.

Franklin, J.F. *et al.* (2002) 'Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example', *Forest Ecology and Management*, 155(1), pp. 399–423. doi:10.1016/S0378-1127(01)00575-8.

Fraser, L.H. *et al.* (2015) 'A call for applying trophic structure in ecological restoration', *Restoration Ecology*, 23(5), pp. 503–507. doi:10.1111/rec.12225.

Fritz, Ö., Brunet, J. and Caldiz, M. (2009) ‘Interacting effects of tree characteristics on the occurrence of rare epiphytes in a Swedish beech forest area’, *The Bryologist*, 112(3), pp. 488–505. doi:10.1639/0007-2745-112.3.488.

Fukami, T. (2015) ‘Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects’, *Annual Review of Ecology Evolution and Systematics*, 46, pp. 1–23. doi:10.1146/annurev-ecolsys-110411-160340.

Fuller, R.J. *et al*. (1995) ‘Population Declines and Range Contractions Among Lowland Farmland Birds in Britain’, *Conservation Biology*, 9(6), pp. 1425–1441.

Galili, T. (2015) ‘dendextend: an R package for visualizing, adjusting and comparing trees of hierarchical clustering’, *Bioinformatics*, 31(22), pp. 3718–3720. doi:10.1093/bioinformatics/btv428.

Gallagher, R.S. (2013) *Seeds, 3rd Edition: The Ecology of Regeneration in Plant Communities*. CABI.

García, D., Donoso, I. and Rodríguez-Pérez, J. (2018) ‘Frugivore biodiversity and complementarity in interaction networks enhance landscape-scale seed dispersal function’, *Functional Ecology*, 32(12), pp. 2742–2752. doi:10.1111/1365-2435.13213.

García-Montiel, D.C. and Scatena, F.N. (1994) ‘The effect of human activity on the structure and composition of a tropical forest in Puerto Rico’, *Forest Ecology and Management*, 63(1), pp. 57–78. doi:10.1016/0378-1127(94)90246-1.

Gardner, C.J. *et al*. (2019) ‘Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis’, *Nature Communications*, 10(1), p. 4590. doi:10.1038/s41467-019-12539-1.

Gardner, T.A. *et al*. (2009) ‘Prospects for tropical forest biodiversity in a human-modified world’, *Ecology letters*, 12(6), pp. 561–582.

Garnier, E. *et al*. (2004) ‘Plant Functional Markers Capture Ecosystem Properties During Secondary Succession’, *Ecology*, 85(9), pp. 2630–2637. doi:10.1890/03-0799.

GBIF.org (2021) *Global biodiversity information facility*. Available at: https://www.gbif.org/.

Geist, H.J. and Lambin, E.F. (2002) ‘Proximate Causes and Underlying Driving Forces of Tropical Deforestation: Tropical forests are disappearing as the result of many pressures, both local and regional, acting in various combinations in different geographical locations’, *BioScience*, 52(2), pp. 143–150. doi:10.1641/0006-3568(2002)052[0143:PCAUDF]2.0.CO;2.

Gibson, L. *et al*. (2011) ‘Primary forests are irreplaceable for sustaining tropical biodiversity’, *Nature*, 478(7369), pp. 378–381. doi:10.1038/nature10425.

Gilman, E.F. and Watson, D.G. (2015) *Quercus robur: English Oak*. University of Florida. Available at: https://edis.ifas.ufl.edu/publication/ST558 (Accessed: 21 May 2022).

Gleason, H.A. (1926) ‘The Individualistic Concept of the Plant Association’, *Bulletin of the Torrey Botanical Club*, 53(1), pp. 7–26. doi:10.2307/2479933.

Gleason, H.A. (1927) ‘Further Views on the Succession-Concept’, *Ecology*, 8(3), pp. 299–326. doi:10.2307/1929332.

Glenn-Lewin, D.C., Peet, R.K. and Veblen, T.T. (1992) *Plant Succession: Theory and prediction*. Springer Science & Business Media.

Global Forest Watch (2020) *Tree cover loss and gain (Global)”*. Available at: www.globalforestwatch.org (Accessed: 20 March 2021).

Godfrey, M. (2014) ‘Guide to mosses and liverworts of woodlands’. FSC.

Godoy, O. and Levine, J.M. (2014) ‘Phenology effects on invasion success: insights from coupling field experiments to coexistence theory’, *Ecology*, 95(3), pp. 726–736. doi:10.1890/13-1157.1.

Gorelick, N. *et al.* (2017) ‘Google Earth Engine: Planetary-scale geospatial analysis for everyone’. doi:10.1016/j.rse.2017.06.031.

Gotelli, N.J. and Entsminger, G.L. (2003) ‘Swap Algorithms in Null Model Analysis’, *Ecology*, 84(2), pp. 532–535.

Gotsch, S.G., Nadkarni, N. and Amici, A. (2016) ‘The functional roles of epiphytes and arboreal soils in tropical montane cloud forests’, *Journal of Tropical Ecology*, 32(5), pp. 455–468. doi:10.1017/S026646741600033X.

Grau, R., Kuemmerle, T. and Macchi, L. (2013) ‘Beyond “land sparing versus land sharing”: environmental heterogeneity, globalization and the balance between agricultural production and nature conservation’, *Current Opinion in Environmental Sustainability*, 5(5), pp. 477–483. doi:10.1016/j.cosust.2013.06.001.

Gregory, R.D., Gibbons, D.W. and Donald, P.F. (2004) ‘Bird census and survey techniques’, in *Bird Ecology and Conservation*. Oxford: Oxford University Press. doi:10.1093/acprof:oso/9780198520863.003.0002.

Griffin, J.N. *et al.* (2009) ‘Biodiversity and the stability of ecosystem functioning’, in *Biodiversity, Ecosystem Functioning, and Human Wellbeing*. Oxford: Oxford University Press. doi:10.1093/acprof:oso/9780199547951.003.0006.

Grime, J.P. (1973) ‘Competitive Exclusion in Herbaceous Vegetation’, *Nature*, 242(5396), pp. 344–347. doi:10.1038/242344a0.

Grime, J.P. (1997) ‘Biodiversity and ecosystem function: The debate deepens’, 277(5330), pp. 1260–1261.

Guariguata, M.R. *et al.* (1997) ‘Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica’, *Plant Ecology*, 132(1), pp. 107–120. doi:10.1023/A:1009726421352.

Guariguata, M.R. and Ostertag, R. (2001) ‘Neotropical secondary forest succession: changes in structural and functional characteristics’, *Forest Ecology and Management*, 148(1), pp. 185–206. doi:10.1016/S0378-1127(00)00535-1.

Gustafsson, L. and Eriksson, I. (1995) ‘Factors of Importance for the Epiphytic Vegetation of Aspen Populus tremula with Special Emphasis on Bark Chemistry and Soil Chemistry’, *Journal of Applied Ecology*, 32(2), pp. 412–424. doi:10.2307/2405107.

Haddad, N.M. *et al.* (2011) ‘Plant diversity and the stability of foodwebs’, *Ecology Letters*, 14(1), pp. 42–46. doi:10.1111/j.1461-0248.2010.01548.x.

Hansen, A.J. *et al.* (1994) ‘Ecological Processes Linking Forest Structure and Avian Diversity in Western Oregon’, in Boyle, T.J.B. and Boyle, C.E.B. (eds) *Biodiversity, Temperate Ecosystems, and Global Change*. Berlin, Heidelberg: Springer (NATO ASI Series), pp. 217–245.

Hansen, M.C. *et al.* (2013) ‘High-Resolution Global Maps of 21st-Century Forest Cover Change’, *Science*, 342(6160), pp. 850–853. doi:10.1126/science.1244693.

Hardin, G. (1960) ‘The competitive exclusion principle’, *Science (New York, N.Y.)*, 131(3409), pp. 1292–1297. doi:10.1126/science.131.3409.1292.

Harrap, S. (2015) *RSPB Pocket Guide to British Birds: Second edition*. Bloomsbury Publishing.

Hautier, Y. *et al.* (2015) ‘Plant ecology. Anthropogenic environmental changes affect ecosystem stability via biodiversity’, *Science (New York, N.Y.)*, 348(6232), pp. 336–340. doi:10.1126/science.aaa1788.

Hayward, G.D. and Rosentreter, R. (1994) ‘Lichens as Nesting Material for Northern Flying Squirrels in the Northern Rocky Mountains’, *Journal of Mammalogy*, 75(3), pp. 663–673. doi:10.2307/1382514.

van der Heijden, M.G.A. *et al.* (1998) ‘Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity’, *Nature*, 396(6706), pp. 69–72. doi:10.1038/23932.

Heino, J. (2008) ‘Patterns of functional biodiversity and function-environment relationships in lake littoral macroinvertebrates’, *Limnology and Oceanography*, 53(4), pp. 1446–1455. doi:10.4319/lo.2008.53.4.1446.

Helmer, E.H. *et al.* (2012) ‘Detailed maps of tropical forest types are within reach: Forest tree communities for Trinidad and Tobago mapped with multiseason Landsat and multiseason fine-resolution imagery’, *Forest Ecology and Management*, 279, pp. 147–166. doi:10.1016/j.foreco.2012.05.016.

Hendrix, S.D. and Marquis, R.J. (1983) ‘Herbivore Damage to Three Tropical Ferns’, *Biotropica*, 15(2), pp. 108–111. doi:10.2307/2387952.

Herman, D.E., Stange, C.M. and Quam, V.C. (1996) *North Dakota tree handbook*. North Dakota State Soil Conservation Committee. Available at: https://scholar.google.com/scholar_lookup?title=North+Dakota+tree+handbook&author=Herman%2C+Dale+E.&publication_year=1996 (Accessed: 21 May 2022).

Hewitt, S. (2005) *Fruit trees of the Caribbean*. Oxford: Macmillan Publishers Limited (Caribbean Pocket Natural History Series).

Hiiesalu, I. *et al.* (2014) 'Species richness of arbuscular mycorrhizal fungi: associations with grassland plant richness and biomass', *New Phytologist*, 203(1), pp. 233–244. doi:10.1111/nph.12765.

Hill, M.O. (1973) 'Diversity and Evenness: A Unifying Notation and Its Consequences', *Ecology*, 54(2), pp. 427–432. doi:https://doi.org/10.2307/1934352.

HilleRisLambers, J. *et al.* (2012) 'Rethinking Community Assembly through the Lens of Coexistence Theory', *Annual Review of Ecology, Evolution, and Systematics*, 43(1), pp. 227–248. doi:10.1146/annurev-ecolsys-110411-160411.

Hirsch, T., Mooney, K. and Cooper, D. (2020) *Global biodiversity outlook 5*.

Hobbs, R.J., Higgs, E. and Harris, J.A. (2009) 'Novel ecosystems: implications for conservation and restoration', *Trends in Ecology & Evolution*, 24(11), pp. 599–605. doi:10.1016/j.tree.2009.05.012.

Hobson, K.A. and Bayne, E. (2000) 'The effects of stand age on avian communities in aspen-dominated forests of central Saskatchewan, Canada', *Forest Ecology and Management*, 136(1), pp. 121–134. doi:10.1016/S0378-1127(99)00287-X.

Hofmeister, J. *et al.* (2009) 'The influence of light and nutrient availability on herb layer species richness in oak-dominated forests in central Bohemia', *Plant Ecology*, 205, pp. 57–75. doi:10.1007/s11258-009-9598-z.

Hooper, D.U. *et al.* (2000) 'Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks: We assess the evidence for correlation between aboveground and belowground diversity and conclude that a variety of mechanisms could lead to positive, negative, or no relationship—depending on the strength and type of interactions among species', *BioScience*, 50(12), pp. 1049–1061. doi:10.1641/0006-3568(2000)050[1049:IBAABB]2.0.CO;2.

Hooper, E.R. (2008) 'Factors Affecting the Species Richness and Composition of Neotropical Secondary Succession: A Case Study of Abandoned Agricultural Land in Panama', in Myster, R.W. (ed.) *Post-Agricultural Succession in the Neotropics*. New York, NY: Springer, pp. 141–164. doi:10.1007/978-0-387-33642-8_6.

Hooper, E.R., Legendre, P. and Condit, R. (2004) 'Factors Affecting Community Composition of Forest Regeneration in Deforested, Abandoned Land in Panama', *Ecology*, 85(12), pp. 3313–3326. doi:https://doi.org/10.1890/03-0655.

Horn, H.S. (1971) *The Adaptive Geometry of Trees*. Princeton University Press.

Horn, H.S. and MacArthur, R.H. (1972) 'Competition among Fugitive Species in a Harlequin Environment', *Ecology*, 53(4), pp. 749–752. doi:10.2307/1934797.

Hosein, F.N. *et al.* (2017) 'Utility of DNA barcoding to identify rare endemic vascular plant species in Trinidad', *Ecology and evolution*, 7(18), pp. 7311–7333.

Hsieh, T.C., Ma, K.H. and Chao, A. (2020) *iNEXT: iNterpolation and EXTrapolation for species diversity*. Available at: http://chao.stat.nthu.edu.tw/wordpress/software-download/.

Hubbell, S. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press. Available at: https://www.jstor.org/stable/j.ctt7rj8w (Accessed: 23 May 2022).

Hume, R. (2014) *RSPB Birds of Britain and Europe: The Definitive Photographic Field Guide*. Dorling Kindersley Ltd.

Huston, M.A. (1997) 'Hidden Treatments in Ecological Experiments: Re-Evaluating the Ecosystem Function of Biodiversity', *Oecologia*, 110(4), pp. 449–460.

Hutchinson, G.E. (1951) 'Copepodology for the Onithologist', *Ecology*, 32(3), pp. 571–577. doi:10.2307/1931745.

ICCO (2021) 'Chocolate Industry', *International Cocoa Organization*. Available at: https://www.icco.org/chocolate-industry/ (Accessed: 19 April 2022).

Ihlen, P.G., Gjerde, I. and Sætersdal, M. (2001) 'Structural indicators of Richness and rarity of epiphytic lichens on Corylus avellana in two different forest types within a nature reserve in south-western Norway', *The Lichenologist*, 33(3), pp. 215–229. doi:10.1006/lich.2000.0315.

Ingle, N.R. (2003) 'Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation', *Oecologia*, 134(2), pp. 251–261. doi:10.1007/s00442-002-1081-7.

Isbell, F. *et al*. (2015) 'Biodiversity increases the resistance of ecosystem productivity to climate extremes', *Nature*, 526(7574), pp. 574–577. doi:10.1038/nature15374.

Isbell, F. *et al*. (2017) 'Linking the influence and dependence of people on biodiversity across scales', *Nature*, 546(7656), pp. 65–72. doi:10.1038/nature22899.

IUCN (2020) *The IUCN Red List of Threatened Species*. Available at: https://www.iucnredlist.org/.

Jagoret, P. *et al*. (2012) 'Afforestation of savannah with cocoa agroforestry systems: a small-farmer innovation in central Cameroon', *Agroforestry Systems*, 86(3), pp. 493–504. doi:10.1007/s10457-012-9513-9.

James, F. (1971) 'Ordinations of habitat relationships among birds', *Wilson Bulletin*, 83.

Jarrett, C. *et al*. (2021) 'Bird communities in African cocoa agroforestry are diverse but lack specialized insectivores', *Journal of Applied Ecology*, 58(6), pp. 1237–1247. doi:10.1111/1365-2664.13864.

Jennings, S., Brown, N. and Sheil, D. (1999) 'Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures', *Forestry: An International Journal of Forest Research*, 72(1), pp. 59–74. doi:10.1093/forestry/72.1.59.

Jezeer, R.E. *et al*. (2017) 'Shaded coffee and cocoa–double dividend for biodiversity and small-scale farmers', *Ecological economics*, 140, pp. 136–145.

John, O.O. (2015) 'Robustness of Quantile Regression to Outliers', *American Journal of Applied Mathematics and Statistics*, 3(2), pp. 86–88. doi:10.12691/ajams-3-2-8.

Johnson, E.A. (1979) 'Succession an Unfinished Revolution', *Ecology*. Edited by F.B. Golley, 60(1), pp. 238–240. doi:10.2307/1936484.

Jones, C.G., Lawton, J.H. and Shachak, M. (1994) 'Organisms as Ecosystem Engineers', *Oikos*, 69(3), pp. 373–386. doi:10.2307/3545850.

Jones, C.G., Lawton, J.H. and Shachak, M. (1997) 'Positive and Negative Effects of Organisms as Physical Ecosystem Engineers', *Ecology*, 78(7), pp. 1946–1957. doi:10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2.

Juggins, S. (2020) *rioja: Analysis of Quaternary Science Data*. Available at: https://CRAN.R-project.org/package=rioja (Accessed: 28 January 2022).

Jüriado, I., Paal, J. and Liira, J. (2003) 'Epiphytic and epixylic lichen species diversity in Estonian natural forests', *Biodiversity & Conservation*, 12(8), pp. 1587–1607. doi:10.1023/A:1023645730446.

Kachhiyapatel, R., Patel, S. and Rajput, Dr.K. (2016) 'Reporting Adiantum capillus-veneris L. and Thelypteris prolifera (Retz.).', *Indian Fern Journal*, 33, pp. 69–80.

Kantvilas, G. and Minchin, P.R. (1989) 'An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest', *Vegetatio*, 84(2), pp. 99–112. doi:10.1007/BF00036510.

Kapusta, P., Szarek-Łukaszewska, G. and Kiszka, J. (2004) 'Spatial analysis of lichen species richness in a disturbed ecosystem (Niepołomice Forest, S Poland)', *The Lichenologist*, 36(3–4), pp. 249–260. doi:10.1017/S0024282904014112.

Karthik, T., Veeraswami, G.G. and Samal, P.K. (2009) 'Forest Recovery Following Shifting Cultivation: An Overview of Existing Research', *Tropical Conservation Science*, 2(4), pp. 374–387. doi:10.1177/194008290900200401.

Kattge, J. *et al*. (2020) 'TRY plant trait database – enhanced coverage and open access', *Global Change Biology*, 26(1), pp. 119–188. doi:10.1111/gcb.14904.

Kayes, L.J., Anderson, P.D. and Puettmann, K.J. (2010) 'Vegetation succession among and within structural layers following wildfire in managed forests', *Journal of Vegetation Science. 21: 233-247*, pp. 233–247.

Keller, J.K., Richmond, M.E. and Smith, C.R. (2003) 'An explanation of patterns of breeding bird species richness and density following clearcutting in northeastern USA forests', *Forest Ecology and Management*, 174(1–3), pp. 541–564.

Kenefick, M., Restall, R. and Hayes, F. (2013) *Birds of Trinidad and Tobago*. Bloomsbury Publishing.

Kennard, D.K. (2002) ‘Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia’, *Journal of Tropical Ecology*, 18(1), pp. 53–66. doi:10.1017/S0266467402002031.

Kew (2021) *Plants of the world online database*, *Royal Botanic Gardens Kew*. Available at: https://powo.science.kew.org/.

Kirby, K.J. (1988) ‘Changes in the Ground Flora under Plantations on Ancient Woodland Sites’, *Forestry: An International Journal of Forest Research*, 61(4), pp. 317–338. doi:10.1093/forestry/61.4.317.

Koenker, R. (2013) ‘quantreg: Quantile Regression. R package version 5.05’, *R Foundation for Statistical Computing: Vienna) Available at: http://CRAN. R-project. org/package= quantreg* [Preprint].

Kraft, N.J.B. *et al*. (2015) ‘Community assembly, coexistence and the environmental filtering metaphor’, *Functional Ecology*, 29(5), pp. 592–599. doi:10.1111/1365-2435.12345.

Krömer, T., Kessler, M. and Gradstein, S.R. (2007) ‘Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory’, *Plant Ecology*, 189(2), pp. 261-278.

Kubínová, Z. *et al*. (2018) ‘Norway spruce needle size and cross section shape variability induced by irradiance on a macro- and microscale and CO2 concentration’, *Trees*, 32(1), pp. 231–244. doi:10.1007/s00468-017-1626-3.

Kubota, Y., Katsuda, K. and Kikuzawa, K. (2005) ‘Secondary succession and effects of clear-logging on diversity in the subtropical forests on Okinawa Island, southern Japan’, *Biodiversity & Conservation*, 14(4), pp. 879–901. doi:10.1007/s10531-004-0657-4.

Kuete, V. (2014) ‘22 - Physical, Hematological, and Histopathological Signs of Toxicity Induced by African Medicinal Plants’, in Kuete, V. (ed.) *Toxicological Survey of African Medicinal Plants*. Elsevier, pp. 635–657. doi:10.1016/B978-0-12-800018-2.00022-4.

Kuusinen, M. (1994) ‘Epiphytic lichen diversity on Salix caprea in old-growth southern and middle boreal forests of Finland’, *Annales Botanici Fennici*, 31(2), pp. 77–92.

Lack, D. and Lack, E. (1951) ‘Further Changes in Bird-Life Caused by Afforestation’, *Journal of Animal Ecology*, 20(2), pp. 173–179. doi:10.2307/1536.

Laiolo, P. (2002) ‘Effects of habitat structure, floral composition and diversity on a forest bird community in north-western Italy’, 51(2), p. 8.

Laliberté, E., Legendre, P. and Shipley, B. (2014) ‘Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology’. CRAN.

Lambin, E.F. *et al*. (2001) ‘The causes of land-use and land-cover change: moving beyond the myths’, *Global Environmental Change*, 11(4), pp. 261–269. doi:10.1016/S0959-3780(01)00007-3.

Laska, M.S. (1997) ‘Structure of Understory Shrub Assemblages in Adjacent Secondary and Old Growth Tropical Wet Forests, Costa Rica1’, *Biotropica*, 29(1), pp. 29–37. doi:10.1111/j.1744-7429.1997.tb00003.x.

Lasky, J.R. *et al.* (2014) ‘Trait-mediated assembly processes predict successional changes in community diversity of tropical forests’, *Proceedings of the National Academy of Sciences of the United States of America*, 111(15), pp. 5616–5621. doi:10.1073/pnas.1319342111.

Lassau, S.A. *et al.* (2005) ‘Using high-resolution multi-spectral imagery to estimate habitat complexity in open-canopy forests: can we predict ant community patterns?’, *Ecography*, 28(4), pp. 495–504. doi:10.1111/j.0906-7590.2005.04116.x.

Laurance, W.F. (1999) ‘Reflections on the tropical deforestation crisis’, *Biological Conservation*, 91(2), pp. 109–117. doi:10.1016/S0006-3207(99)00088-9.

Le Borgne, H., Dupuch, A. and Fortin, D. (2018) ‘Ecological processes determining the distribution dynamics of vole populations during forest succession’, *Oecologia*, 188(3), pp. 721–732. doi:10.1007/s00442-018-4261-9.

Lebrija-Trejos, E. *et al.* (2008) ‘Successional Change and Resilience of a Very Dry Tropical Deciduous Forest Following Shifting Agriculture’, *Biotropica*, 40(4), pp. 422–431. doi:https://doi.org/10.1111/j.1744-7429.2008.00398.x.

Lebrija-Trejos, E., Pérez-García, E.A., *et al.* (2010) ‘Functional traits and environmental filtering drive community assembly in a species-rich tropical system’, *Ecology*, 91(2), pp. 386–398. doi:10.1890/08-1449.1.

Lebrija-Trejos, E., Meave, J.A., *et al.* (2010) ‘Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession’, *Perspectives in Plant Ecology, Evolution and Systematics*, 12(4), pp. 267–275. doi:10.1016/j.ppees.2010.09.002.

Lee, M.-B. *et al.* (2020) ‘Avian taxonomic and functional diversity in early stage of longleaf pine (Pinus palustris) stands restored at agricultural lands: variations in scale dependency’, *Restoration Ecology*, 28(1), pp. 147–155. doi:10.1111/rec.13053.

Lehmkuhl, J.F. and Ruggiero, L.F. (1991) ‘Forest fragmentation in the Pacific Northwest and its potential effects on wildlife’, *USDA Forest Service general technical report PNW-GTR - Pacific Northwest Research Station (USA)*, pp. 34–36.

Lennox, G.D. *et al.* (2018) ‘Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests’, *Global Change Biology*, 24(12), pp. 5680–5694. doi:10.1111/gcb.14443.

Leppik, E., Jüriado, I. and Liira, J. (2011) ‘Changes in stand structure due to the cessation of traditional land use in wooded meadows impoverish epiphytic lichen communities’, *The Lichenologist*, 43(3), pp. 257–274. doi:10.1017/S002428291100003X.

Letcher, S.G. (2010) ‘Phylogenetic Structure of Angiosperm Communities during Tropical Forest Succession’, *Proceedings: Biological Sciences*, 277(1678), pp. 97–104.

Lewis, S.L., Edwards, D.P. and Galbraith, D. (2015) 'Increasing human dominance of tropical forests', *Science*, 349(6250), pp. 827–832. doi:10.1126/science.aaa9932.

Lindenmayer, D.B. *et al.* (2008) 'How Predictable Are Reptile Responses to Wildfire?', *Oikos*, 117(7), pp. 1086–1097.

Little, E.L. and Skolmen, R.G. (1989) 'Common forest trees of hawaii (native and introduced)', 679, p. 327.

Liu, Xiaofei *et al.* (2017) 'Recovery of woody plant species richness in secondary forests in China: a meta-analysis', *Scientific Reports*, 7(1), p. 10614. doi:10.1038/s41598-017-10898-7.

Löbel, S., Snäll, T. and Rydin, H. (2006) 'Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes', *Journal of Ecology*, 94(4), pp. 856–868. doi:10.1111/j.1365-2745.2006.01114.x.

Lohbeck, M. *et al.* (2012) 'Functional diversity changes during tropical forest succession', *Perspectives in Plant Ecology, Evolution and Systematics*, 14(2), pp. 89–96. doi:10.1016/j.ppees.2011.10.002.

Lohbeck, M., Poorter, L., Martínez-Ramos, M., *et al.* (2013) 'Changing drivers of species dominance during tropical forest succession', *Functional Ecology*, 28(4), pp. 1052–1058. doi:10.1111/1365-2435.12240.

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., *et al.* (2013) 'Successional changes in functional composition contrast for dry and wet tropical forest', *Ecology*, 94(6), pp. 1211–1216. doi:10.1890/12-1850.1.

Loreau, M. (2003) 'Biodiversity and ecosystem functioning: recent theoretical advances', *Oikos*, 91(1), pp. 3–17. doi:10.1034/j.1600-0706.2000.910101.x.

Loreau, M. and de Mazancourt, C. (2013) 'Biodiversity and ecosystem stability: a synthesis of underlying mechanisms', *Ecology Letters*, 16(s1), pp. 106–115. doi:10.1111/ele.12073.

Lugo, A.E. and Brown, S. (1991) 'Comparing Tropical and Temperate Forests', in Cole, J., Lovett, G., and Findlay, S. (eds) *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*. New York, NY: Springer, pp. 319–330. doi:10.1007/978-1-4612-3122-6_16.

Macarthur, R. and Levins, R. (1967) 'The Limiting Similarity, Convergence, and Divergence of Coexisting Species', *The American Naturalist*, 101(921), pp. 377–385.

Mace, G.M. (2014) 'Whose conservation?', *Science*.

Maechler, M. *et al.* (2019) *cluster: Cluster Analysis Basics and Extensions*. (R package).

Magurran, A.E. (2004) *Measuring Biological Diversity*. Wiley.

Magurran, A.E. *et al.* (2010) 'Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time', *Trends in Ecology & Evolution*, 25(10), pp. 574–582. doi:10.1016/j.tree.2010.06.016.

Magurran, A.E. (2016) 'How ecosystems change', *Science*, 351(6272), pp. 448–449. doi:10.1126/science.aad6758.

Magurran, A.E. *et al.* (2018) 'Divergent biodiversity change within ecosystems', *Proceedings of the National Academy of Sciences*, 115(8), pp. 1843–1847.

Magurran, A.E. and Dornelas, M. (2010) 'Biological diversity in a changing world', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1558), pp. 3593–3597. doi:10.1098/rstb.2010.0296.

Malhi, Y. *et al.* (2014) 'Tropical Forests in the Anthropocene', *Annual Review of Environment and Resources*, 39(1), pp. 125–159. doi:10.1146/annurev-environ-030713-155141.

Mandl, N. *et al.* (2010) 'A comparison of alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane forests of southern Ecuador', *Biodiversity and Conservation*, 19(8), pp. 2359–2369.

Måren, I.E. *et al.* (2018) 'Changing contributions of stochastic and deterministic processes in community assembly over a successional gradient', *Ecology*, 99(1), pp. 148–157. doi:10.1002/ecy.2052.

Marteinsdóttir, B., Svavarsdóttir, K. and Thórhallsdóttir, T.E. (2018) 'Multiple mechanisms of early plant community assembly with stochasticity driving the process', *Ecology*, 99(1), pp. 91–102. doi:10.1002/ecy.2079.

Martin, P.A., Newton, A.C. and Bullock, J.M. (2013) 'Carbon pools recover more quickly than plant biodiversity in tropical secondary forests', *Proceedings of the Royal Society B: Biological Sciences*, 280(1773), p. 20132236. doi:10.1098/rspb.2013.2236.

Martin, P.H., Sherman, R.E. and Fahey, T.J. (2004) 'Forty Years of Tropical Forest Recovery from Agriculture: Structure and Floristics of Secondary and Old-growth Riparian Forests in the Dominican Republic', *Biotropica*, 36(3), pp. 297–317. doi:10.1111/j.1744-7429.2004.tb00322.x.

Maunder, M. *et al.* (2008) 'Plant conservation in the Caribbean Island biodiversity hotspot', *The Botanical Review*, 74(1), pp. 197–207.

Maurer, B.A. and McGill, B.J. (2011) 'Measurement of species diversity. Biological diversity: frontiers in measurement and assessment', pp.55-65.

Mayfield, M.M. *et al.* (2010) 'What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change', *Global Ecology and Biogeography*, 19(4), pp. 423–431. doi:10.1111/j.1466-8238.2010.00532.x.

Mayfield, M.M. and Levine, J.M. (2010) 'Opposing effects of competitive exclusion on the phylogenetic structure of communities', *Ecology Letters*, 13(9), pp. 1085–1093. doi:10.1111/j.1461-0248.2010.01509.x.

McCormick, J. (1968) 'Succession', *Student Publication, Graduate School of Fine Arts*, (1), pp. 22–35.

McCouch, S. *et al.* (2020) 'Mobilizing Crop Biodiversity', *Molecular Plant*, 13(10), pp. 1341–1344. doi:10.1016/j.molp.2020.08.011.

McGill, B.J. *et al.* (2015) 'Fifteen forms of biodiversity trend in the Anthropocene', *Trends in Ecology & Evolution*, 30(2), pp. 104–113. doi:10.1016/j.tree.2014.11.006.

McGinley, M.A. *et al.* (1990) 'Morphological Constraints on Seed Mass in Lodgepole Pine', *Functional Ecology*, 4(2), pp. 183–192. doi:10.2307/2389337.

McIntire, E.J.B. and Fajardo, A. (2014) 'Facilitation as a ubiquitous driver of biodiversity', *New Phytologist*, 201(2), pp. 403–416. doi:10.1111/nph.12478.

McKinney, M.L. (2006) 'Urbanization as a major cause of biotic homogenization', *Biological Conservation*, 127(3), pp. 247–260. doi:10.1016/j.biocon.2005.09.005.

McKinney, M.L. and Lockwood, J.L. (1999) 'Biotic homogenization: a few winners replacing many losers in the next mass extinction', *Trends in Ecology & Evolution*, 14(11), pp. 450–453. doi:10.1016/S0169-5347(99)01679-1.

McLellan, R. *et al.* (2014) *Living Planet Report 2014: species and spaces, people and places*. WWF International. Available at: https://www.worldwildlife.org/pages/living-planet-report-2014 (Accessed: 19 April 2022).

McShea, W.J. and Rappole, J.H. (2000) 'Managing the Abundance and Diversity of Breeding Bird Populations through Manipulation of Deer Populations', *Conservation Biology*, 14(4), pp. 1161–1170. doi:10.1046/j.1523-1739.2000.99210.x.

Meiners, S.J. *et al.* (2015) 'Is successional research nearing its climax? New approaches for understanding dynamic communities', *Functional Ecology*, 29(2), pp. 154–164. doi:10.1111/1365-2435.12391.

Melo, A.S. (2019) *CommEcol: Community Ecology Analyses*. Available at: https://CRAN.R-project.org/package=CommEcol.

Millennium Ecosystem Assessment (2005) 'Ecosystems and human well-being', 5, p. 563.

Milliken, W. and Ratter, J.A. (1998) 'The vegetation of the Ilha de Maraca', in *XF2006289546*.

Mondragón, D., Valverde, T. and Hernández-Apolinar, M. (2015) 'Population ecology of epiphytic angiosperms: a review.', *Tropical Ecology*, 56(1), pp. 1–39.

Moning, C. *et al.* (2009) 'Lichen diversity in temperate montane forests is influenced by forest structure more than climate', *Forest Ecology and Management*, 258(5), pp. 745–751. doi:10.1016/j.foreco.2009.05.015.

Montgomery, R. and Chazdon, R. (2002) ‘Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps’, *Oecologia*, 131(2), pp. 165–174. doi:10.1007/s00442-002-0872-1.

Mora, F. *et al*. (2015) ‘Testing Chronosequences through Dynamic Approaches: Time and Site Effects on Tropical Dry Forest Succession’, *Biotropica*, 47(1), pp. 38–48. doi:https://doi.org/10.1111/btp.12187.

Morales-Hidalgo, D., Oswalt, S.N. and Somanathan, E. (2015) ‘Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015’, *Forest Ecology and Management*, 352, pp. 68–77. doi:10.1016/j.foreco.2015.06.011.

Moss, D. (1978) ‘Diversity of Woodland Song-Bird Populations’, *Journal of Animal Ecology*, 47(2), pp. 521–527. doi:10.2307/3798.

Mottl, O. *et al*. (2019) ‘Secondary succession has surprisingly low impact on arboreal ant communities in tropical montane rainforest’, *Ecosphere*, 10(8), p. e02848. doi:10.1002/ecs2.2848.

Mouchet, M.A., Villéger, S., Mason, N.W. and Mouillot, D. (2010) ‘Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules’, *Functional Ecology*, 24(4), pp. 867-876.

Muggeo, V.M.R. (2017) ‘Interval estimation for the breakpoint in segmented regression: a smoothed score-based approach’, *Australian & New Zealand Journal of Statistics*, 59(3), pp. 311–322. doi:10.1111/anzs.12200.

Muiruri, E.W., Rainio, K. and Koricheva, J. (2016) ‘Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae’, *Oecologia*, 180(3), pp. 619–630. doi:10.1007/s00442-015-3391-6.

Muñiz-Castro, M.A., Williams-Linera, G. and Martínez-Ramos, M. (2012) ‘Dispersal mode, shade tolerance, and phytogeographical affinity of tree species during secondary succession in tropical montane cloud forest’, *Plant Ecology*, 213(2), pp. 339–353. doi:10.1007/s11258-011-9980-5.

Muscarella, R. *et al*. (2016) ‘Functional convergence and phylogenetic divergence during secondary succession of subtropical wet forests in Puerto Rico’, *Journal of Vegetation Science*, 27(2), pp. 283–294. doi:10.1111/jvs.12354.

Myers, N. (1980) ‘Conversion of Tropical Moist Forests.’, *Conversion of Tropical Moist Forests*. [Preprint]. Available at: https://www.cabdirect.org/cabdirect/abstract/19802607080 (Accessed: 5 April 2021).

Myers, N. *et al*. (2000) ‘Biodiversity hotspots for conservation priorities’, *Nature*, 403(6772), pp. 853–858. doi:10.1038/35002501.

Nadkarni, N.M. (1994) ‘Diversity of Species and Interactions in the Upper Tree Canopy of Forest Ecosystems1’, *American Zoologist*, 34(1), pp. 70–78. doi:10.1093/icb/34.1.70.

Nadkarni, N.M. and Matelson, T.J. (1989) ‘Bird Use of Epiphyte Resources in Neotropical Trees’, *The Condor*, 91(4), pp. 891–907. doi:10.2307/1368074.

Nadrowski, K., Wirth, C. and Scherer-Lorenzen, M. (2010) ‘Is forest diversity driving ecosystem function and service?’, *Current Opinion in Environmental Sustainability, v.2, 75-79 (2010)*, 2. doi:10.1016/j.cosust.2010.02.003.

NATT (2018) ‘Honouring our Industrial Roots: Sugar, Cocoa, Asphalt and Oil’. Available at: https://natt.gov.tt/sites/default/files/pdfs/Honouring-Our-Industrial-Roots.pdf.

NC State University (2021) *Alternanthera ficoidea (Bloodleaf, Calico Plant, Copperleaf, Joseph’s Coat, Joyweed, Parrot Leaf)*. Available at: https://plants.ces.ncsu.edu/plants/alternanthera-ficoidea/ (Accessed: 24 May 2022).

Neitlich, P.N. and McCune, B. (1997) ‘Hotspots of Epiphytic Lichen Diversity in Two Young Managed Forests’, *Conservation Biology*, 11(1), pp. 172–182. doi:10.1046/j.1523-1739.1997.95492.x.

Newbold, T. *et al.* (2015) ‘Global effects of land use on local terrestrial biodiversity’, *Nature*, 520(7545), pp. 45–50. doi:10.1038/nature14324.

Nieder, J., Engwald, S. and Barthlott, W. (1999) ‘Patterns of neotropical epiphyte diversity’, *Selbyana*, pp. 66-75.

Nilsson, S.G. (1979) ‘Density and Species Richness of Some Forest Bird Communities in South Sweden’, *Oikos*, 33(3), pp. 392–401. doi:10.2307/3544327.

Nimmo, Dale.G. *et al.* (2012) ‘Predicting the century-long post-fire responses of reptiles’, *Global Ecology and Biogeography*, 21(11), pp. 1062–1073. doi:10.1111/j.1466-8238.2011.00747.x.

Nobel, I.R. and Slatyer, R.O. (1977) ‘Post-fire succession of plants in Mediterranean ecosystems’, *Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems*, pp. 27–36.

Norden, N. *et al.* (2015) ‘Successional dynamics in Neotropical forests are as uncertain as they are predictable’, *Proceedings of the National Academy of Sciences*, 112(26), pp. 8013–8018. doi:10.1073/pnas.1500403112.

Nparks (2021) *Flora and fauna web*, *Singapore Government Agency, National Parks*. Available at: https://www.nparks.gov.sg/florafaunaweb.

Odum, E.P. (1969) ‘The Strategy of Ecosystem Development’, *Science*, 164(3877), pp. 262–270. doi:10.1126/science.164.3877.262.

Oksanen, J. *et al.* (2010) ‘Vegan: community ecology package. R package version 1.17-4’, *URL http://CRAN. R-project. org/package= vegan* [Preprint].

Oksuz, D.P., Palmeirim, J.M. and Correia, R.A. (2021) ‘Bird taxonomic and functional responses to land abandonment in wood-pastures’, *Agroforestry Systems*, 95(6), pp. 1167–1176. doi:10.1007/s10457-021-00649-z.

Oliver, T.H. *et al*. (2015) ‘Declining resilience of ecosystem functions under biodiversity loss’, *Nature Communications*, 6(1), p. 10122. doi:10.1038/ncomms10122.

Owen, K. *et al*. (2020) ‘Bioacoustic analyses reveal that bird communities recover with forest succession in tropical dry forests’, *Avian Conservation and Ecology*, 15(1). doi:10.5751/ACE-01615-150125.

Pandolfi, J.M. and Lovelock, C.E. (2014) ‘Novelty trumps loss in global biodiversity’, *Science*, 344(6181), pp. 266–267.

Paradis, E. *et al*. (2022) *ape: Analyses of Phylogenetics and Evolution*. Available at: https://CRAN.R-project.org/package=ape (Accessed: 28 January 2022).

Parrotta, J.A. (1995) ‘Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site’, *Journal of Vegetation Science*, 6(5), pp. 627–636. doi:10.2307/3236433.

Parrotta, J.A., Turnbull, J.W. and Jones, N. (1997) ‘Catalyzing native forest regeneration on degraded tropical lands’, *Forest Ecology and Management*, 99(1), pp. 1–7. doi:10.1016/S0378-1127(97)00190-4.

Pärt, T. and Söderström, B. (1999) ‘Conservation value of semi-natural pastures in Sweden: contrasting botanical and avian measures’, *Conservation Biology*, 13(4), pp. 755–765.

Pecl, G.T. *et al*. (2017) ‘Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being’, *Science*, 355(6332), p. eaai9214. doi:10.1126/science.aai9214.

Peintinger, M., Bergamini, A. and Schmid, B. (2003) ‘Species-area relationships and nestedness of four taxonomic groups in fragmented wetlands’, *Basic and Applied Ecology*, 4(5), pp. 385–394.

Pellissier, L. *et al*. (2014) ‘Soil fungal communities of grasslands are environmentally structured at a regional scale in the Alps’, *Molecular Ecology*, 23(17), pp. 4274–4290. doi:10.1111/mec.12854.

Peña-Claros, M. (2003) ‘Changes in Forest Structure and Species Composition during Secondary Forest Succession in the Bolivian Amazon1’, *Biotropica*, 35(4), pp. 450–461. doi:10.1111/j.1744-7429.2003.tb00602.x.

Petchey, O.L. and Gaston, K.J. (2006) ‘Functional diversity: back to basics and looking forward’, *Ecology letters*, 9(6), pp. 741–758.

Phillips, R. and Grant, S. (1980) *Grasses, Ferns, Mosses & Lichens of Great Britain and Ireland*. Pan Books.

Pickett, S.T.A. (1976) ‘Succession: An Evolutionary Interpretation’, *The American Naturalist*, 110(971), pp. 107–119. doi:10.1086/283051.

Piertro, P. and Beltramini, M. (2021) *Monaco Nature Encyclopedia*. Available at: https://www.monaconatureencyclopedia.com/?lang=en.

Pimm, S.L. *et al.* (2014) 'The biodiversity of species and their rates of extinction, distribution, and protection', *Science*, 344(6187), p. 1246752. doi:10.1126/science.1246752.

Plowman, T.C. (2012) *Acnistus arborescens (L.) Schltdl. [family SOLANACEAE].*

Poelmans, E. and Rousseau, S. (2016) 'How do chocolate lovers balance taste and ethical considerations?', *British Food Journal* [Preprint].

Porley, R. (2008) *Arable Bryophytes: A Field Guide to the Mosses, Liverworts and Hornworts of Cultivated Land in Britain and Ireland*. WildGuides.

Press, B. (2016) *Green Guide to Trees Of Britain And Europe*. Bloomsbury Publishing.

Pulsford, S.A., Lindenmayer, D.B. and Driscoll, D.A. (2014) *A succession of theories: purging redundancy from disturbance theory. - PDF Download Free*, *docksci.com*. Available at: https://docksci.com/a-succession-of-theories-purging-redundancy-from-disturbance-theory_5a7e5339d64ab24eecbbcf45.html (Accessed: 2 May 2022).

Purschke, O. *et al.* (2013) 'Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes', *Journal of Ecology*, 101(4), pp. 857–866. doi:10.1111/1365-2745.12098.

QGIS Development Team (2021) *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. Available at: http://qgis.osgeo.org/.

Quesnel, V. and Farrell, T.F. (2000) *Native trees of Trinidad and Tobago*. Trinidad and Tobago Field Naturalists' Club.

R Core Team (2021) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: http://www.R-project.org/.

Raevel, V., Violle, C. and Munoz, F. (2012) 'Mechanisms of ecological succession: insights from plant functional strategies', *Oikos*, 121(11), pp. 1761–1770. doi:10.1111/j.1600-0706.2012.20261.x.

Rajab, Y.A. *et al.* (2016) 'Cacao Cultivation under Diverse Shade Tree Cover Allows High Carbon Storage and Sequestration without Yield Losses', *PLOS ONE*, 11(2), p. e0149949. doi:10.1371/journal.pone.0149949.

Ramirez, A.H.M., Jhala, A.J. and Singh, M. (2012) 'Germination and Emergence Characteristics of Common Beggar's-Tick (Bidens alba)', *Weed Science*, 60(3), pp. 374–378. doi:10.1614/WS-D-11-00167.1.

Rasingam, L. and Parthasarathy, N. (2009) 'Diversity of understory plants in undisturbed and disturbed tropical lowland forests of Little Andaman Island, India', *Biodiversity and Conservation*, 18(4), pp. 1045–1065. doi:10.1007/s10531-008-9496-z.

Rey-Benayas, J.M., Galván, I. and Carrascal, L.M. (2010) 'Differential effects of vegetation restoration in Mediterranean abandoned cropland by secondary succession and pine plantations on bird assemblages', *Forest Ecology and Management*, 260(1), pp. 87–95.

Revelle, W. and Revelle, M.W. (2015). 'Package 'psych'. The comprehensive R archive network', 337, pp. 338.

Rice, R.A. and Greenberg, R. (2000) 'Cacao Cultivation and the Conservation of Biological Diversity', *AMBIO: A Journal of the Human Environment*, 29(3), pp. 167–173. doi:10.1579/0044-7447-29.3.167.

Riswan, S., Kenworthy, J.B. and Kartawinata, K. (1985) 'The Estimation of Temporal Processes in Tropical Rain Forest: A Study of Primary Mixed Dipterocarp Forest in Indonesia', *Journal of Tropical Ecology*, 1(2), pp. 171–182.

Rocha, J. *et al.* (2019) 'The conservation value of cacao agroforestry for bird functional diversity in tropical agricultural landscapes', *Ecology and Evolution*, 9(14), pp. 7903–7913. doi:10.1002/ece3.5021.

Rolim, S.G. *et al.* (2017) 'Recovery of Forest and Phylogenetic Structure in Abandoned Cocoa Agroforestry in the Atlantic Forest of Brazil', *Environmental Management*, 59(3), pp. 410–418. doi:10.1007/s00267-016-0800-5.

Rolim, S.G., Machado, R.E. and Pillar, V.D. (2017) 'Divergence in a Neotropical forest during 33 years of succession following clear-cutting', *Journal of Vegetation Science*, 28(3), pp. 495–503. doi:https://doi.org/10.1111/jvs.12502.

Rolo, V., Olivier, P.I. and van Aarde, R. (2017) 'Tree and bird functional groups as indicators of recovery of regenerating subtropical coastal dune forests', *Restoration Ecology*, 25(5), pp. 788–797. doi:10.1111/rec.12501.

Rozendaal, D.M.A. *et al.* (2019) 'Biodiversity recovery of Neotropical secondary forests', *Science Advances*, 5(3), p. eaau3114. doi:10.1126/sciadv.aau3114.

Ruf, F. and Schroth, G. (2004) 'Chocolate forests and monocultures - an historical review of cocoa growing and its conflicting role in tropical deforestation and forest conservation', in, pp. 107–134.

Russell, T., Cutler, C. and Walters, M. (2014) *The Complete Encyclopedia of Trees of the World*. Anness Publishing.

Sadalmelik (2007) *Topographic map of Trinidad and Tobago. Created with GMT from SRTM data*. Available at: https://commons.wikimedia.org/wiki/File:Trinidad_Topography.png (Accessed: 3 May 2022).

Sanaphre-Villanueva, L. *et al.* (2016) 'Functional Diversity of Small and Large Trees along Secondary Succession in a Tropical Dry Forest', *Forests*, 7(8), p. 163. doi:10.3390/f7080163.

Sanaphre-Villanueva, L. *et al.* (2017) 'Patterns of Plant Functional Variation and Specialization Along Secondary Succession and Topography in a Tropical Dry Forest', *Environmental Research Letters*, 12, p. 055004. doi:10.1088/1748-9326/aa6baa.

Sandor, M.E. and Chazdon, R.L. (2014) 'Remnant Trees Affect Species Composition but Not Structure of Tropical Second-Growth Forest', *PLOS ONE*, 9(1), p. e83284. doi:10.1371/journal.pone.0083284.

San-Miguel-Ayanz, J. *et al.* (2016) *European Atlas of Forest Tree Species.*

dos Santos, D. *et al.* (2021) ‘Crop functional diversity drives multiple ecosystem functions during early agroforestry succession’, *Journal of Applied Ecology*, 58(8), pp. 1718–1727. doi:10.1111/1365-2664.13930.

Santos Jr, A. *et al.* (2006) ‘Appraisal of the age of the trees used as nest by the Hyacinth Macaw in the Pantanal’, *Mato Grosso. Natureza & Conservacao*, 4, pp. 180–188.

dos Santos-Junior, R. *et al.* (2017) ‘Composition and diversity patterns of terrestrial herb communities in old-growth and secondary South Brazilian Atlantic Forest’, *Brazilian Journal of Botany*, 40(4), pp. 951–961. doi:10.1007/s40415-017-0411-2.

Sax, D.F. (2002) ‘Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California’, *Global Ecology and Biogeography*, 11(1), pp. 49–57. doi:10.1046/j.1466-822X.2001.00262.x.

Sayer, C.A., Bullock, J.M. and Martin, P.A. (2017) ‘Dynamics of avian species and functional diversity in secondary tropical forests’, *Biological Conservation*, 211, pp. 1–9. doi:10.1016/j.biocon.2017.05.004.

Sberze, M., Cohn-Haft, M. and Ferraz, G. (2010) ‘Old growth and secondary forest site occupancy by nocturnal birds in a Neotropical landscape’, *Animal Conservation*, 13, pp. 3–11. doi:10.1111/j.1469-1795.2009.00312.x.

Scariot, A., Lleras, E. and Hay, J.D. (1995) ‘Flowering and Fruiting Phenologies of the Palm Acrocomia aculeata: Patterns and Consequences’, *Biotropica*, 27(2), pp. 168–173. doi:10.2307/2388992.

Schieck, J., Nietfeid, M. and Stelfox, J.B. (1995) ‘Differences in bird species richness and abundance among three successional stages of aspen-dominated boreal forests’, *Canadian Journal of Zoology*, 73(8), pp. 1417–1431. doi:10.1139/z95-167.

Schiller, A., Hunsaker, C.T., Kane, M.A., Wolfe, A.K., Dale, V.H., Suter, G.W., Russell, C.S., Pion, G., Jensen, M.H. and Konar, V.C. (2001). ‘Communicating ecological indicators to decision makers and the public’, *Conservation Ecology*, *5*(1).

Schleuning, M., Fründ, J. and García, D. (2014) ‘Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions’, 38, pp. 380–392. doi:10.1111/ecog.00983.

Schoonmaker, P. and McKee, A. (1988) ‘Species Composition and Diversity During Secondary Succession of Coniferous Forests in the Western Cascade Mountains of Oregon’, *Forest Science*, 34(4), pp. 960–979. doi:10.1093/forestscience/34.4.960.

Schuler, H. *et al.* (2022) ‘Ecosystem Services from Ecological Agroforestry in Brazil: A Systematic Map of Scientific Evidence’, *Land*, 11, p. 83. doi:10.3390/land11010083.

Schwab, F.E. and Sinclair, A. (1994) ‘Biodiversity of diurnal breeding bird communities related to succession in the dry Douglas-fir forests of southeastern British Columbia’, *Canadian Journal of Forest Research*, 24(10), pp. 2034–2040. doi:10.1139/x94-261.

Schweiger, A.K. *et al.* (2018) 'Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function', *Nature Ecology & Evolution*, 2(6), pp. 976–982. doi:10.1038/s41559-018-0551-1.

Seedial, M. (2009) 'Cocoa production a producer's manual'. Edited by M. of A.L. and M. Resources. Trinidad and Tobago.

Seedial, M. (2013) 'Shade management in cocoa production'. Edited by E.T. and I.S.D.M. of F. Production. Trinidad and Tobago.

Semper-Pascual, A. *et al.* (2019) 'Biodiversity loss in deforestation frontiers: Linking occupancy modelling and physiological stress indicators to understand local extinctions', *Biological Conservation*, 236, pp. 281–288. doi:10.1016/j.biocon.2019.05.050.

Sett, R. and Kundu, M. (2016) 'Epiphytic Lichens: Their Usefulness as Bio-indicators of Air Pollution', *Donnish Journal of Research in Environmental Studies*, 3(3), pp. 17–24.

Shahabuddin, G. and Kumar, R. (2006) 'Influence of anthropogenic disturbance on bird communities in a tropical dry forest: role of vegetation structure', *Animal Conservation*, 9(4), pp. 404–413. doi:10.1111/j.1469-1795.2006.00051.x.

Shelford, V.E. (1911) 'Ecological Succession. II. Pond Fishes', *Biological Bulletin*, 21(3), pp. 127–151. doi:10.2307/1535882.

Sheridan, R.P. (1994) 'Adaptive morphology of the tropical wet montane epiphyte Anthurium hookeri', *Selbyana*, 15(2), pp. 18–23.

Sherry, T.W. *et al.* (2020) 'Insectivorous birds in the Neotropics: Ecological radiations, specialization, and coexistence in species-rich communities', *The Auk*, 137(4), p. ukaa049. doi:10.1093/auk/ukaa049.

Shi, X.-M. *et al.* (2017) 'Epiphytic bryophytes as bio-indicators of atmospheric nitrogen deposition in a subtropical montane cloud forest: Response patterns, mechanism, and critical load', *Environmental Pollution*, 229, pp. 932–941. doi:10.1016/j.envpol.2017.07.077.

Shvidenko, A., McCallum, I. and Nilsson, S. (2005) 'Forest and woodlands systems', in Hassan, R., Scholes, R., and Ash, N. (eds) *Ecosystems and Human Well-being: Current State and Trends*. Washington: Island Press. Available at: http://www.unep.org/maweb/documents/document.290.aspx.pdf (Accessed: 5 April 2021).

Sillett, S.C. *et al.* (2000) 'Dispersal Limitations of Epiphytic Lichens Result in Species Dependent on Old-Growth Forests', *Ecological Applications*, 10(3), pp. 789–799. doi:10.1890/1051-0761(2000)010[0789:DLOELR]2.0.CO;2.

Skujins, J. (1991) *Semiarid Lands and Deserts: Soil Resource and Reclamation*. CRC Press.

Smith, A.J.E. (1980) *The Moss Flora of Britain and Ireland*. Cambridge University Press.

Smith, A.L., Michael Bull, C. and Driscoll, D.A. (2013) 'Successional specialization in a reptile community cautions against widespread planned burning and complete fire suppression', *Journal of Applied Ecology*, 50(5), pp. 1178–1186. doi:10.1111/1365-2664.12119.

Smithsonian (2021) *STRI Symbiota Portal*, *Smithsonian Tropical Research Institute*. Available at: https://panamabiota.org/stri/index.php.

Sobek, S. *et al*. (2009) 'Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata?', *Forest Ecology and Management*, 258(5), pp. 609–615. doi:10.1016/j.foreco.2009.04.026.

Socolar, J.B. *et al*. (2016) 'How should beta-diversity inform biodiversity conservation?', *Trends in ecology & evolution*, 31(1), pp. 67–80.

Spicer, M.E. and Woods, C.L. (2022) 'A case for studying biotic interactions in epiphyte ecology and evolution', *Perspectives in Plant Ecology, Evolution and Systematics*, 54, p. 125658. doi:10.1016/j.ppees.2021.125658.

Sporn, S.G., Bos, M.M. and Gradstein, S.R. (2007) 'Is productivity of cacao impeded by epiphytes? An experimental approach', *Agriculture, Ecosystems & Environment*, 122(4), pp. 490–493. doi:10.1016/j.agee.2007.02.009.

Stachowicz, J.J. (2001) 'Mutualism, Facilitation, and the Structure of Ecological Communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend', *BioScience*, 51(3), pp. 235–246. doi:10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2.

Stary, F. and Jirásek, V. (1975) *Herbs: concise guide in colour*. Prague: Hamlyn.

Sterry, P. (2008) *Collins Complete Guide to British Wild Flowers*. Collins.

Sterry, P. (2015) *Collins Complete Guide to British Trees: A Photographic Guide to every common species*. HarperCollins UK.

Sullivan, J. (1994) *Picea abies*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Available at: https://www.fs.fed.us/database/feis/plants/tree/picabi/all.html (Accessed: 21 May 2022).

Supp, S.R. and Ernest, S.K.M. (2014) 'Species-level and community-level responses to disturbance: a cross-community analysis', *Ecology*, 95(7), pp. 1717–1723. doi:10.1890/13-2250.1.

Sutton, D. (1988) *Field guide to the wild flowers of Britain and Northern Europe*. Kingfisher Books.

Tabarelli, M. *et al*. (2012) 'Secondary forests as biodiversity repositories in human-modified landscapes: insights from the Neotropics', *Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais*, 7, pp. 319–328. doi:10.46357/bcnaturais.v7i3.593.

Tadesse, G., Zavaleta, E. and Shennan, C. (2014) ‘Coffee landscapes as refugia for native woody biodiversity as forest loss continues in southwest Ethiopia’, *Biological Conservation*, 169, pp. 384–391. doi:10.1016/j.biocon.2013.11.034.

Tedersoo, L. *et al*. (2016) ‘Tree diversity and species identity effects on soil fungi, protists and animals are context dependent’, *The ISME Journal*, 10(2), pp. 346–362. doi:10.1038/ismej.2015.116.

The Brasso Seco Chocolate Company (2022). Available at: https://www.facebook.com/brassosecochocolates/.

Thomas, L. *et al*. (2013) ‘Distance Sampling’, in *Encyclopedia of Environmetrics*. John Wiley & Sons, Ltd. doi:10.1002/9780470057339.vad033.pub2.

Tilman, D. (1985) ‘The Resource-Ratio Hypothesis of Plant Succession’, *The American Naturalist*, 125(6), pp. 827–852. doi:10.1086/284382.

Tilman, D. (1990) ‘Constraints and Tradeoffs: Toward a Predictive Theory of Competition and Succession’, *Oikos*, 58(1), pp. 3–15. doi:10.2307/3565355.

Tilman, D. *et al*. (1997) ‘The Influence of Functional Diversity and Composition on Ecosystem Processes’, *Science*, 277(5330), pp. 1300–1302. doi:10.1126/science.277.5330.1300.

Tilman, D. (1999) ‘The Ecological Consequences of Changes in Biodiversity: A Search for General Principles’, *Ecology*, 80(5), pp. 1455–1474. doi:10.1890/0012-9658(1999)080[1455:TECOCI]2.0.CO;2.

Tilman, D., Reich, P.B. and Knops, J.M.H. (2006) ‘Biodiversity and ecosystem stability in a decade-long grassland experiment’, *Nature*, 441(7093), pp. 629–632. doi:10.1038/nature04742.

Tinya, F. *et al*. (2021) ‘Environmental drivers of forest biodiversity in temperate mixed forests – A multi-taxon approach’, *Science of The Total Environment*, 795, p. 148720. doi:10.1016/j.scitotenv.2021.148720.

Toky, O.P. and Ramakrishnan, P.S. (1983) ‘Secondary Succession Following Slash and Burn Agriculture in North-Eastern India: I. Biomass, Litterfall and Productivity’, *Journal of Ecology*, 71(3), pp. 735–745. doi:10.2307/2259589.

Tscharntke, T. *et al*. (2002) ‘Contribution of small habitat fragments to conservation of insect communities of grassland–cropland landscapes’, *Ecological Applications*, 12(2), pp. 354–363.

Tscharntke, T. *et al*. (2012) ‘Landscape moderation of biodiversity patterns and processes-eight hypotheses’, *Biological reviews*, 87(3), pp. 661–685.

Uhl, C. and Jordan, C.F. (1984) ‘Succession and Nutrient Dynamics Following Forest Cutting and Burning in Amazonia’, *Ecology*, 65(5), pp. 1476–1490. doi:10.2307/1939128.

Uliczka, H. and Angelstam, P. (1999) ‘Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest’, *Ecography*, 22(4), pp. 396–405. doi:10.1111/j.1600-0587.1999.tb00576.x.

Ulrich, W. *et al*. (2016) ‘Species interactions and random dispersal rather than habitat filtering drive community assembly during early plant succession’, *Oikos*, 125(5), pp. 698–707. doi:10.1111/oik.02658.

UN (2007) ‘United Nations Forum on Forests’. Available at: https://www.un.org/esa/forests/wp-content/uploads/2013/09/E-2007-42-UNFF7Report.pdf.

UNEP (1992) *Convention on Biological Diversity*. Nairobi: Environmental Law and Institutions Activity Center. Available at: www.biodiv.org/convention/articles.asp.

UNFCCC (2015) ‘New York Declaration on Forests - Halving the loss of natural forest by 2020, striving to end it by 2030’. New York Declaration on Forests. Available at: https://unfccc.int/news/new-york-declaration-on-forests (Accessed: 17 April 2022).

University of Florida (2021) *Plant directory*, *Center for aquatic and invasive plants*. Available at: https://plants.ifas.ufl.edu/.

Urban, D.L. and Smith, T.M. (1989) ‘Microhabitat Pattern and the Structure of Forest Bird Communities’, *The American Naturalist*, 133(6), pp. 811–829. doi:10.1086/284954.

Vaast, P. and Somarriba, E. (2014) ‘Trade-offs between crop intensification and ecosystem services: the role of agroforestry in cocoa cultivation’, *Agroforestry Systems*, 88(6), pp. 947–956. doi:10.1007/s10457-014-9762-x.

Vandermeer, J. *et al*. (2004) ‘Multiple Basins of Attraction in a Tropical Forest: Evidence for Nonequilibrium Community Structure’, *Ecology*, 85(2), pp. 575–579.

Vellend, M. *et al*. (2013) ‘Global meta-analysis reveals no net change in local-scale plant biodiversity over time’, *Proceedings of the National Academy of Sciences*, 110(48), pp. 19456–19459. doi:10.1073/pnas.1312779110.

Vieira, D.L.M., Holl, K.D. and Peneireiro, F.M. (2009) ‘Agro-Successional Restoration as a Strategy to Facilitate Tropical Forest Recovery’, *Restoration Ecology*, 17(4), pp. 451–459. doi:10.1111/j.1526-100X.2009.00570.x.

Villéger, S., Grenouillet, G. and Brosse, S. (2013) ‘Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages’, *Global Ecology and Biogeography*, 22(6), pp. 671–681. doi:10.1111/geb.12021.

Villéger, S., Mason, N.W.H. and Mouillot, D. (2008) ‘New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology’, *Ecology*, 89(8), pp. 2290–2301. doi:10.1890/07-1206.1.

Vockenhuber, E.A. *et al*. (2011) ‘Tree diversity and environmental context predict herb species richness and cover in Germany’s largest connected deciduous forest’, *Perspectives in Plant Ecology, Evolution and Systematics*, 13(2), pp. 111–119. doi:10.1016/j.ppees.2011.02.004.

Vogeler, J.C. *et al*. (2014) 'Terrain and vegetation structural influences on local avian species richness in two mixed-conifer forests', *Remote Sensing of Environment*, 147, pp. 13–22. doi:10.1016/j.rse.2014.02.006.

Vogelsang, K.M., Reynolds, H.L. and Bever, J.D. (2006) 'Mycorrhizal fungal identity and richness determine the diversity and productivity of a tallgrass prairie system', *New Phytologist*, 172(3), pp. 554–562. doi:10.1111/j.1469-8137.2006.01854.x.

Waldron, A. *et al*. (2012) 'Conservation through Chocolate: a win-win for biodiversity and farmers in Ecuador's lowland tropics', *Conservation Letters*, 5(3), pp. 213–221.

Waldrop, M.P. *et al*. (2006) 'Resource availability controls fungal diversity across a plant diversity gradient', *Ecology Letters*, 9(10), pp. 1127–1135. doi:10.1111/j.1461-0248.2006.00965.x.

Walewski, J. (2007) *Lichens of the North Woods*. Kollath+Stensaas Pub.

Walker, L. and Del Moral, R. (2011) 'Primary Succession', in. doi:10.1002/9780470015902.a0003181.pub2.

Wall, S., Borchert, M. and Gworek, J. (2006) 'Secondary dispersal of bigcone Douglas-fir (Pseudotsuga macrocarpa) seeds', *Acta Oecologica*, 30, pp. 100–106. doi:10.1016/j.actao.2006.02.004.

Waltert, M. *et al*. (2005) 'From Forest to Farmland: Habitat Effects on Afrotropical Forest Bird Diversity', *Ecological Applications*, 15(4), pp. 1351–1366.

Weeda, E.J. (2003) *Nederlandse Oecologische Flora*. Wageningen University. Available at: https://www.wur.nl/upload_mm/0/2/8/8411be71-ecc7-4368-8338-bd21b285d6a4_salcinf.pdf.

Weiher, E. (2011) 'A primer of trait and functional diversity', in Magurran, A.E. and McGill, B.J. (eds) *Biological diversity: frontiers in measurement and assessment*. Oxford University Press, pp. 175–193.

Weiher, E. and Keddy, P.A. (1995) 'The Assembly of Experimental Wetland Plant Communities', *Oikos*, 73(3), pp. 323–335. doi:10.2307/3545956.

West, D.C., Shugart, H.H. and Botkin, D.B. (eds) (1981) *Forest Succession: Concepts and Application*. New York, NY: Springer (Springer Advanced Texts in Life Sciences). doi:10.1007/978-1-4612-5950-3.

Westoby, M., Walker, B. and Noy-Meir, I. (1989) 'Opportunistic Management for Rangelands Not at Equilibrium', *Journal of Range Management*, 42(4), p. 266. doi:10.2307/3899492.

Whitfeld, T.J.S. *et al*. (2014) 'Species Richness, Forest Structure, and Functional Diversity During Succession in the New Guinea Lowlands', *Biotropica*, 46(5), pp. 538–548. doi:10.1111/btp.12136.

Wickham, H. *et al*. (2021) *ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics*. Available at: https://CRAN.R-project.org/package=ggplot2 (Accessed: 30 January 2022).

Wildlife Trusts (2010) *Concise wild flower guide*. London: New Holland.

Wilman, H. *et al*. (2014) 'EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals', *Ecology*, 95(7), pp. 2027–2027. doi:10.1890/13-1917.1.

Wilson, E.O. and Frances, P.M. (eds) (1988) *Biodiversity*. Washington, D.C.: National Academy Press.

Winfree, R. (2013) 'Global change, biodiversity, and ecosystem services: What can we learn from studies of pollination?', *Basic and Applied Ecology*, 14(6), pp. 453–460. doi:10.1016/j.baae.2013.07.004.

Winter, M.-B. *et al*. (2015) 'Multi-taxon alpha diversity following bark beetle disturbance: Evaluating multi-decade persistence of a diverse early-seral phase', *Forest Ecology and Management*, 338, pp. 32–45. doi:10.1016/j.foreco.2014.11.019.

Wolseley, P.A. *et al*. (2013) 'Guide to using a lichen based index to nitrogen air quality'. Edited by FSC. Centre for Ecology and Hydrology, Natural History Museum and University of Nottingham.

Wolters, V., Bengtsson, J. and Zaitsev, A.S. (2006) 'Relationship among the species richness of different taxa', *Ecology*, 87(8), pp. 1886–1895.

Woods, P. (1989) 'Effects of Logging, Drought, and Fire on Structure and Composition of Tropical Forests in Sabah, Malaysia', *Biotropica*, 21(4), pp. 290–298. doi:10.2307/2388278.

Woodward, F.I. and Diament, A.D. (1991) 'Functional Approaches to Predicting the Ecological Effects of Global Change', *Functional Ecology*, 5(2), pp. 202–212. doi:10.2307/2389258.

Yeung, P. (2019) 'Ivory Coast law could see chocolate industry "wipe out" protected forests', *The Guardian*, 16 October. Available at: https://www.theguardian.com/environment/2019/oct/16/ivory-coast-law-could-see-chocolate-industry-wipe-out-protected-forests (Accessed: 19 April 2022).

Young, K. (2017) 'Mimicking Nature: A Review of Successional Agroforestry Systems as an Analogue to Natural Regeneration of Secondary Forest Stands', in, pp. 179–209. doi:10.1007/978-3-319-69371-2_8.

Zhang, H., Qi, W. and Liu, K. (2018) 'Functional traits associated with plant colonizing and competitive ability influence species abundance during secondary succession: Evidence from subalpine meadows of the Qinghai–Tibetan Plateau', *Ecology and Evolution*, 8(13), pp. 6529–6536. doi:10.1002/ece3.4110.

Zhang, Q. *et al*. (2013) 'Linking vegetation structure and bird organization: response of mixed-species bird flocks to forest succession in subtropical China', *Biodiversity and Conservation*, 22(9), pp. 1965–1989. doi:10.1007/s10531-013-0521-5.

Zhou, J. *et al*. (2014) ‘Stochasticity, succession, and environmental perturbations in a fluidic ecosystem’, *Proceedings of the National Academy of Sciences of the United States of America*, 111(9), pp. E836-845. doi:10.1073/pnas.1324044111.

Appendices

Appendices

Appendix 2.1 The role of starting point

While there are some well supported aspects of in successional theory, empirical data can often deviate from expectation due to the role of starting point (West, Shugart and Botkin, 1981; Glenn-Lewin, Peet and Veblen, 1992). Starting point refers to any underlying processes which affect resource availability and species availability include local environmental conditions, land management and disturbance history, and the state of the landscape when a forest begins to regenerate altering the trajectory and rate of successional processes (Chazdon, 2014). The trajectory and ultimate state of secondary forests is determined by the interaction of abiotic and biotic factors (Gibson *et al.*, 2011; Mora *et al.*, 2015; Norden *et al.*, 2015). The cause of deforestation, and the intensity, duration and frequency of disturbance all shape secondary succession. Environmental and substrate conditions, and the habitat surrounding a deforested area also influence forest characteristics and recovery rate. While some secondary forests recover their species diversity, composition and functioning quickly, severely degraded areas may never regain their historic condition naturally (Chazdon, 2003).

Secondary succession is variable even between forests with comparable disturbance histories and environmental conditions. Many combinations of factors operating throughout succession can influence the trajectory and ultimate climax conditions of secondary forests. The underlying environmental conditions, how land was cleared, the type and intensity of disturbance, the duration of disturbance and the condition of the surrounding habitat are all instrumental in forest recovery. I will now explore some of these factors in more detail.

Environment and forest type

The capacity of a forest to recover over secondary succession depends on local abiotic conditions. There are many forest types, differentiated by the mean annual temperature, precipitation, and potential evapotranspiration (Lugo and Brown, 1991). These forest types vary in their baseline complexity, diversity, and biomass, and recover differently following

disturbances. Thus, generalisations of successional processes and recovery rates across forest types are misleading.
For example, successional processes vary across latitudinal gradients (Gibson et al., 2011). There are few studies on secondary forest succession across ecoregions. Comparing similar forest types (such as those with comparable water availability) between tropical and temperate regions may yield meaningful results (Lugo and Brown, 1991). Tropical moist broadleaf forests typically accumulate aboveground biomass faster than temperate moist broadleaf forests over the first 40 years of succession (Cole, Lovett and Findlay, 2012). Although the ultimate aboveground biomass is comparable between the forest types, the recovery process is slower in the temperate forests (Lugo and Brown, 1991).

Furthermore, successional processes can differ between habitat types within the same ecoregion. For example, studies in tropical regions highlight that dry and wet forests should be considered independently (Kennard, 2002; Lebrija-Trejos *et al.*, 2008; Lohbeck *et al.*, 2013; Rozendaal *et al.*, 2017). Differences in liquid water availability affect the dominant community traits, tree dispersal ability and forest structure. Above-ground biomass recovery is usually faster in wet forests within the initial stages (first 20 years) of succession (Silver, Ostertag and Lugo, 2000; Becknell, Kissing Kucek and Powers, 2012). Research suggests, however, that overall dry tropical forests recover more quickly than wet forests (Lebrija-Trejos *et al.*, 2008; Becknell, Kissing Kucek and Powers, 2012). Wet tropical forests commonly have a successional stage dominated by long-lived pioneer trees which slows succession. In contrast, a meta-analysis by Lebrija-Trejos *et al.* (2008) showed that climax trees began to dominate after 40 years of succession following an early-pioneer tree phase in dry tropical forests. Overall, wet forests have greater tree species richness, tree basal area cover, aboveground biomass, soil carbon and more canopy trees (Lugo and Brown, 1991; Lebrija-Trejos *et al.*, 2008; Lebrija-Trejos *et al.*, 2010). Thus, succession in wet forests is complex, with more stages and slower recovery, especially in species composition (Lebrija-Trejos *et al.*, 2008).

The inconsistencies in how assemblages change over succession in dry and wet forests is seen across taxa as well. For example, Sitters et al. (2016) found contrasting trends in vegetation species richness and functional diversity indices in dry forests and wet forests following forest fires in south-eastern Australia. Furthermore, bird species richness, functional richness and functional dispersion were negatively correlated with vegetation diversity in wet forests, but positively correlated in dry forests (Sitters *et al.*, 2016).

Natural disturbance

Secondary forests may regenerate following natural or anthropogenic disturbances (Chazdon, 2003). Natural disturbances include cyclones, hurricanes, and fires. Wind-disturbances can severely damage forests, but primarily effect the forest canopy and many trees re-sprout. Forests usually recover from wind-disturbances quickly and there is seldom lasting damage. Some studies indicate that wind-driven deforestation can increase tree species richness. Wind-storms often produce an intermediate-intensity disturbance which prevents any pioneer species from becoming dominant, and from which many damaged trees can re-grow. Thus, more tree species coexist in the area (Chazdon, 2003). Vandermeer *et al.* (2000) found that large hurricane-damaged sites had greater tree species richness than undisturbed sites 10 years after Hurricane Joan hit Nicaragua. The authors propose that diversity is increased because pioneer species cannot entirely dominate the large deforested areas, allowing more species to coexist (Vandermeer *et al.*, 2000).

Fires are another common source of disturbance in secondary forests, especially in areas with a distinct dry season (Chazdon, 2003). Many damaged trees can re-sprout following low-intensity forest fires, and large trees may survive. Small trees (diameter at breast height <10cm) are at greater risk from forest fires and often ~40% are killed (Holdsworth and Uhl, 1997; Cochrane and Schulze, 1999; Chazdon, 2003). Cochran and Shulze (1999) found that burned forests had lower biomass, tree density and canopy cover. Habitat heterogeneity increased, however, due to patchiness in burn severity and age since regeneration. Hooper *et al.* (2004) found that fire reduced tree species richness and altered tree composition through degrading the soil seed bank and limiting the forest's ability to re-sprout from remnant vegetation (Hooper, Legendre and Condit, 2004). Forests recover from fires more rapidly if trees can re-sprout or if many large trees survive. Intense fires can damage the soil seed bank, limit the regenerative ability of trees, and alter tree composition by favouring fire-tolerant species, however. Repeated or high intensity fires kill more trees, impeding secondary forest succession (Uhl, Buschbacher and Serrao, 1988; Cochrane and Schulze, 1999; Chazdon, 2003).

Anthropogenic disturbance

Anthropogenic deforestation is primarily caused by small-scale shifting cultivation (or 'slash-and-burn'), conventional agriculture, pasture, and timber harvesting (Guariguata and Ostertag, 2001; Chazdon, 2003). While natural and anthropogenic disturbances can have similar outcomes, the imprint of human disturbance is often strong and longer lasting (Donohue, Foster and Motzkin, 2000; Chazdon, 2003).

Many studies have shown that anthropogenic disturbances have a greater impact than natural disturbances. Boucher *et al.* (2001), for example, compared five-year-old secondary forests regenerating from hurricanes and from agriculture in Nicaragua. Though the forests had similar basal area cover and tree density, those recovering from agriculture had lower tree species richness and the species composition remained altered. Forests regenerating from hurricanes overall showed greater similarity to old-growth forests (Boucher *et al.*, 2001). Similarly, Zimmerman *et al.* (1995) studied the effect of a hurricane on 60-year-old secondary forests in Puerto Rico. These forests still showed traces of their historic agriculture and pasture use despite the more recent hurricane suggesting that anthropogenic land-use was more important in determining species composition than natural disturbance (Zimmerman *et al.*, 1995). A study by Burslem *et al.* (2000) in the Solomon Islands likewise concluded that the impact of anthropogenic land-use history on vegetation composition was more pervasive than regular cyclones (Burslem, Whitmore and Brown, 2000). Furthermore, Dupouey *et al.* (2002), found that the impact of agriculture was still visible 2,000 years after abandonment in France. The authors uncovered that the old-secondary forest soil had higher pH and nutrient content, but less organic matter than true old-growth forests which highlights the lasting effects of human disturbance (Dupouey *et al.*, 2002).

Natural disturbances mostly damage the forest canopy, and remnant vegetation greatly contributes to regeneration. Following anthropogenic disturbances however, seed dispersal and pioneer tree colonisation are more important to regeneration. Human land management can directly alter the tree species composition through selective tree removal and planting, or by introducing exotic species. For example, García-Montiel and Scatena (1994) found that secondary forests regenerating from agroforestry included naturalised crop species such as bananas. The compositional changes in areas used for timber harvesting likewise reflected patterns expected from long-term selective tree removal (García-Montiel and Scatena, 1994).

The successional trajectory of secondary forests is slower and less predictable following human-disturbances. Land management type, intensity and duration can all impact the trajectory, but some anthropogenic land-uses are more impactful than others. For example, land subjected to severe vegetation removal such as overgrazing, bulldozing and repeated burning or weeding recovers slowly or lacks forest regeneration entirely once abandoned (Chazdon, 2003). With any disturbance, the secondary forest's recovery rate and successional trajectory will depend on the extent of the damage and the size of the deforested area (Everham and Brokaw, 1996).

Agriculture

Land abandonment following conversion for agriculture and pasture is a major source of secondary forests, though regeneration is slow. The imprint of agricultural and pastureland can remain long into succession. Agriculture and pastureland have fewer tree seeds and remnant trees, greater seed predation, altered environmental and soil conditions, and more herbs and grasses which suppress tree germination (Aide *et al*., 1995; Wijdeven and Kuzee, 2000; Cubiña and Aide, 2001; Guariguata and Ostertag, 2001).

Forests are often prepared for agriculture and pastureland by felling trees and burning the remaining vegetation to prevent woody-plant growth. Using fire in land management further alters the physical and chemical properties of the soil which affects vegetation colonisation (Aide *et al*., 1995; Guariguata and Ostertag, 2001). Álvarez-Yépiz *et al* (2008) found significantly lower soil cation exchange capacity and greater soil bulk density in secondary forests which had been slash-and-burn cultivated compared to uncultivated forests. Conventional agriculture generally decreases soil fertility as well, though can increase soil nutrients if the land was fertilised (Derroire et al., 2016). Forests regenerating after small-scale shifting cultivation tend to recover more rapidly compared to other forms of agricultural management which are often more intensive (Moran *et al.*, 2000; Guariguata and Ostertag, 2001; Gehring, Denich and Vlek, 2005).

Forest recovery from pasture is generally slower than following agriculture. Nepstad *et al.* (1996) found that tree recruitment was lower in secondary forests regenerating from pastureland due to the lack of remnant vegetation, reduced animal seed dispersal, and greater seed predation. Pastures often have changed soil properties and a prominent grass and herb layer as well (Nepstad *et al.*, 1996). Reiners et al. (1994) found that soil properties were altered with forest conversion to pastures, including decreased soil acidity and nitrogen mineralisation rates (Reiners *et al.*, 1994). Aide *et al.* (1995) found that tree density and species richness remained low until ~15 years after pasture abandonment likely due to soil degradation, compaction and altered structural properties, especially early in secondary succession. The early pioneer tree composition was also different in forests regenerating from pastures, likely due to the dense grass and herb layer impeding and filtering which tree species colonise (Aide *et al.*, 1995).

Agroforestry, orchards, and tree plantations

The effect of agroforestry and orchards on successional processes depends on the nature and intensity of land management. The types of crop trees planted in an agroforest can affect forest functioning and succession. For example, Fernandes and Sanford Jr. (1995) found that palm plantations had significantly lower soil nitrate levels as well as lower nitrification and nitrogen mineralisation rates compared to cacao plantations (Fernandes and Sanford Jr., 1995). Agricultural forests can also have varying levels of management regarding the use of fertilisers and pesticides, and the extent to which the ground vegetation and epiphytes are removed (Seedial, 2009, 2013). This can affect which plant species are able to colonise abandoned agricultural forests.

The impact of logging depends on the extent of the tree removal. Low-intensity logging has a comparable impact to natural disturbances. Some research indicates that low-intensity selective-logging can even increase tree species diversity. If the abundance of dominant trees is lowered, new species, especially small trees, can become established. Cannon et al. (1998) reported that 8-year-old selectively logged Indonesian forests had lower tree density and fewer large trees, but comparable or greater species richness than non-logged forests (Cannon, Peart and Leighton, 1998). Molino and Sabatier (2001) likewise reported 10-year-old secondary forests in French Guiana had greater species richness following intermediate-intensity logging, particularly among light-demanding trees (Molino and Sabatier, 2001). If rare trees are targeted in selective logging, however, the relative abundances of species can become less even (Ferry Slik, Verburg and Keßler, 2002).

It is further hypothesised that logging can increase landscape-level heterogeneity where different forest stands sustained varied levels of damage or are different ages of regeneration. Logging roads and trails add further habitat diversity by creating spaces with compacted soil and greater light availability (Chazdon, 2003).

Clear-cut forests take much longer to return to pre-disturbance conditions. Clear-cutting can alter soil properties, nutrient, and carbon cycling (Uhl, Buschbacher and Serrao, 1988), and damage the soil seed bank. Rolim et al. (2017) found tree species richness increased throughout succession, but that it was still lower in 33-year-old clear-cut secondary forests compared with old-growth. The tree species composition also remained altered, though it became increasingly similar to the surrounding forest (Rolim, Machado and Pillar, 2017).

Disturbance intensity and duration

The nature, severity and duration of a disturbance shapes the initial conditions in which a forest regenerates. For example, Uhl and Kauffman (1990) found that pastures were on average 10°C hotter and 30% less humid than old-growth forests in the Brazilian Amazon (Uhl and Kauffman, 1990), which is a very different starting point for succession. Long-term land use and deforestation can decrease soil organic matter and increase nutrient leaching. This ultimately decreases soil fertility and increases acidity over time (Guariguata and Ostertag, 2001). With agriculture, the extent of soil damage also depends on duration and intensity of cultivation, and the number of cultivation cycles (Lawrence, 2005; Sovu *et al.*, 2009; Derroire *et al.*, 2016). Sovu *et al.* (2009), for example, found that forests recovering from shifting cultivation with only one cultivation cycle had greater tree species diversity and stem density, and lower exotic bamboo abundance compared to areas with three cultivation cycles.

Soil fertility and texture influence the rate of secondary succession. Specifically, high quality soil catalyses recovery and degraded soil impedes regeneration (Guariguata and Ostertag, 2001; Chazdon, 2003). Herbert et al. (1999) found that tree damage was higher in forest plots artificially fertilised with phosphorus following Hurricane Iniki in Kauai, Hawaii, but that primary productivity and biomass was greater in fertilised plots after two years of recovery (Herbert, Fownes and Vitousek, 1999). Changes in soil nutrients can further alter the vegetation species composition where more nutrient-rich soils, for example when land has been fertilised, tend to favour fast-growing pioneer-type species (Guariguata and Ostertag, 2001).

Generally, the recovery of functional characteristics, species diversity and composition is faster when disturbance intensity is low and brief (Uhl, Buschbacher and Serrao, 1988; Guariguata *et al.*, 1997; Chazdon, 2003). Studies found that areas abandoned immediately after being deforested had three to six times greater tree species richness than those subsequently used for agriculture or pasture before abandonment (Finegan, 1996). Uhl *et al.* (1988) found forests regenerated quickly when pastures had been managed less intensely, largely due to re-sprouting vegetation. Nepstad *et al.* (1996) found that land which had been managed for pasture over long periods of time had fewer instances of re-sprouting and a diminished soil seed bank (Nepstad et al., 1996). In large and intensely disturbed deforested areas the colonisation of pioneer plants is more important than re-sprouting vegetation, and forest recovery takes longer. This is especially so if the management continues for a long time (>10 years). Secondary forests are thus better able to recover when the initial damage and human management was minimal.

Isolation and colonisation

The recolonisation of vegetation in deforested areas relies on the abundance of surviving or re-sprouting trees and seed availability (soil seed bank and seed rain from nearby mature trees). Remnant vegetation, including surviving trees, re-sprouted trees and living seeds, increase vegetation recruitment and the recovery rate of forests.

Many trees can re-sprout after being injured but not entirely killed (Chazdon, 2003; Nepstad et al., 1996). Others colonise as direct progeny of surviving mature trees, grow from the soil seed bank or seed into a deforested area by biotic or abiotic dispersal agents (commonly vertebrate and wind-dispersal; Lambin *et al.*, 2001; Mora *et al.*, 2015). Surviving mature trees thus catalyse forest regeneration as a direct seed source. They further offer habitat for animals which encourages vertebrate-distributed seed germination (Chazdon, 2003). Fruiting trees are particularly attractive (Derroire et al., 2016), though all remnant trees increase local seed deposition. Even remnant structures such as standing dead trees and logs can increase the habitat quality (Franklin *et al.*, 2002).

Remnant trees also generate microclimates suitable for germination (Chazdon, 2003; Derroire et al., 2016). The detritus produced by trees (eg. leaf litter) enhances soil quality, and their roots stabilise soil and enhance water cycling. Trees that fix nitrogen (eg. leguminous trees) directly increase soil fertility. Lastly, shade provided by the tree canopy both regulates temperature and inhibits grass or herb growth which would otherwise suppress tree and shrub germination. Remnant trees are therefore focal points of tree growth and diversity in secondary forests (Franklin *et al.*, 2002; Chazdon, 2014; Sandor and Chazdon, 2014).

Nearby mature forests also influence the regeneration rate, tree diversity and species composition of secondary forests (Cubiña and Aide, 2001; Hooper, Legendre and Condit, 2004; Derroire *et al.*, 2016; Rolim, Machado and Pillar, 2017). The matrix habitats surrounding deforested areas are principal seed sources. Deforested areas typically begin to regrow along any remnant forest edges (Chinea and Helmer, 2003). The species diversity and composition of nearby remnant forest limits the diversity and composition of seed rain into deforested areas. Old-growth forests are often refuges for shade-tolerant plants and specialist species with limited colonisation abilities. They are therefore valuable sources of sensitive species (Arroyo-Rodríguez *et al.*, 2017).

The distance and direction to the nearest seed source further influences seed rain (Derroire et al., 2016). Wind-dispersed plants depend on both the proximity of seed sources and their position relative to the dominant wind direction. Wind-dispersed trees are common, especially early in succession, since seeds can travel long distances (Finegan and Delgado, 2000; Cubiña and Aide, 2001; Derroire *et al.*, 2016). The distance and orientation of secondary forests relative to nearby mature forests further affects the behaviour of biotic seed dispersal agents (Ingle, 2003). Ingle (2003), for example, found that bird seed dispersal diminished with increasing distance to a seed source.

The soil seed bank quality also effects tree colonisation (Hyatt and Casper, 2000). As with seed rain, the soil seed bank composition is affected by seed dispersal from nearby mature trees and forests. Seeds from diverse plants build up in the soil and may remain dormant for years. If regeneration is delayed from prolonged disturbance, such as with agricultural or pastureland, seeds can become inviable. This is particularly important in wet-tropical forests where seed longevity is often short (Vázquez-Yanes and Orozco-Segovia, 1993; Cubiña and Aide, 2001). The type of disturbance effects the seed bank quality as well. For example, slash-and-burn reduces seed density through direct mortality and greater seed predation (Guariguata and Ostertag, 2001). Managed burning regimes for pasture maintenance likewise decrease tree seed viability and inhibit re-sprouting (Derroire et al., 2016). Thus, the seed bank quality depends on the disturbance, seed influx rate, seed longevity and quality of the seed source.

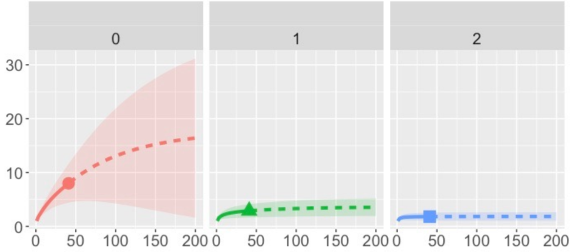
Multiple disturbances

Forests commonly undergo multiple disturbances simultaneously, or are disturbed at some point during regeneration. Some disturbances increase the likelihood that an area will be disturbed again. For example, burnt forests are at greater risk of fire (Woods, 1989; Cochrane and Schulze, 1999). Uhl and Kauffman (1990) likewise predict that logged forests and pastureland are more susceptible to wildfires due to their greater fuel load and drier climate. Multiple disturbances can alter or disrupt the recovery process, further slowing regeneration. Woods (1989), for example, studied two and six-year-old Malaysian secondary forests re-growing after logging, which were both burnt in a wildfire in 1983. In both forest, most of the young trees were killed by the fire leaving the species community altered and diversity diminished. The author proposes that the recovery capacity of the forests declined due to the cumulative damage of the two disturbances.

Appendix 3.1 Extrapolated rarefaction curves for Trinidad field research

Extrapolated rarefaction curves generated from taxonomic alpha-diversity analyses presented in Chapter 4. The labels 0, 1 and 2 refer to the diversity index: Hill numbers of the order q: species richness (q=0), Shannon diversity (q=1) and Simpson diversity (q=2; Hill, 1973). Solid lines represent interpolated data, while dashed lines are extrapolated. The diversity index increases along the Y axis, and number of individuals along the X axis. Confidence intervals are shaded around line.

Tree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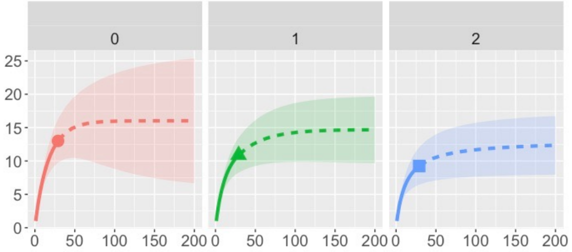
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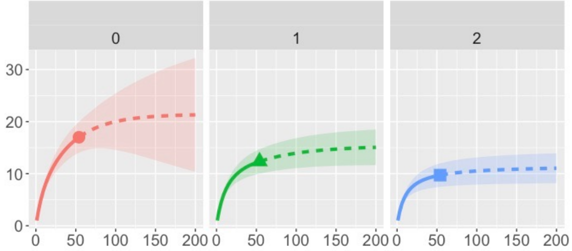
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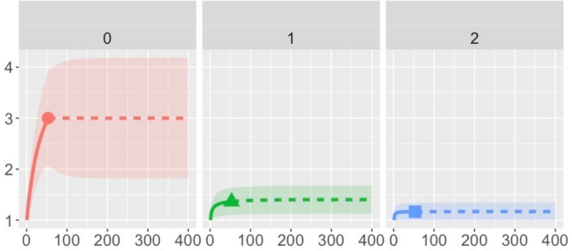
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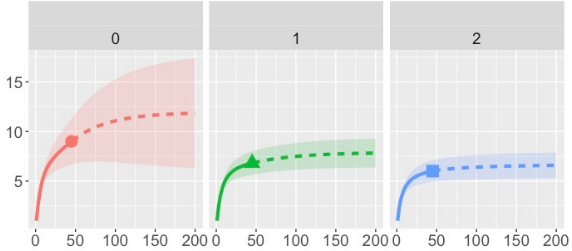
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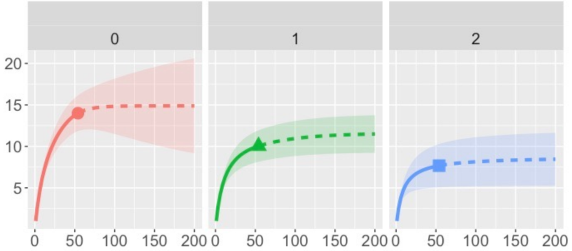
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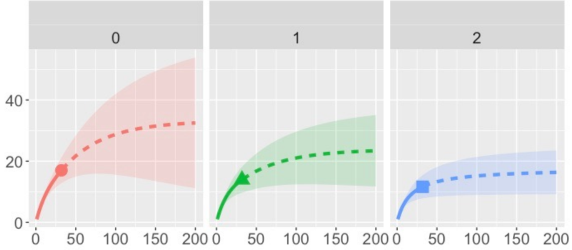
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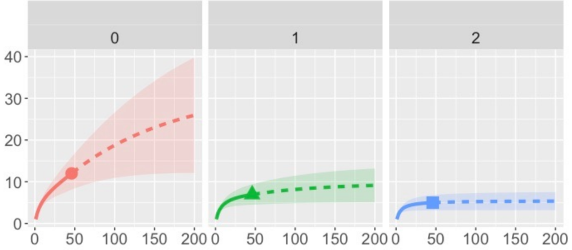
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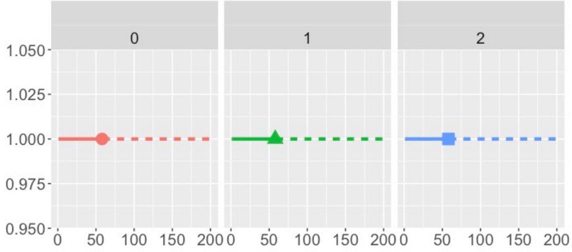
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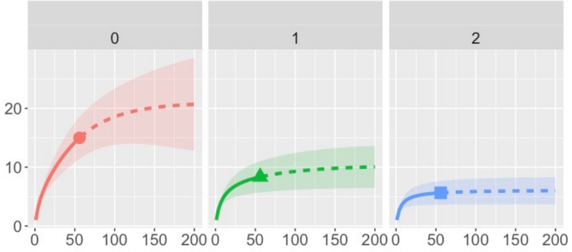
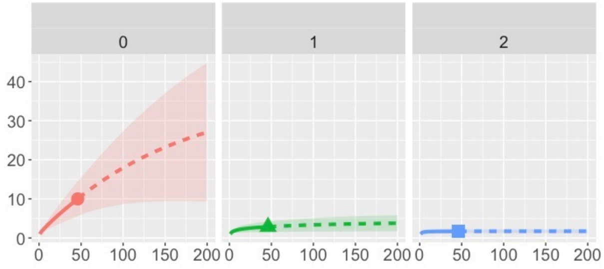

GL

Tree

LAL



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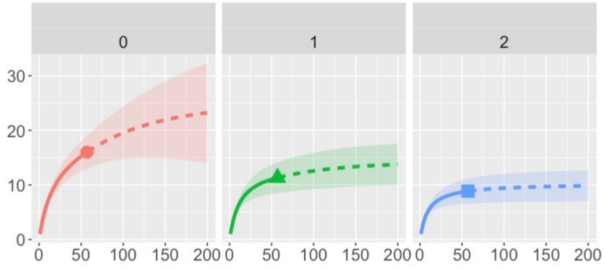

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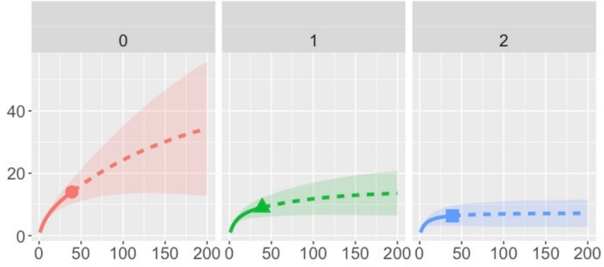

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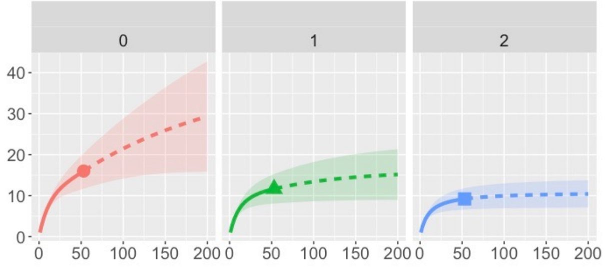

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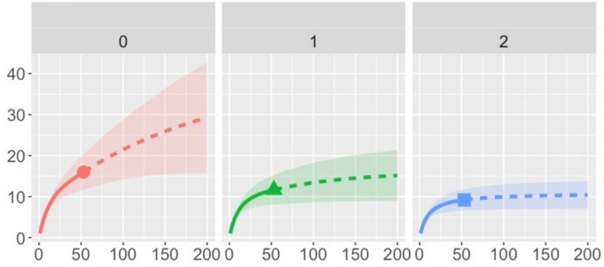

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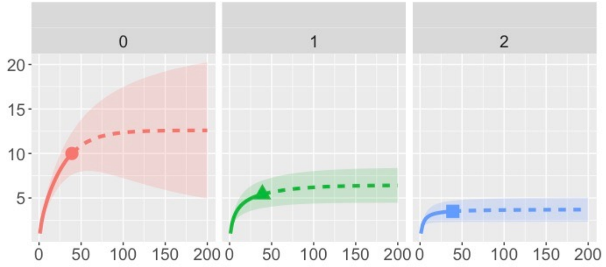

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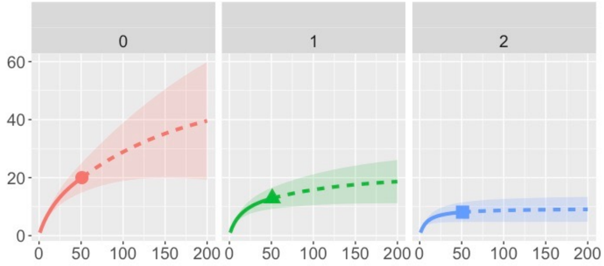

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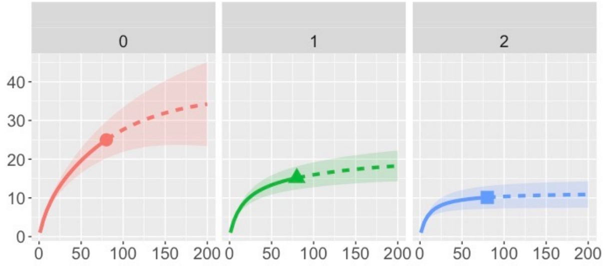

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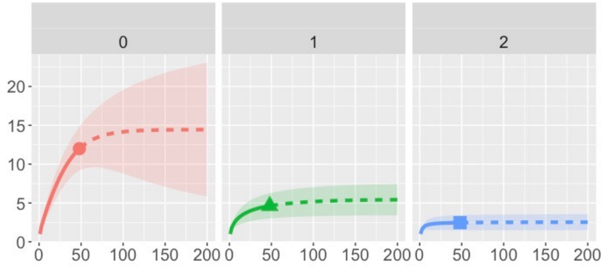

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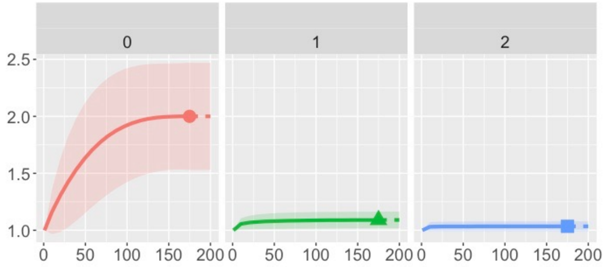

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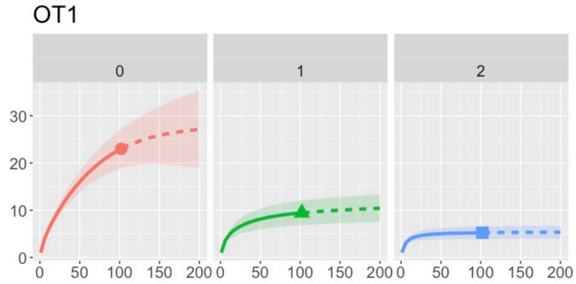
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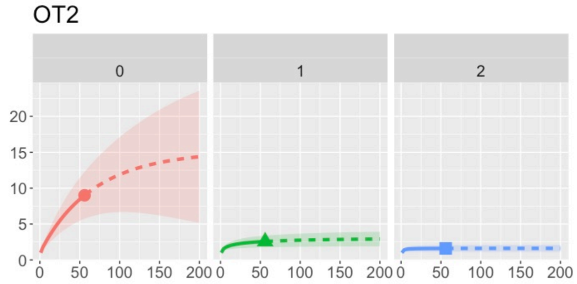
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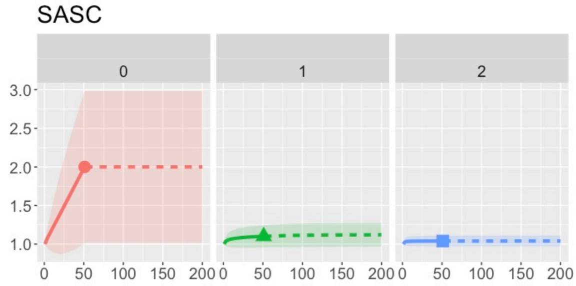
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1.0
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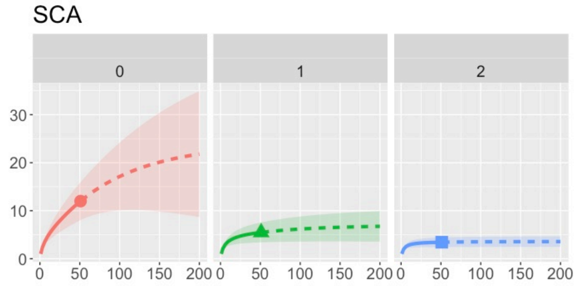
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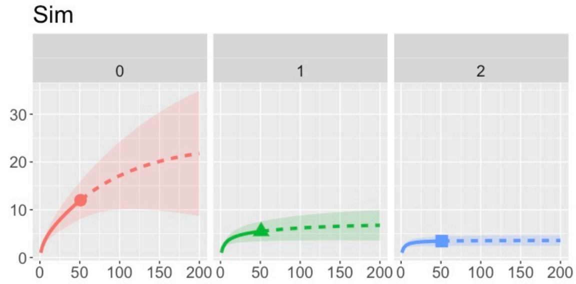
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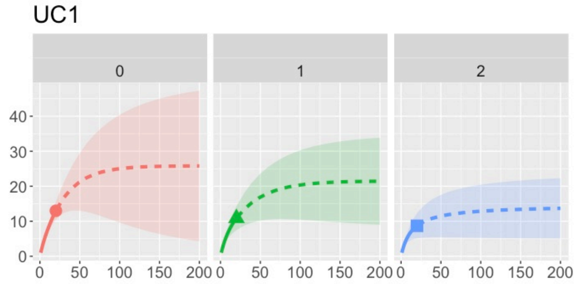
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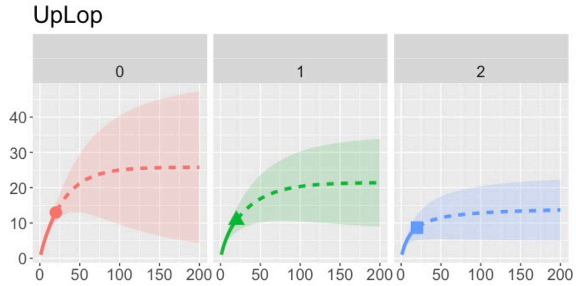
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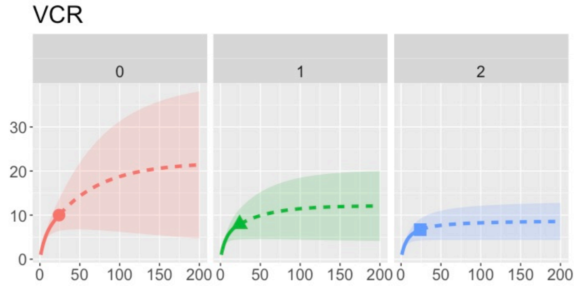
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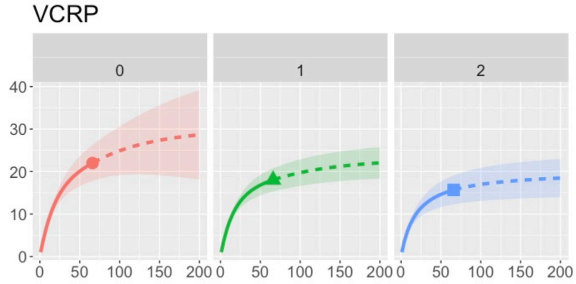
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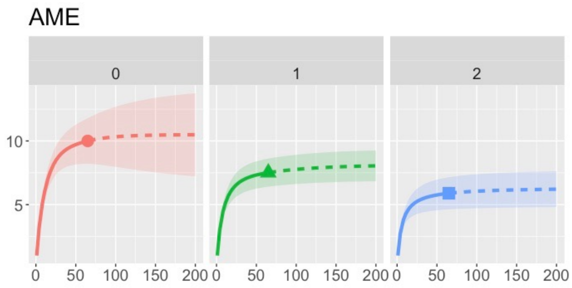
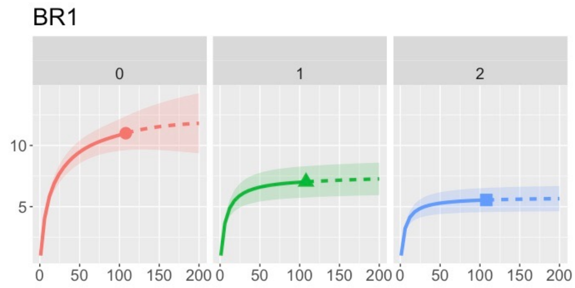
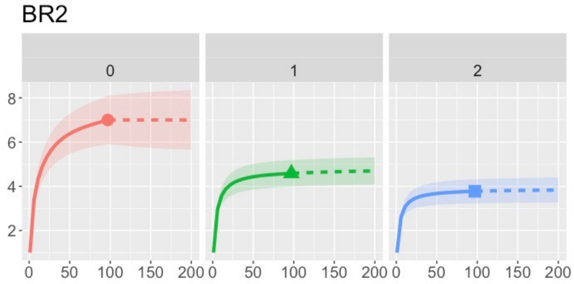
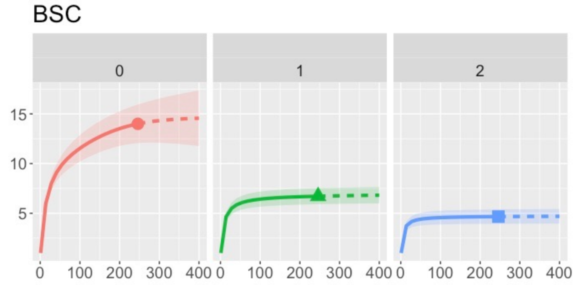
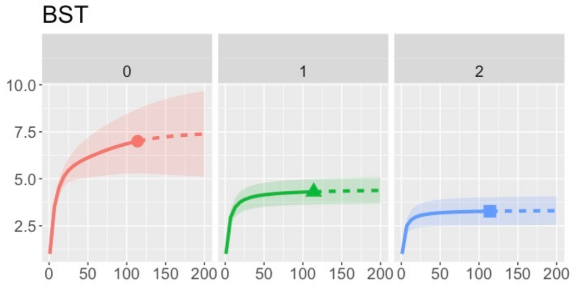
Ground vegetation

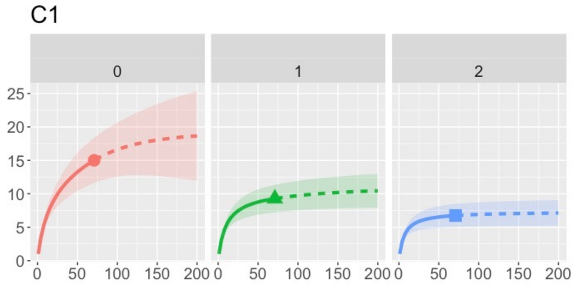


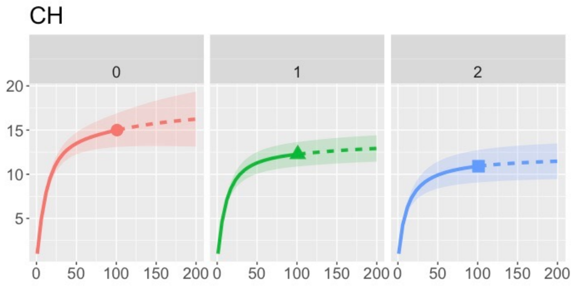


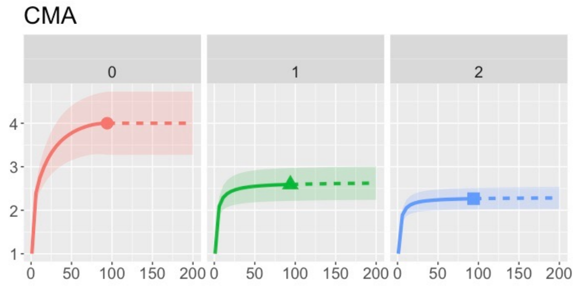


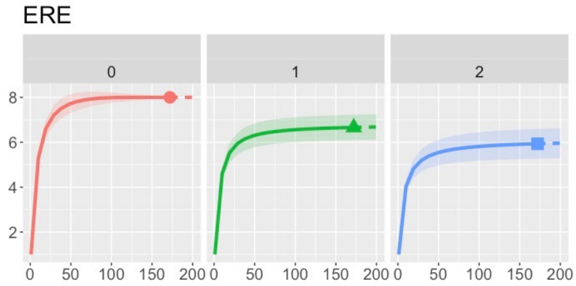


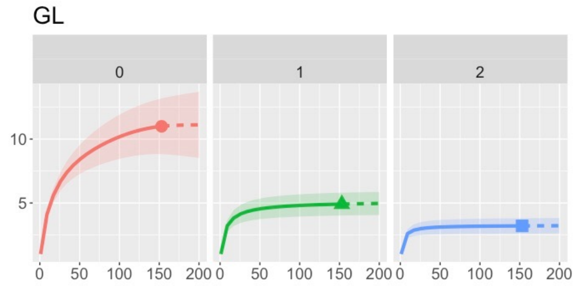












Ground vegetation

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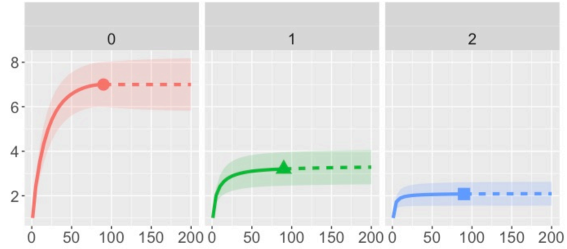

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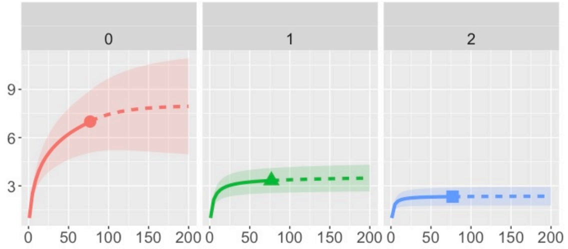

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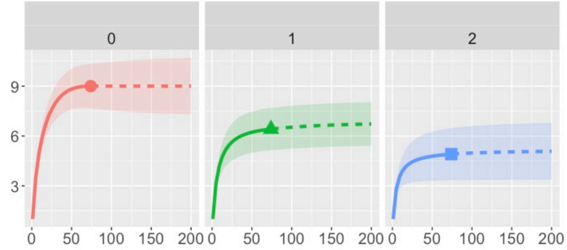

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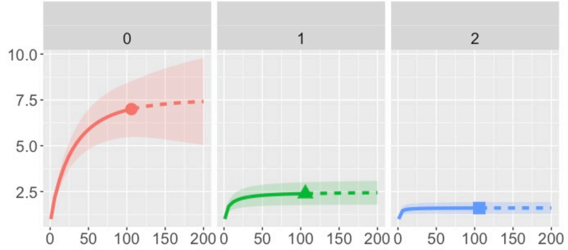

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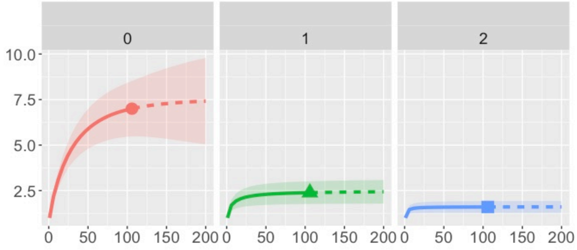

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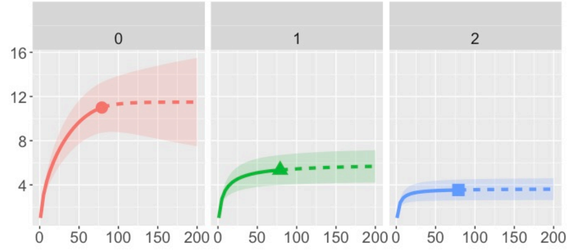

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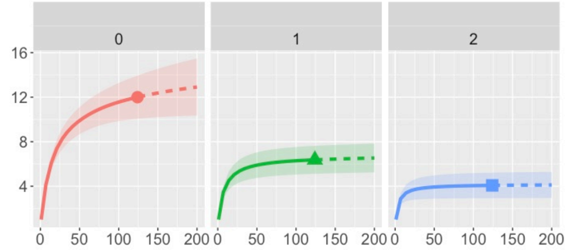

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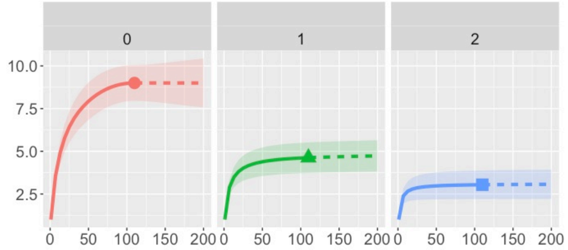

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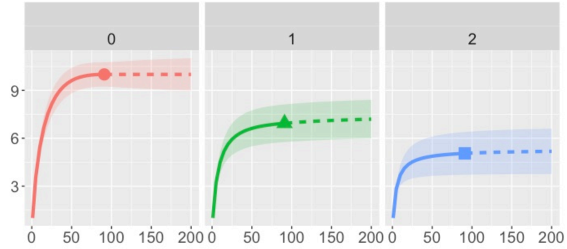
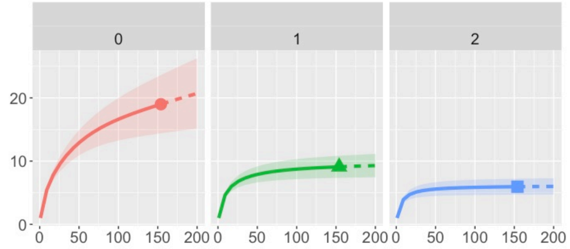
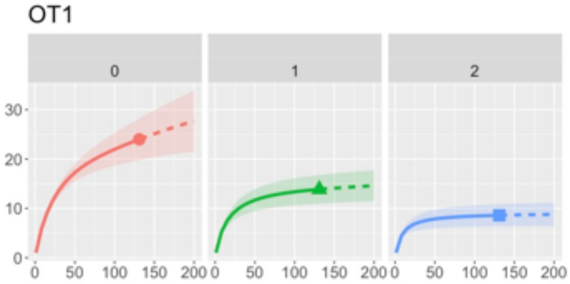


OA



Ground vegetation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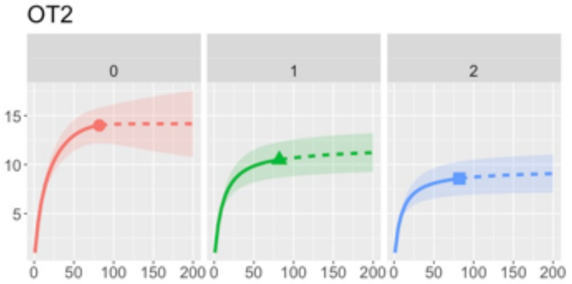
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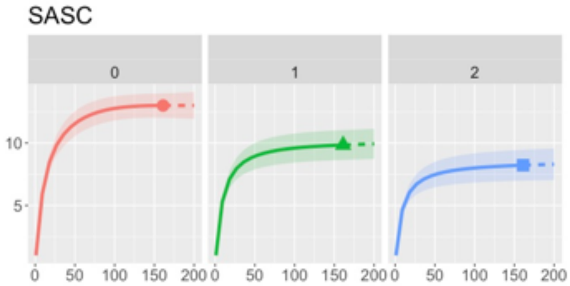
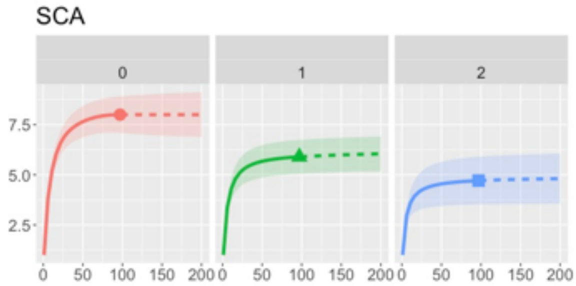

SASC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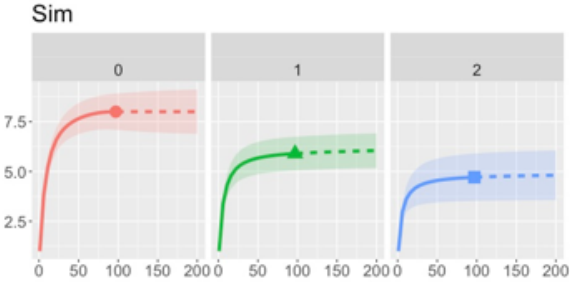
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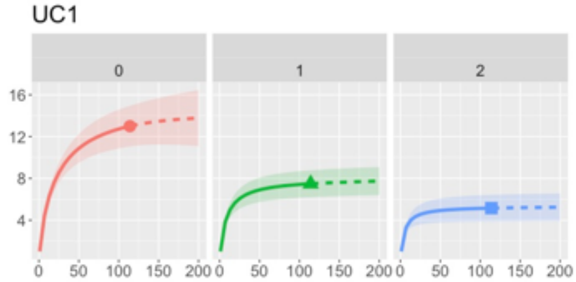
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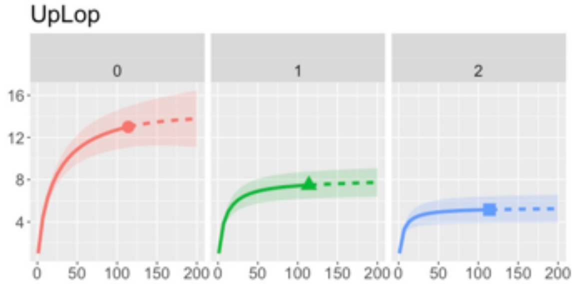
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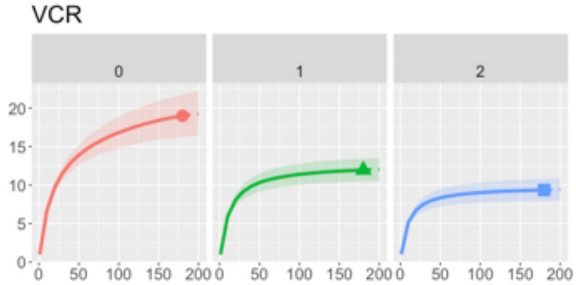
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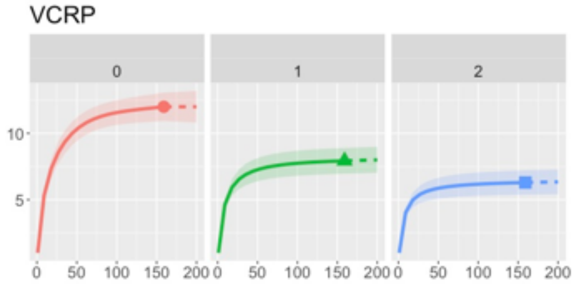
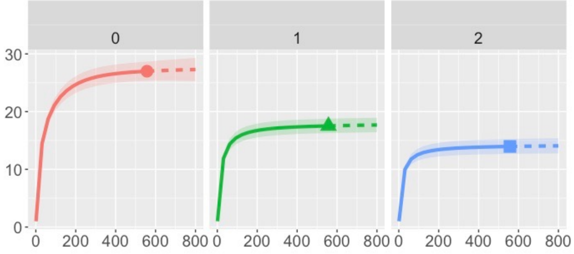

VCRP

Epiphytes

AME



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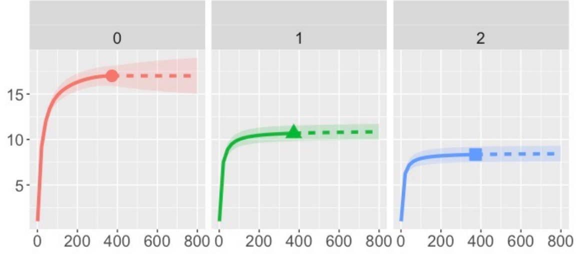
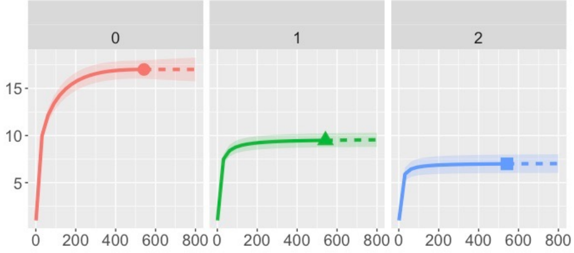
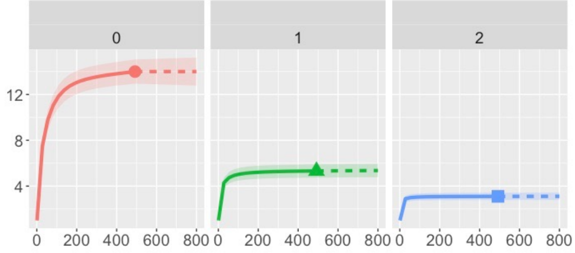


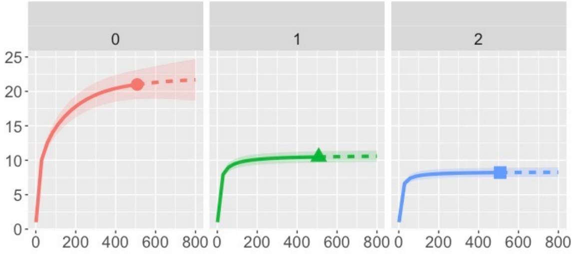
BR2



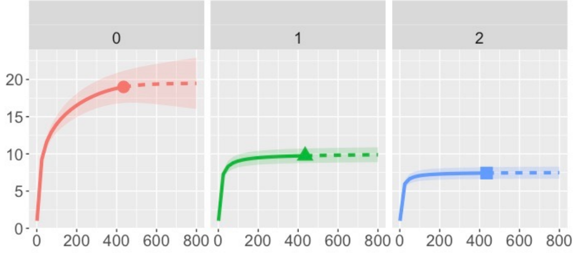
BSC



BST



C1



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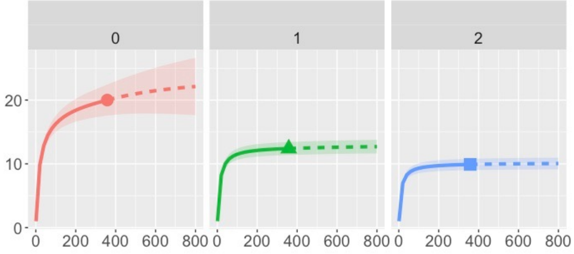

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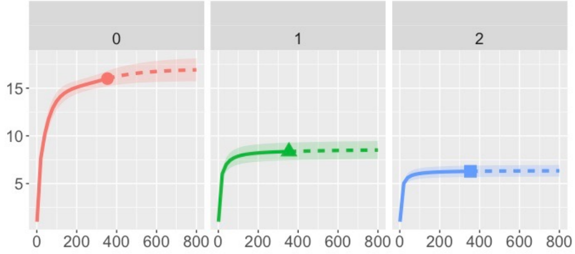

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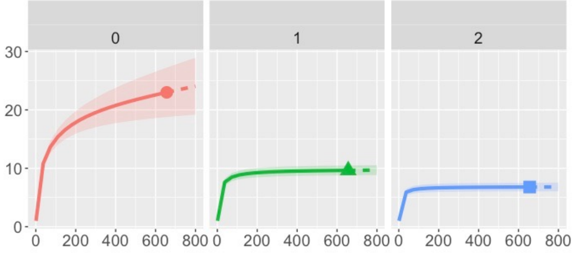

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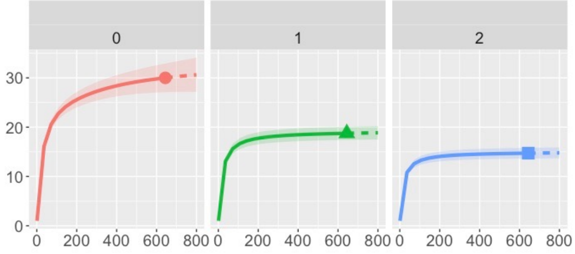
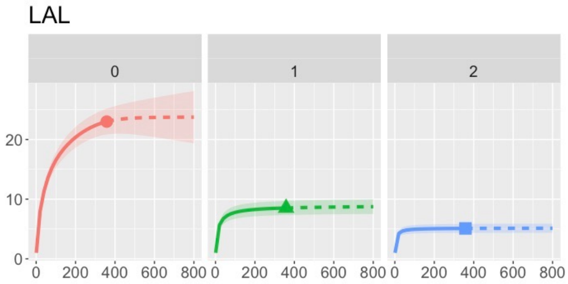


Epiphytes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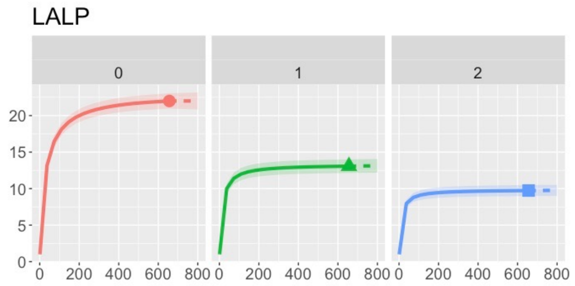
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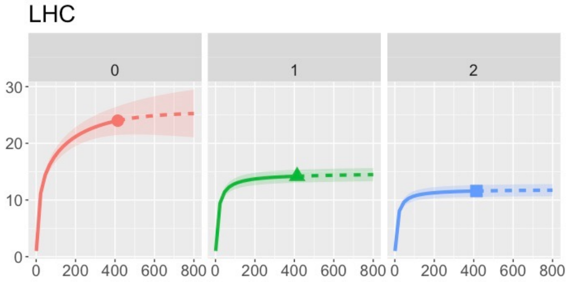
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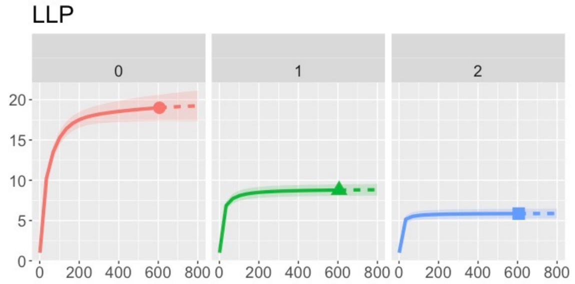
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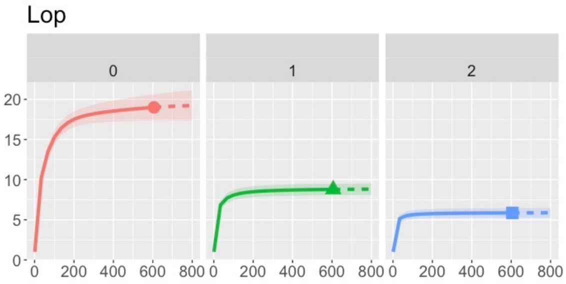
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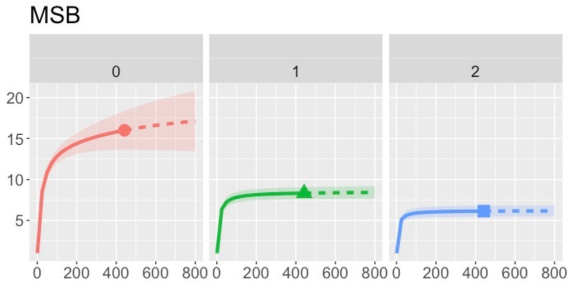
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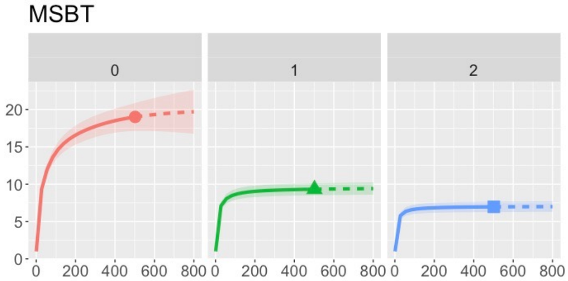
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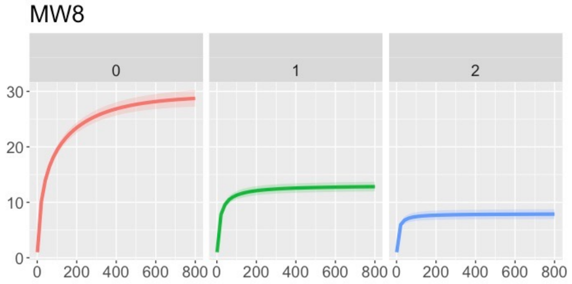
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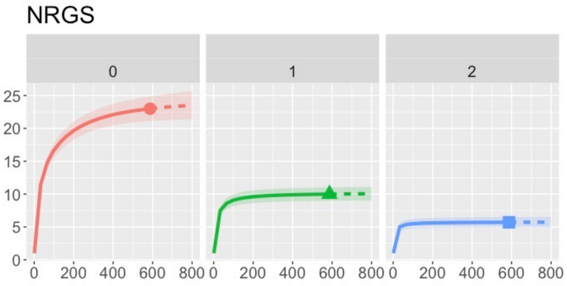
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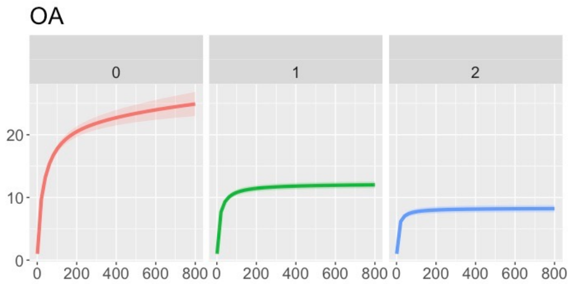
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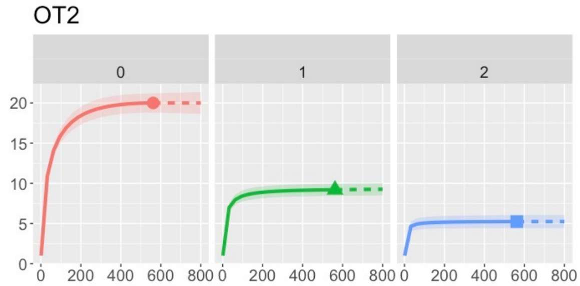
Epiphytes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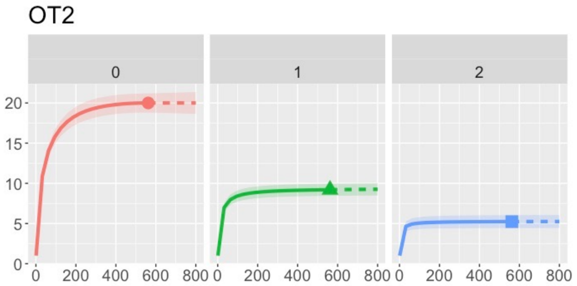
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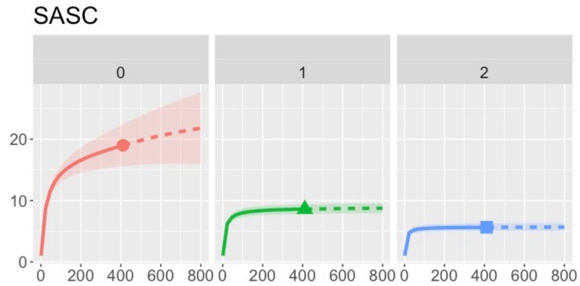
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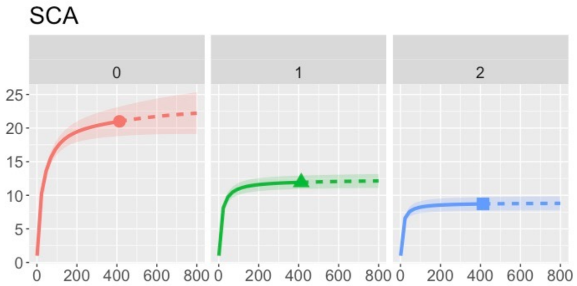
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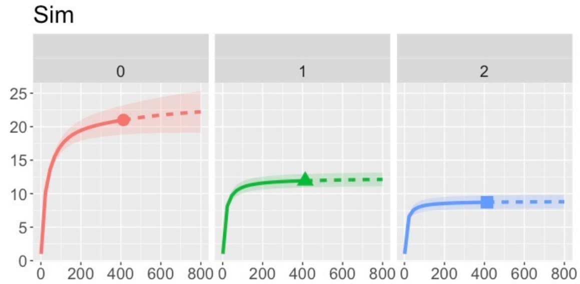
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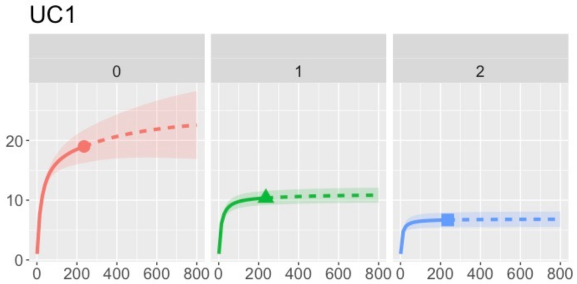
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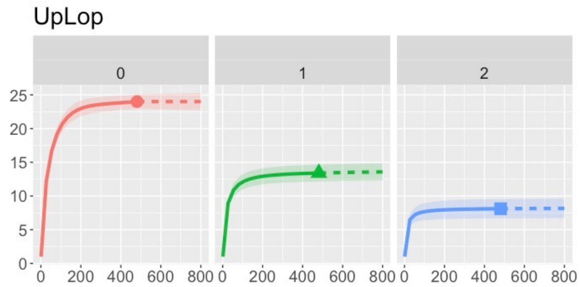
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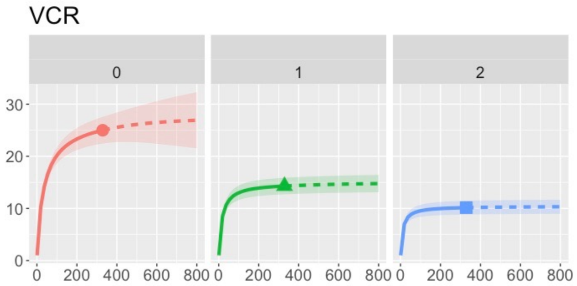
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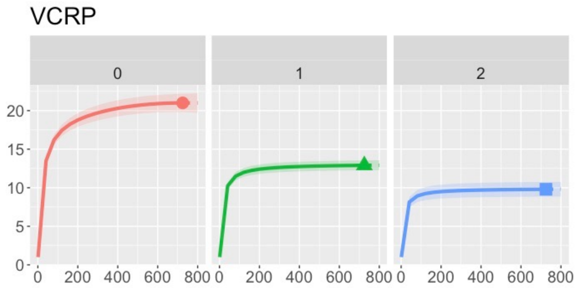
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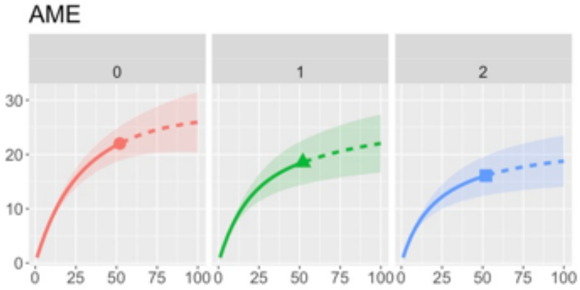
Birds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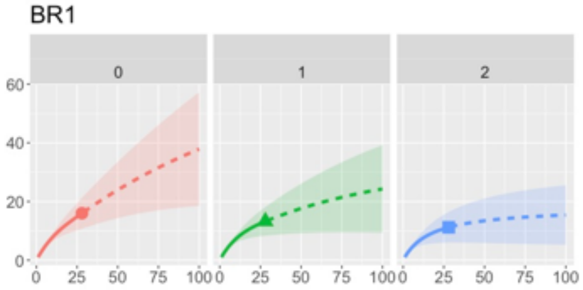
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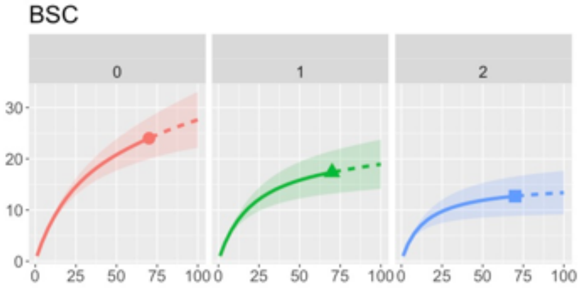
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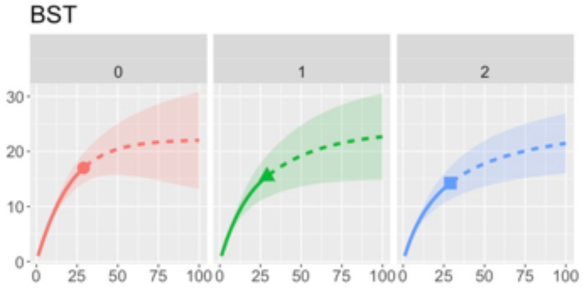
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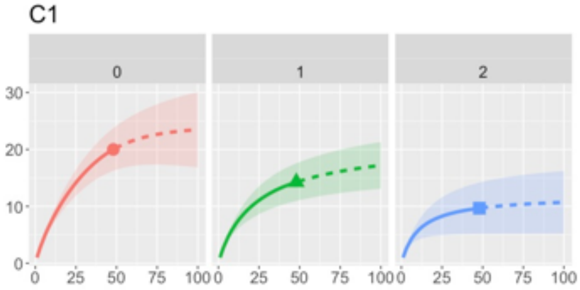
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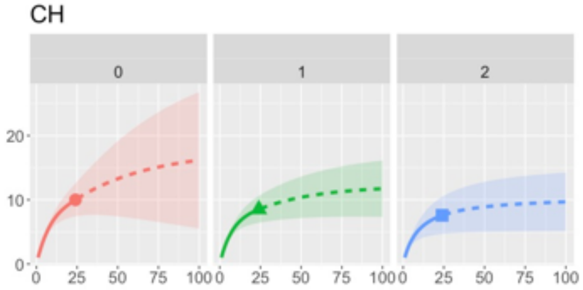
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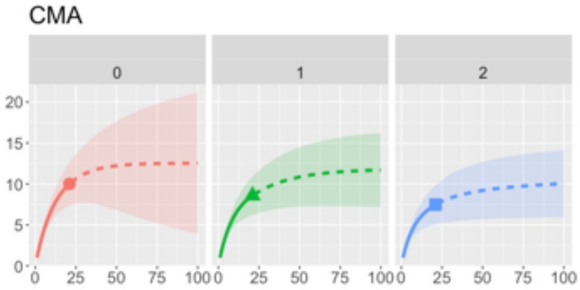
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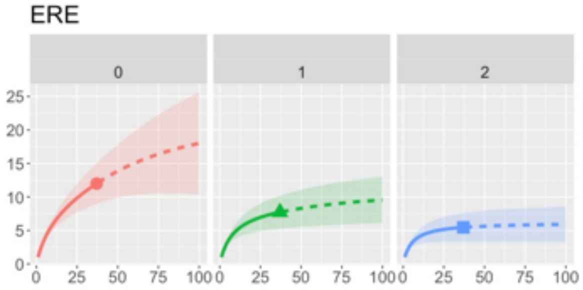
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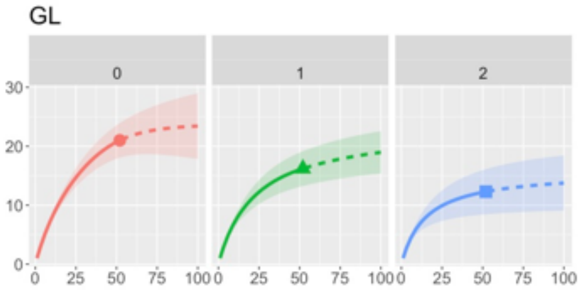
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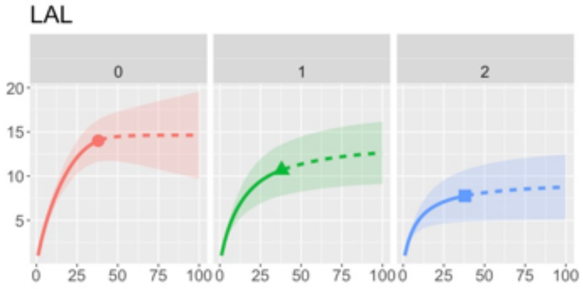
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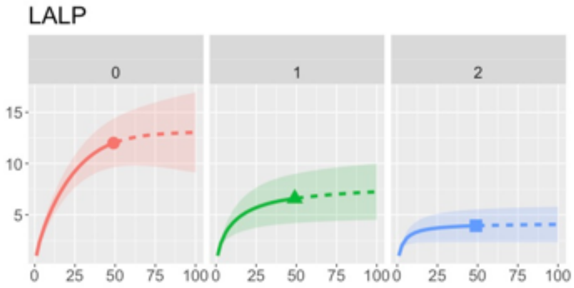
Birds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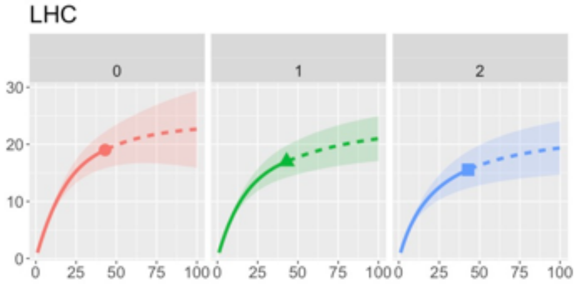
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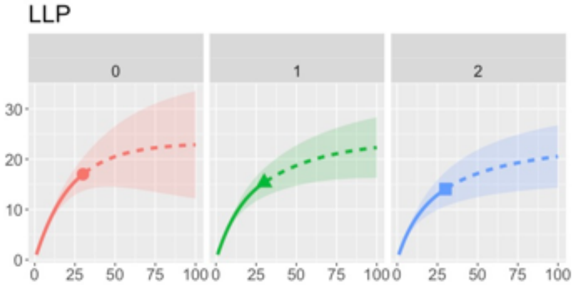
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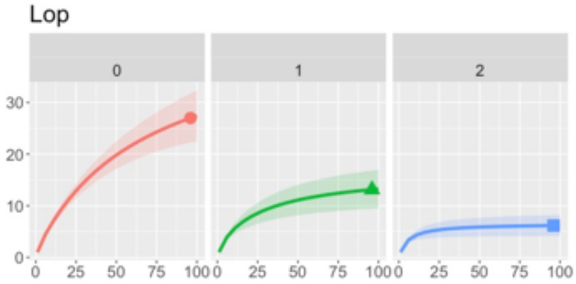
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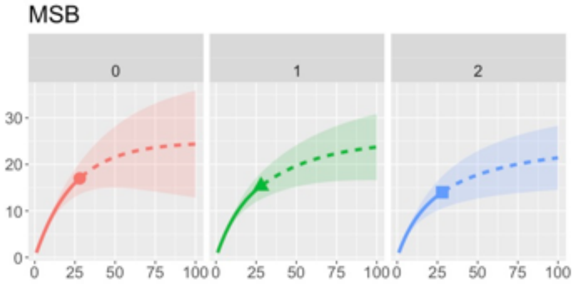
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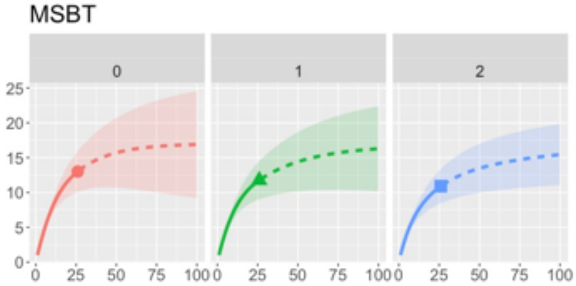
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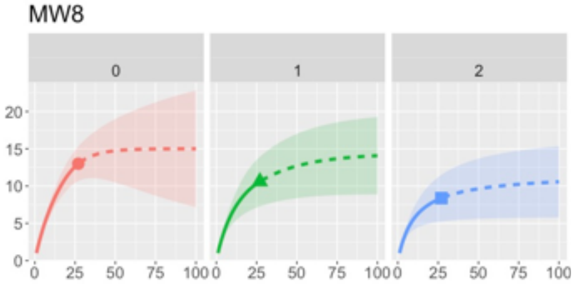
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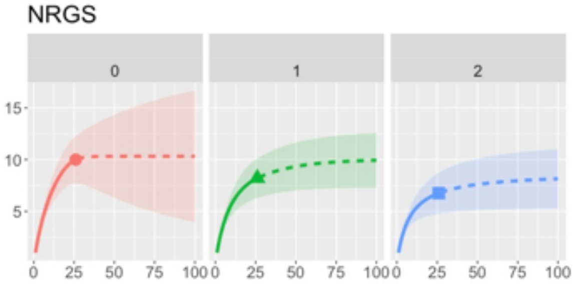
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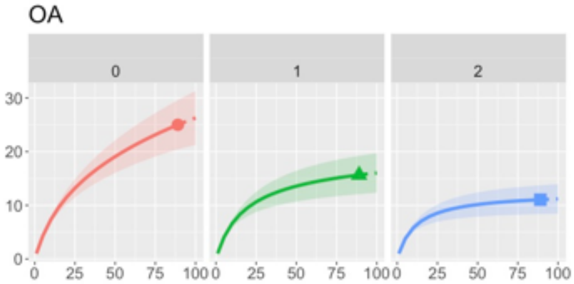
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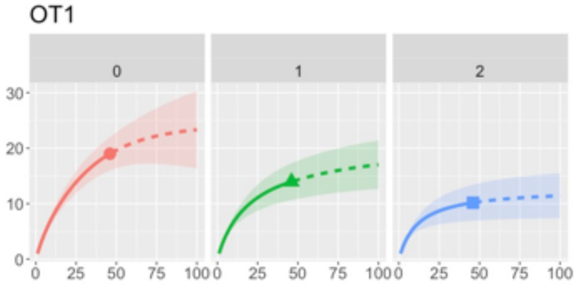
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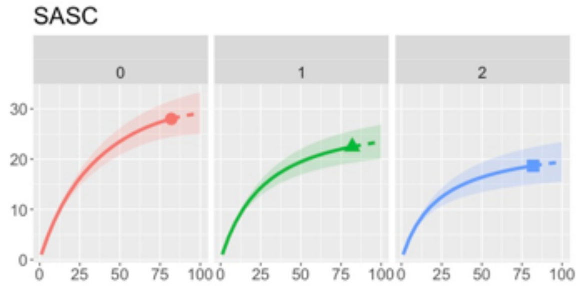
Birds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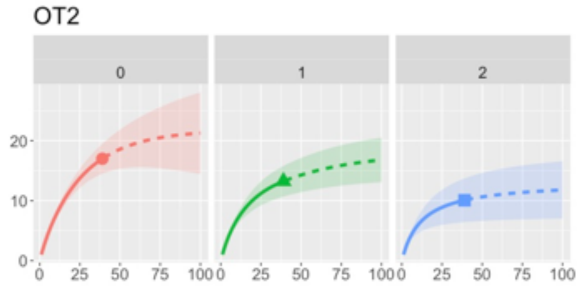
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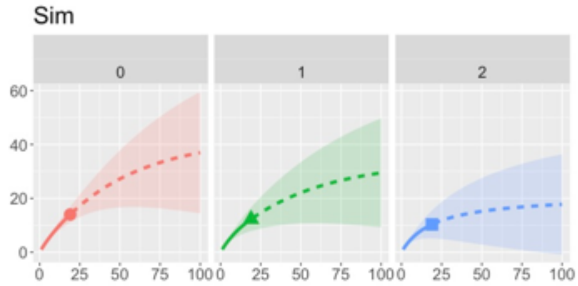
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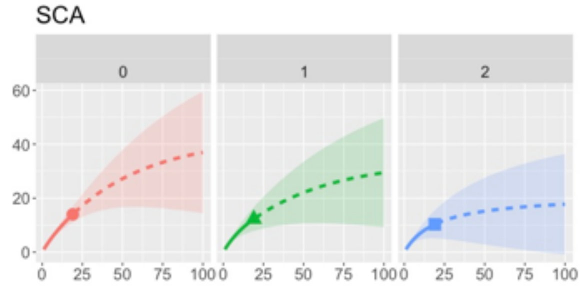
SCA
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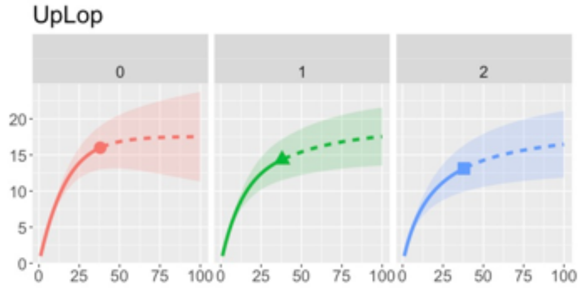
UpLop
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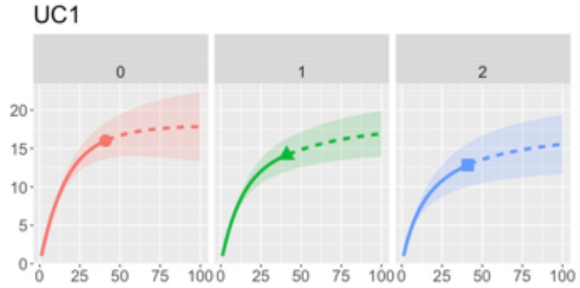
0
0 25 50 75 100


UC1
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1
2
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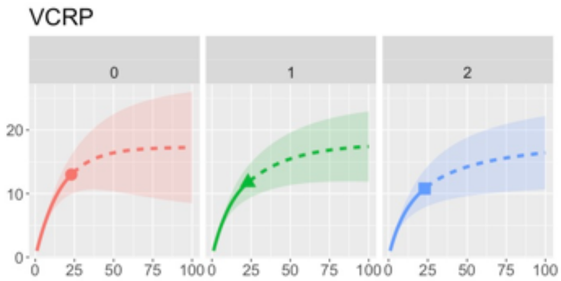
15
10
5
0
0 25 50 75 100


VCRP
0
1
2
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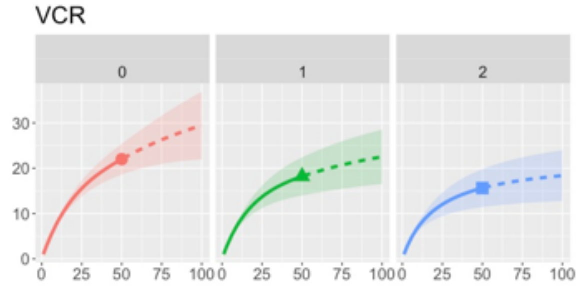
10
0
0 25 50 75 100


VCR
0
1
2
30
20
10
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0 25 50 75 100

Appendix 3.2 Trinidad lichen morphospecies photo library

Lichen 1 Black leprose lichen

Lichen 2 Pale blue leprose lichen

Lichen 3 Pale bluish-grey crustose lichen with white lirellate apothecia

Lichen 4 Bright green crustose lichen with large white lecanorine apothecia

Lichen 5 Green crustose lichen with grey arthonioid apothecia

Lichen 6 Bright green leprose lichen with reddish lecideine apothecia

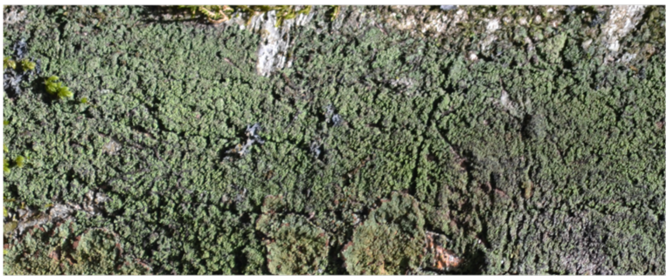
Lichen 7 Brownish-green crustose lichen with dark grey lecideine apothecia

Lichen 8 Dark brown folios lichen

Lichen 9 Greenish-brown crustose lichen with black arthonioid apothecia

Lichen 10 Brown crustose lichen with black prothallus and small lecideine apothecia

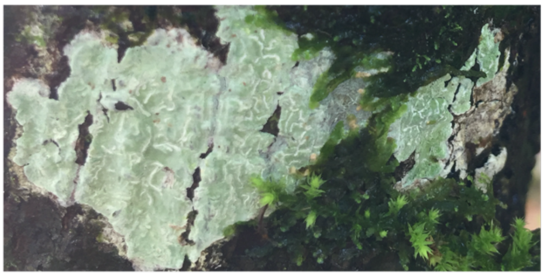
Lichen 11 Dark green crustose lichen with brown lecideine apothecia



Lichen 12 Green crustose lichen with slightly lobed margins and darker isidia

Lichen 13 Pale green crustose lichen with fine isidia and lobed white margins

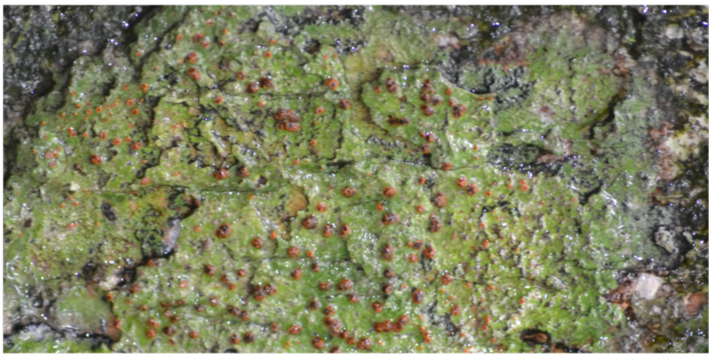
Lichen 14 Bluish-green placodioid lichen with fine isidia and lobed margins similar to L13 but with visible black prothallus



Lichen 15 Green crustose lichen with white lirellate apothecia

Lichen 16 Dark green crustose lichen with black prothallus and arthonioid apothecia

Lichen 17 White crustose lichen with grey-black lirellate apothecia



Lichen 18 Yellowish-green crustose lichen with orange lecideine apothecia

Lichen 19 Yellowish-green crustose lichen with black prothallus and arthonioid apothecia

Lichen 20 Orange leprose lichen or algae

Lichen 21 Pale bluish-green encrusting lichen with small lecanorine apothecia

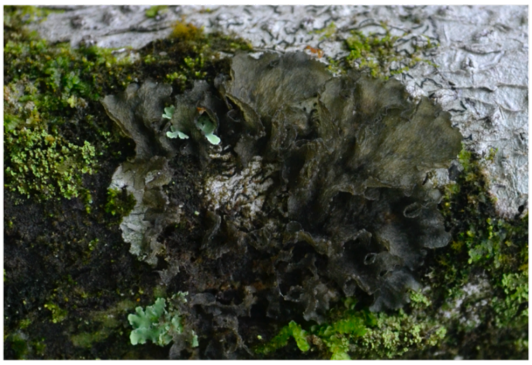
Lichen 22 Pale green leprose lichen with black lecideine apothecia

Lichen 23 Pale green crustose lichen with pink prothallus

Lichen 24 Bright green crustose lichen with white and brown margins, and small white lecideine apothecia

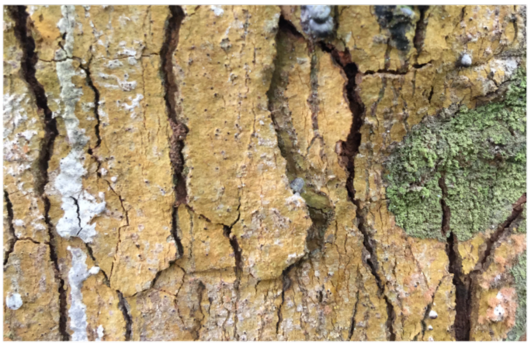
Lichen 25 Green crustose lichen with white lecideine apothecia

Lichen 26 Pale bluish-green crustose lichen with white lirellate apothecia and white margins



Lichen 27 Dark green folios lichen

Lichen 28 Pale blue crustose lichen with white soredia



Lichen 29 Orange-yellow crustose lichen with perithecia

Lichen 30 White leprose lichen with black margins

Lichen 31 Pale bluish-green crustose lichen with black lirellate apothecia

Lichen 32 Pale yellow crustose lichen with black slightly lobed margins

Lichen 33 A green filamentous lichen cf *Coenogonium linkii*

Appendix 3.3 Analyses on truncated bird data

Birds were observed up to 200m away on surveys and the full dataset was used in the analyses presented in the main thesis. The bird data were truncated to only include observations which were within 50 metres of the transect line in order to test whether varying levels of detectability and different matrix habitat types influenced the results on the whole dataset which included observations up to 200m. The analysis on the truncated data yielded similar results: there was no significant change in bird species richness ($F_{(1,26)}$=1.722, R^2=0.02, p=0.20), Shannon diversity ($F_{(1,26)}$=0.85, R^2=-0.01, p=0.37) or Simpson diversity estimates with forest age ($F_{(1,26)}$=0.18, R^2=-0.03, p=0.67).

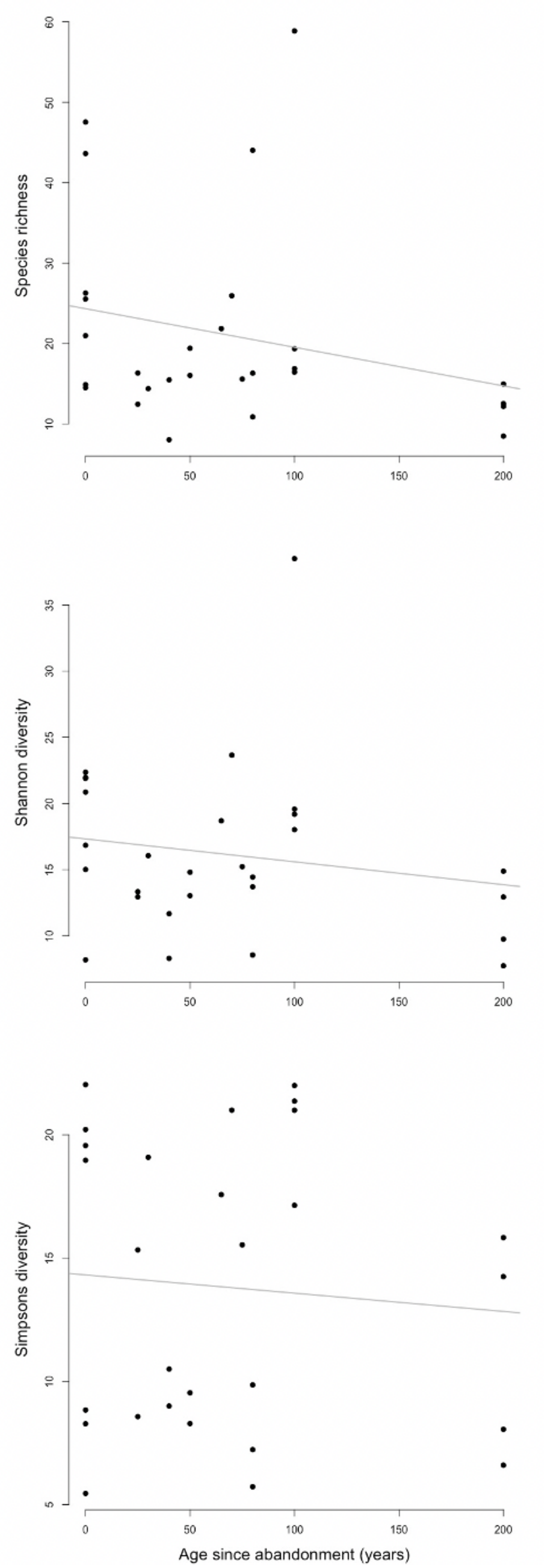


Figure 3.4.1 Bird species richness, Shannon diversity and Simpson diversity with forest age. The data used in these analyses were truncated to only include bird observed within 50m from the transect line.

A 0.5 quantile regression found a significant increase in the probability of compositional dissimilarity (Raup Crick index) with increasing age (p=<0.01; Koenker, 2013), but no significant change with environmental distance (p=0.09) between sites. These results indicate that neither the potential variation in detectability between sites, nor the inclusion of birds over 50m away which may have been outside of a site in differing matrix habitats influenced the diversity assessments presented in this thesis.

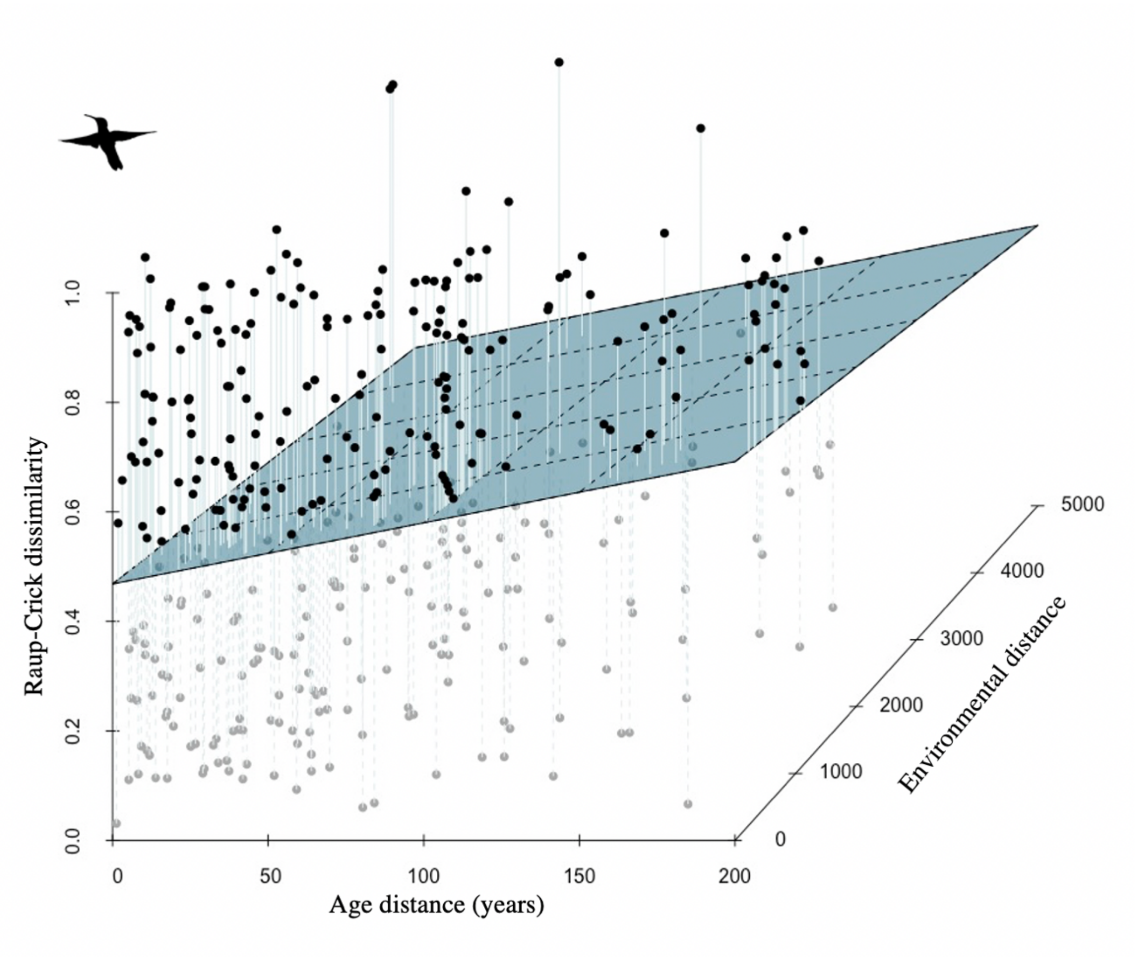


Figure 3.4.2. Change in bird species compositional dissimilarity (Raup-Crick index) with age difference and environmental distance between site pairs. Age difference is the age difference between site pairs, and environmental distance is the pairwise distance of sites in Euclidean space built using the environmental factors: annual average precipitation, average site altitude, distance of site from nearest settlement and average land gradient (Chapter 3).

Appendix 3.4 Bird repeatability

The precision of data collection was tested by re-surveying birds in all sites. Each transects was walked three times, 20 minutes apart. The first bird survey was used in the main analysis presented in Chapter 4. The coefficient of variation (CV) between species richness for the three transects within each site was measured. The CV value between the three transects was under 23% for all sites, which suggests that species richness remained consistent within sites.

Table 3.5.1. Coefficient of variation (CV) of species richness between three bird surveys along the same transect conducted 20 minutes apart in each site.

Site	CV
AME	11.2
BR1	11.5
BSC	11.8
BST	5.9
C1	12.6
Chag	22.9
CMA	5.4
ERE	9.1
GL	7.9
LAL	10.9
LALP	5.1
LHC	18.3
LLP	10.7
Lop1	15.0
MSB	17.6
MSBT	15.2
MW8	13.1
NRGS	16.9
OA	11.0
OT1	9.6
OT2	6.3
SASC	14.9
SCA	12.4
Sim1	10.4
UC1	5.9
UpLop	9.4
VCR	5.4
VCRP	13.3

Additionally, the results from each of the bird transect repeats within each site were further compared using extrapolated rarefaction to test for differences in species richness between the three bird transects within each site. The confidence intervals of the extrapolated rarefaction curves for the three transects within site overlap, which indicates there is no significant difference in species richness between the repeated surveys within each of the sites.

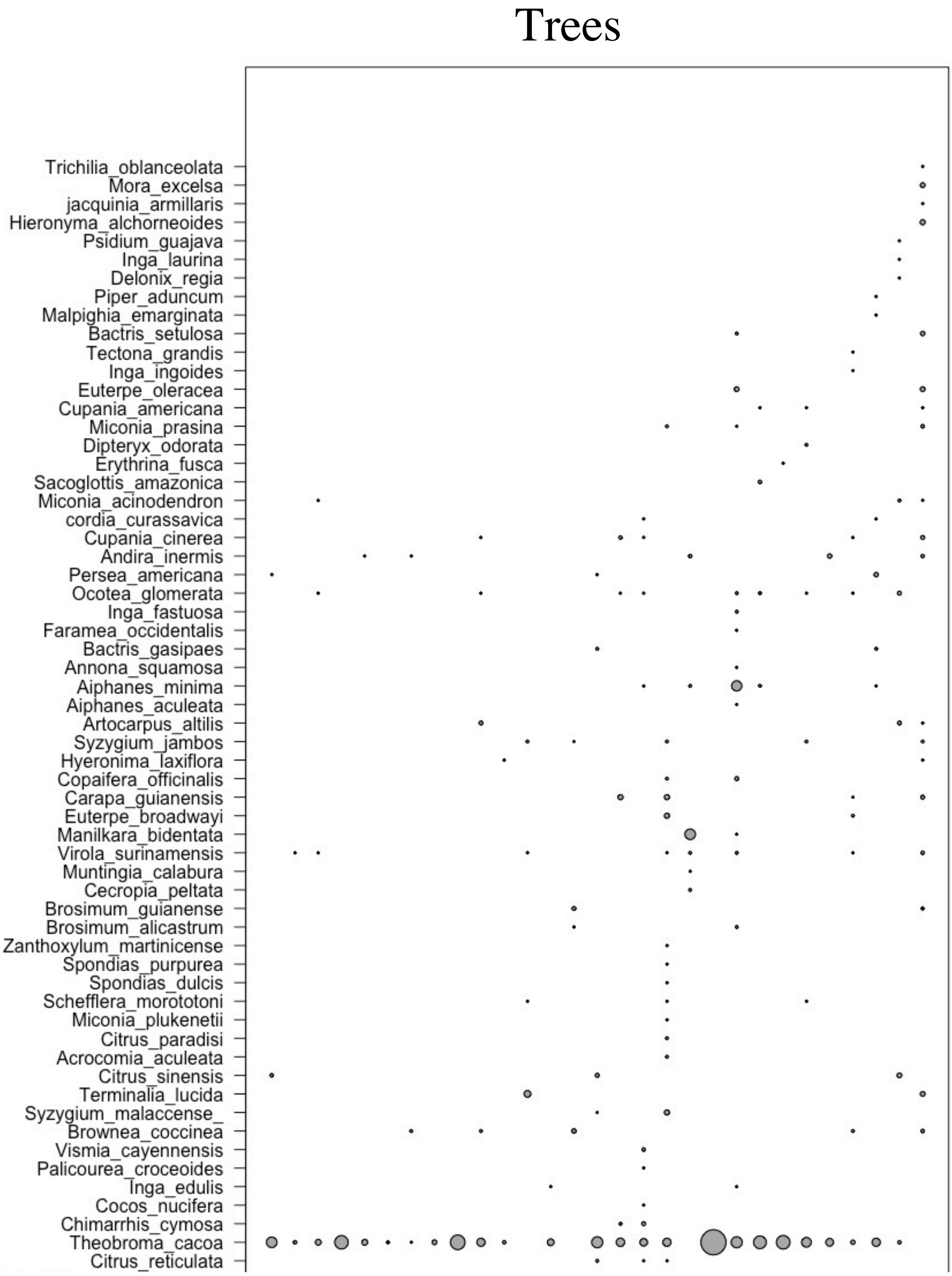
Furthermore, the Raup Crick index was further to test the degree of within-site compositional variance. Results found that there was little compositional change between surveys within each site. All Raup Crick values were below 0.13 which suggests that there was strong compositional similarity between the replicates. These results demonstrate that the field methods used to survey birds in Trinidad sites are repeatable and provide a representative sample of the bird communities.

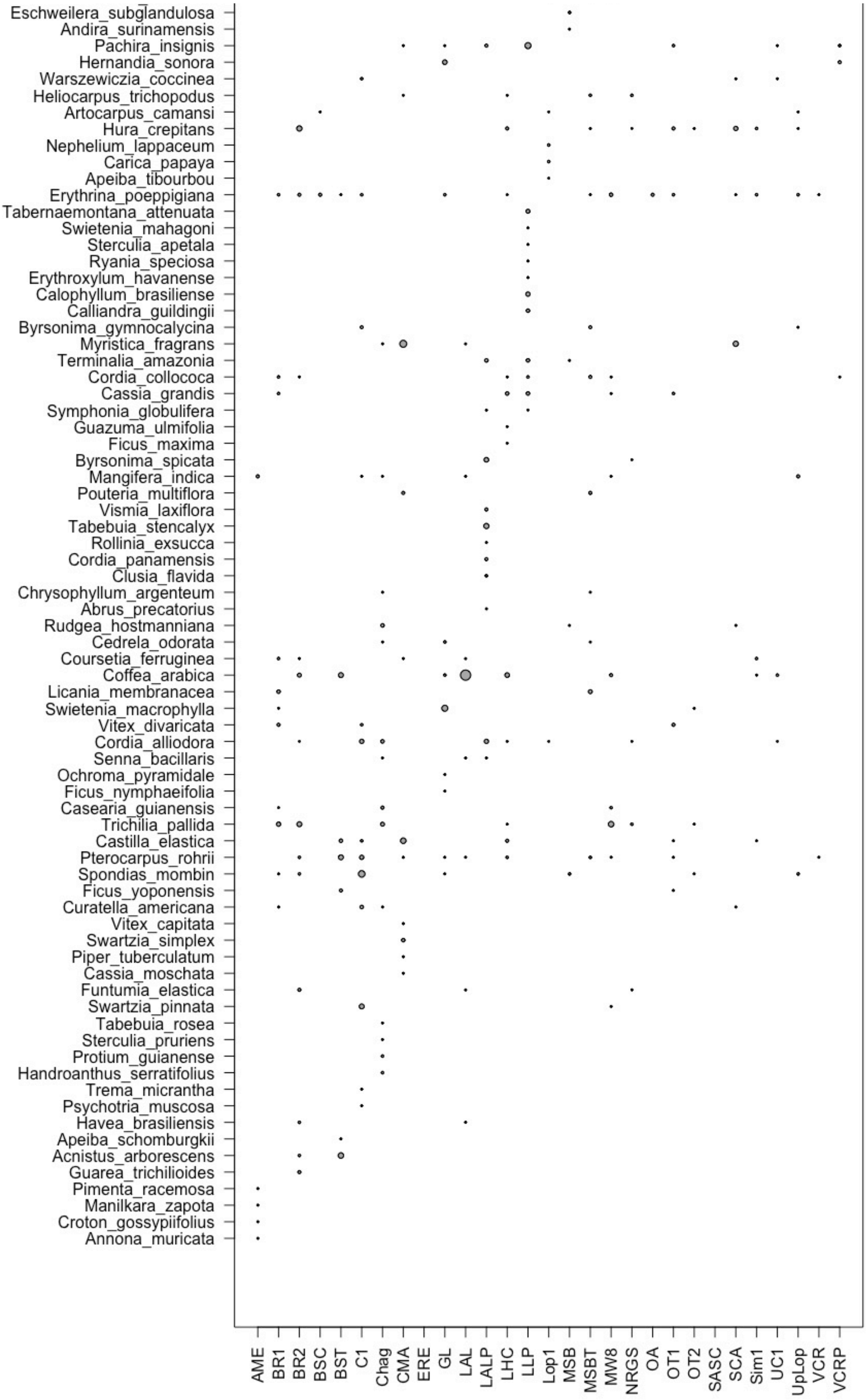
Lastly, a linear regression was used to test whether CV varied with forest age. A linear regression found no significant relationship between CV and forest age ($F_{(1,26)}$=0.02, R^2= -0.04, p=0.9) which suggests that the precision and repeatability of the methods was not affected by forest age.

Figure 3.5.1. Change in the Coefficient of variation with forest age.

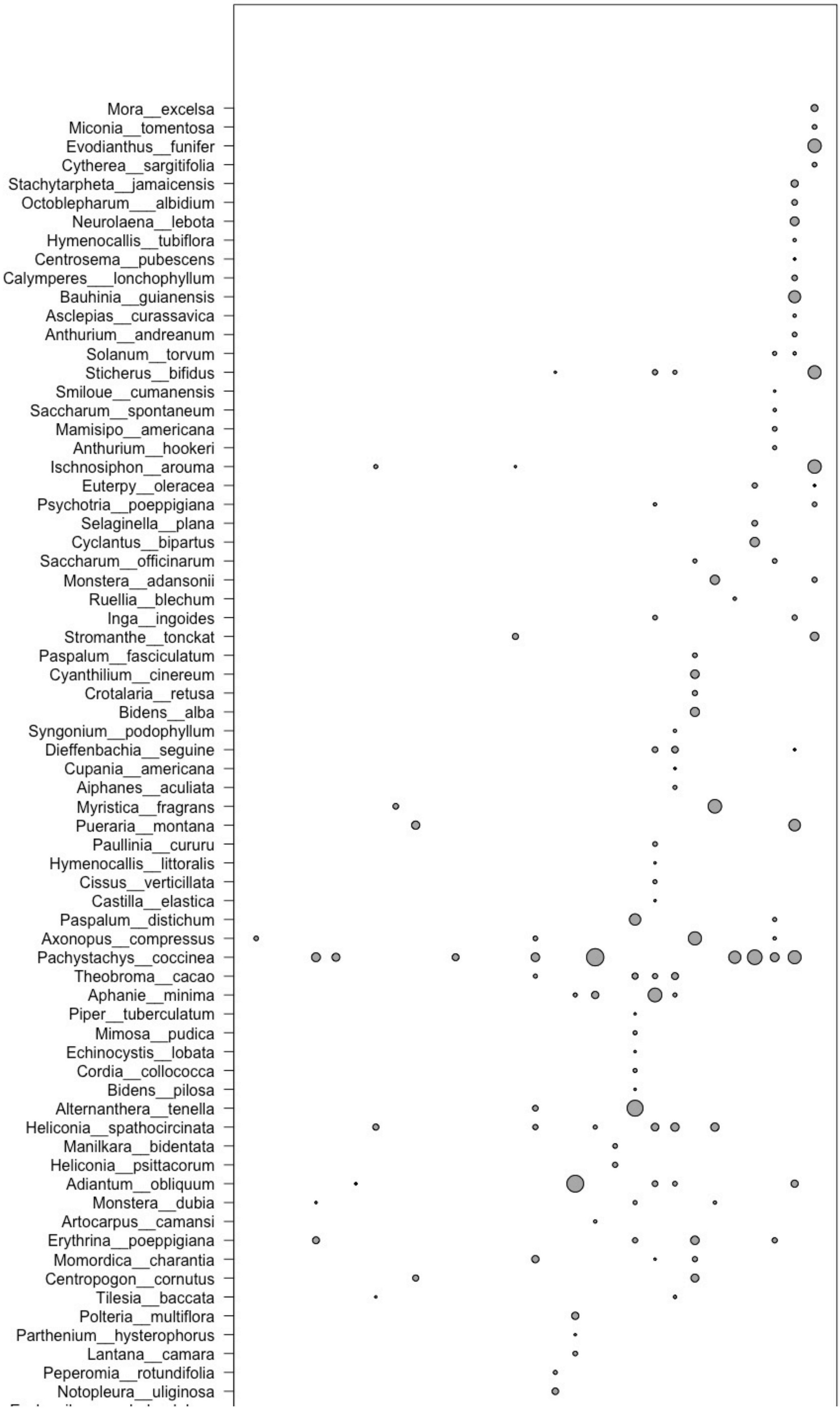
Appendix 4.1 Bubble plots

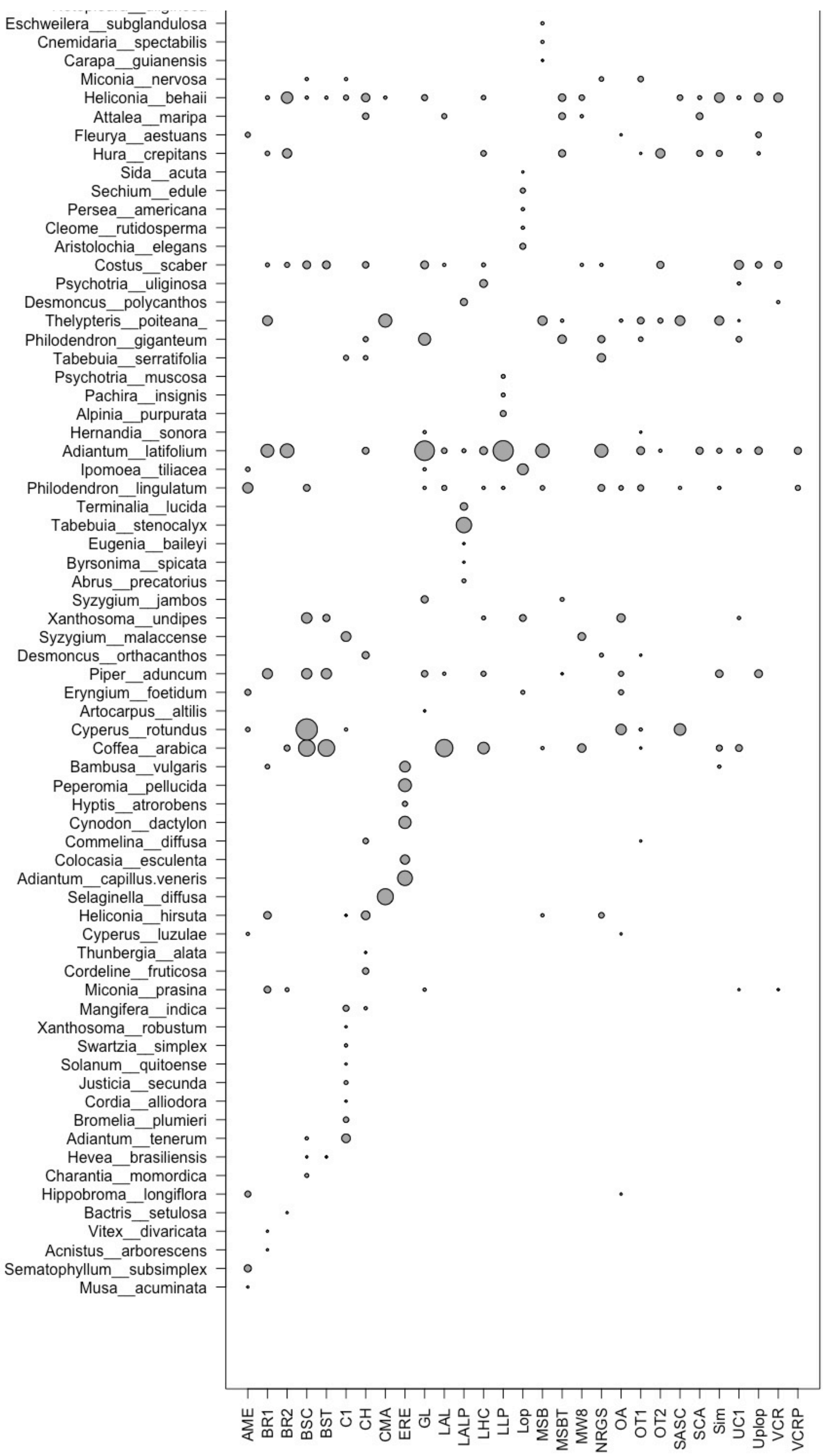
Bubble blots were used to assess changes in species composition with forest age, presented in part in Chapter 4. The following appendix provides the full bubble plots. The size of each of the circles on the plot represents the abundance of a given species in a given sites.




Eschweilera_subglandulosa
Andira_surinamensis
Pachira_insignis
Hernandia_sonora
Warszewiczia_coccinea
Heliocarpus_trichopodus
Artocarpus_camansi
Hura_crepitans
Nephelium_lappaceum
Carica_papaya
Apeiba_tibourbou
Erythrina_poeppigiana
Tabernaemontana_attenuata
Swietenia_mahagoni
Sterculia_apetala
Ryania_speciosa
Erythroxylum_havanense
Calophyllum_brasiliense
Calliandra_guildingii
Byrsonima_gymnocalycina
Myristica_fragrans
Terminalia_amazonia
Cordia_collococa
Cassia_grandis
Symphonia_globulifera
Guazuma_ulmifolia
Ficus_maxima
Byrsonima_spicata
Mangifera_indica
Pouteria_multiflora
Vismia_laxiflora
Tabebuia_stencalyx
Rollinia_exsucca
Cordia_panamensis
Clusia_flavida
Chrysophyllum_argenteum
Abrus_precatorius
Rudgea_hostmanniana
Cedrela_odorata
Coursetia_ferruginea
Coffea_arabica
Licania_membranacea
Swietenia_macrophylla
Vitex_divaricata
Cordia_alliodora
Senna_bacillaris
Ochroma_pyramidale
Ficus_nymphaeifolia
Casearia_guianensis
Trichilia_pallida
Castilla_elastica
Pterocarpus_rohrii
Spondias_mombin
Ficus_yoponensis
Curatella_americana
Vitex_capitata
Swartzia_simplex
Piper_tuberculatum
Cassia_moschata
Funtumia_elastica
Swartzia_pinnata
Tabebuia_rosea
Sterculia_pruriens
Protium_guianense
Handroanthus_serratifolius
Trema_micrantha
Psychotria_muscosa
Havea_brasiliensis
Apeiba_schomburgkii
Acnistus_arborescens
Guarea_trichilioides
Pimenta_racemosa
Manilkara_zapota
Croton_gossypiifolius
Annona_muricata
AME
BR1
BR2
BSC
BST
C1
Chag
CMA
ERE
GL
LAL
LALP
LHC
LLP
Lop1
MSB
MSBT
MW8
NRGS
OA
OT1
OT2
SASC
SCA
Sim1
UC1
UpLop
VCR
VCRP

Ground vegetation

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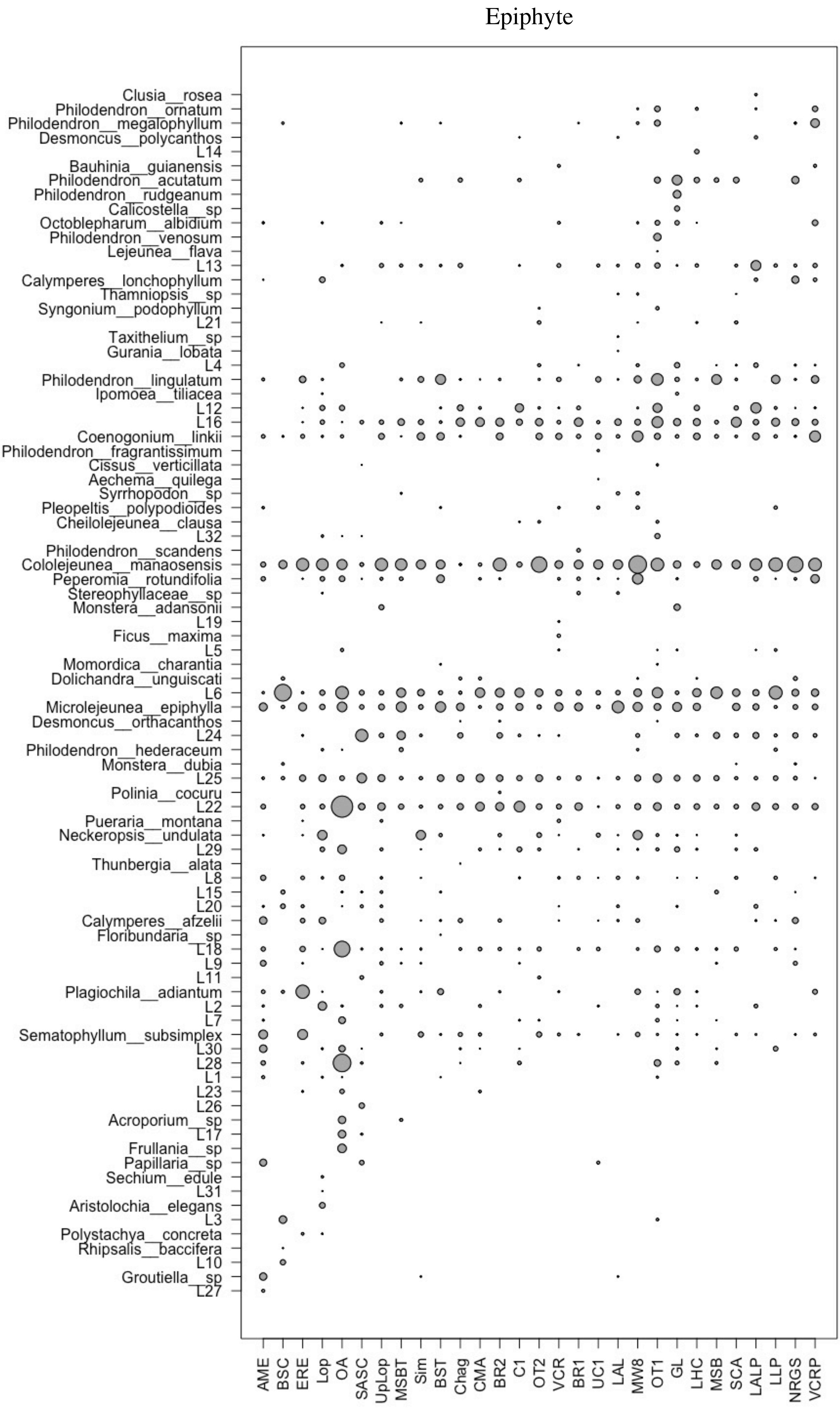
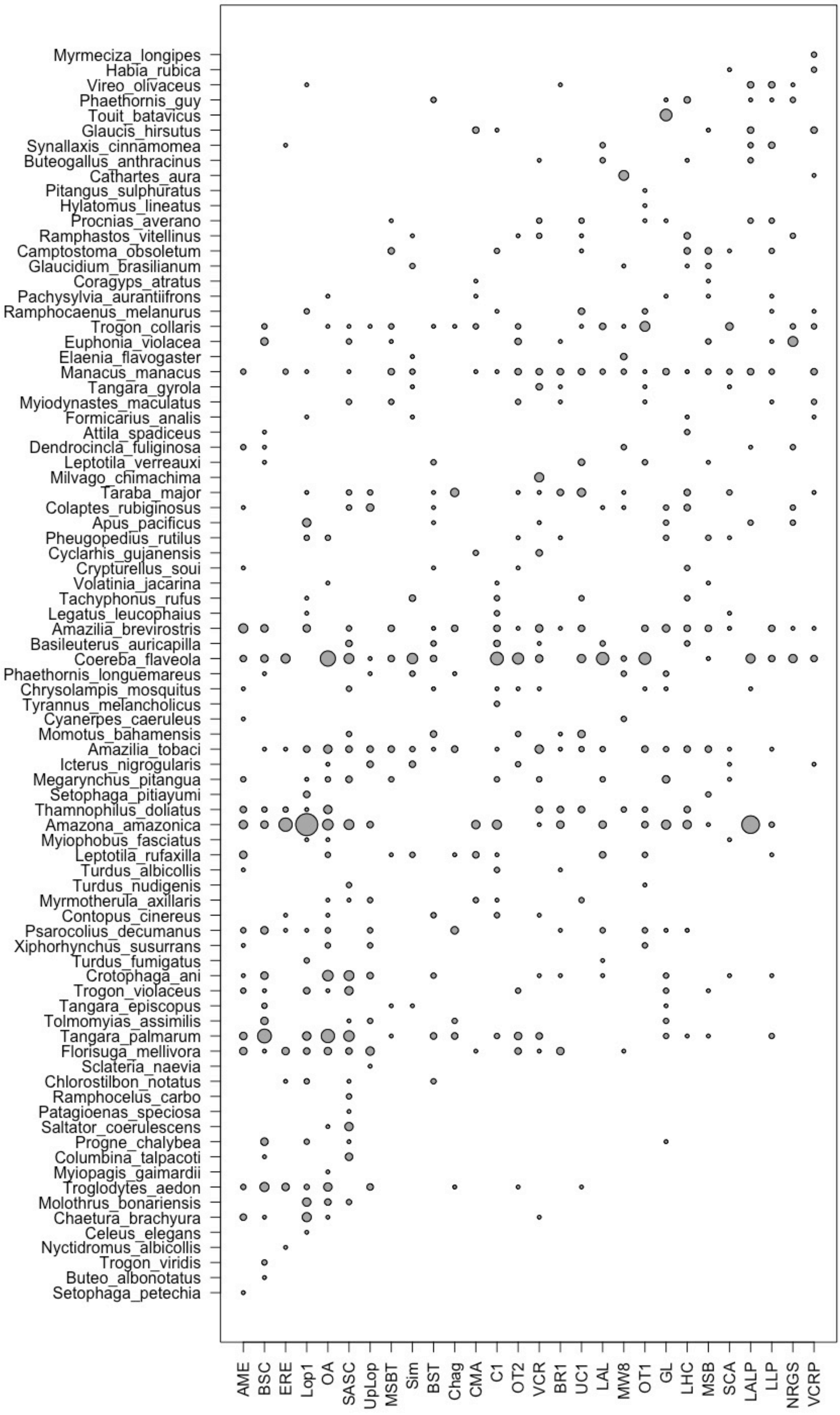
Cnemidaria__spectabilis
Carapa__guianensis
Miconia__nervosa
Heliconia__behaii
Attalea__maripa
Fleurya__aestuans
Hura__crepitans
Sida__acuta
Sechium__edule
Persea__americana
Cleome__rutidosperma
Aristolochia__elegans
Costus__scaber
Psychotria__uliginosa
Desmoncus__polycanthos
Thelypteris__poiteana_
Philodendron__giganteum
Tabebuia__serratifolia
Psychotria__muscosa
Pachira__insignis
Alpinia__purpurata
Hernandia__sonora
Adiantum__latifolium
Ipomoea__tiliacea
Philodendron__lingulatum
Terminalia__lucida
Tabebuia__stenocalyx
Eugenia__baileyi
Byrsonima__spicata
Abrus__precatorius
Syzygium__jambos
Xanthosoma__undipes
Syzygium__malaccense
Desmoncus__orthacanthos
Piper__aduncum
Eryngium__foetidum
Artocarpus__altilis
Cyperus__rotundus
Coffea__arabica
Bambusa__vulgaris
Peperomia__pellucida
Hyptis__atrorobens
Cynodon__dactylon
Commelina__diffusa
Colocasia__esculenta
Adiantum__capillus.veneris
Selaginella__diffusa
Heliconia__hirsuta
Cyperus__luzulae
Thunbergia__alata
Cordeline__fruticosa
Miconia__prasina
Mangifera__indica
Xanthosoma__robustum
Swartzia__simplex
Solanum__quitoense
Justicia__secunda
Cordia__alliodora
Bromelia__plumieri
Adiantum__tenerum
Hevea__brasiliensis
Charantia__momordica
Hippobroma__longiflora
Bactris__setulosa
Vitex__divaricata
Acnistus__arborescens
Sematophyllum__subsimplex
Musa__acuminata
AME
BR1
BR2
BSC
BST
C1
CH
CMA
ERE
GL
LAL
LALP
LHC
LLP
Lop
MSB
MSBT
MW8
NRGS
OA
OT1
OT2
SASC
SCA
Sim
UC1
Uplop
VCR
VCRP



Epiphyte

Clusia__rosea
Philodendron__ornatum
Philodendron__megalophyllum
Desmoncus__polycanthos
L14
Bauhinia__guianensis
Philodendron__acutatum
Philodendron__rudgeanum
Calicostella__sp
Octoblepharum__albidium
Philodendron__venosum
Lejeunea__flava
L13
Calymperes__lonchophyllum
Thamniopsis__sp
Syngonium__podophyllum
L21
Taxithelium__sp
Gurania__lobata
L4
Philodendron__lingulatum
Ipomoea__tiliacea
L12
L16
Coenogonium__linkii
Philodendron__fragrantissimum
Cissus__verticillata
Aechema__quilega
Syrrhopodon__sp
Pleopeltis__polypodioides
Cheilolejeunea__clausa
L32
Philodendron__scandens
Cololejeunea__manaosensis
Peperomia__rotundifolia
Stereophyllaceae__sp
Monstera__adansonii
L19
Ficus__maxima
L5
Momordica__charantia
Dolichandra__unguiscati
L6
Microlejeunea__epiphylla
Desmoncus__orthacanthos
L24
Philodendron__hederaceum
Monstera__dubia
L25
Polinia__cocuru
L22
Pueraria__montana
Neckeropsis__undulata
L29
Thunbergia__alata
L8
L15
L20
Calymperes__afzelii
Floribundaria__sp
L18
L9
L11
Plagiochila__adiantum
L2
L7
Sematophyllum__subsimplex
L30
L28
L1
L23
L26
Acroporium__sp
L17
Frullania__sp
Papillaria__sp
Sechium__edule
L31
Aristolochia__elegans
L3
Polystachya__concreta
Rhipsalis__baccifera
L10
Groutiella__sp
L27
AME
BSC
ERE
Lop
OA
SASC
UpLop
MSBT
Sim
BST
Chag
CMA
BR2
C1
OT2
VCR
BR1
UC1
LAL
MW8
OT1
GL
LHC
MSB
SCA
LALP
LLP
NRGS
VCRP

Birds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Habia_rubica
Vireo_olivaceus
Phaethornis_guy
Touit_batavicus
Glaucis_hirsutus
Synallaxis_cinnamomea
Buteogallus_anthracinus
Cathartes_aura
Pitangus_sulphuratus
Hylatomus_lineatus
Procnias_averano
Ramphastos_vitellinus
Camptostoma_obsoletum
Glaucidium_brasilianum
Coragyps_atratus
Pachysylvia_aurantiifrons
Ramphocaenus_melanurus
Trogon_collaris
Euphonia_violacea
Elaenia_flavogaster
Manacus_manacus
Tangara_gyrola
Myiodynastes_maculatus
Formicarius_analis
Attila_spadiceus
Dendrocincla_fuliginosa
Leptotila_verreauxi
Milvago_chimachima
Taraba_major
Colaptes_rubiginosus
Apus_pacificus
Pheugopedius_rutilus
Cyclarhis_gujanensis
Crypturellus_soui
Volatinia_jacarina
Tachyphonus_rufus
Legatus_leucophaius
Amazilia_brevirostris
Basileuterus_auricapilla
Coereba_flaveola
Phaethornis_longuemareus
Chrysolampis_mosquitus
Tyrannus_melancholicus
Cyanerpes_caeruleus
Momotus_bahamensis
Amazilia_tobaci
Icterus_nigrogularis
Megarynchus_pitangua
Setophaga_pitiayumi
Thamnophilus_doliatus
Amazona_amazonica
Myiophobus_fasciatus
Leptotila_rufaxilla
Turdus_albicollis
Turdus_nudigenis
Myrmotherula_axillaris
Contopus_cinereus
Psarocolius_decumanus
Xiphorhynchus_susurrans
Turdus_fumigatus
Crotophaga_ani
Trogon_violaceus
Tangara_episcopus
Tolmomyias_assimilis
Tangara_palmarum
Florisuga_mellivora
Sclateria_naevia
Chlorostilbon_notatus
Ramphocelus_carbo
Patagioenas_speciosa
Saltator_coerulescens
Progne_chalybea
Columbina_talpacoti
Myiopagis_gaimardii
Troglodytes_aedon
Molothrus_bonariensis
Chaetura_brachyura
Celeus_elegans
Nyctidromus_albicollis
Trogon_viridis
Buteo_albonotatus
Setophaga_petechia
AME
BSC
ERE
Lop1
OA
SASC
UpLop
MSBT
Sim
BST
Chag
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Appendix 4.2: Results without primary forests

Taxonomic alpha-diversity

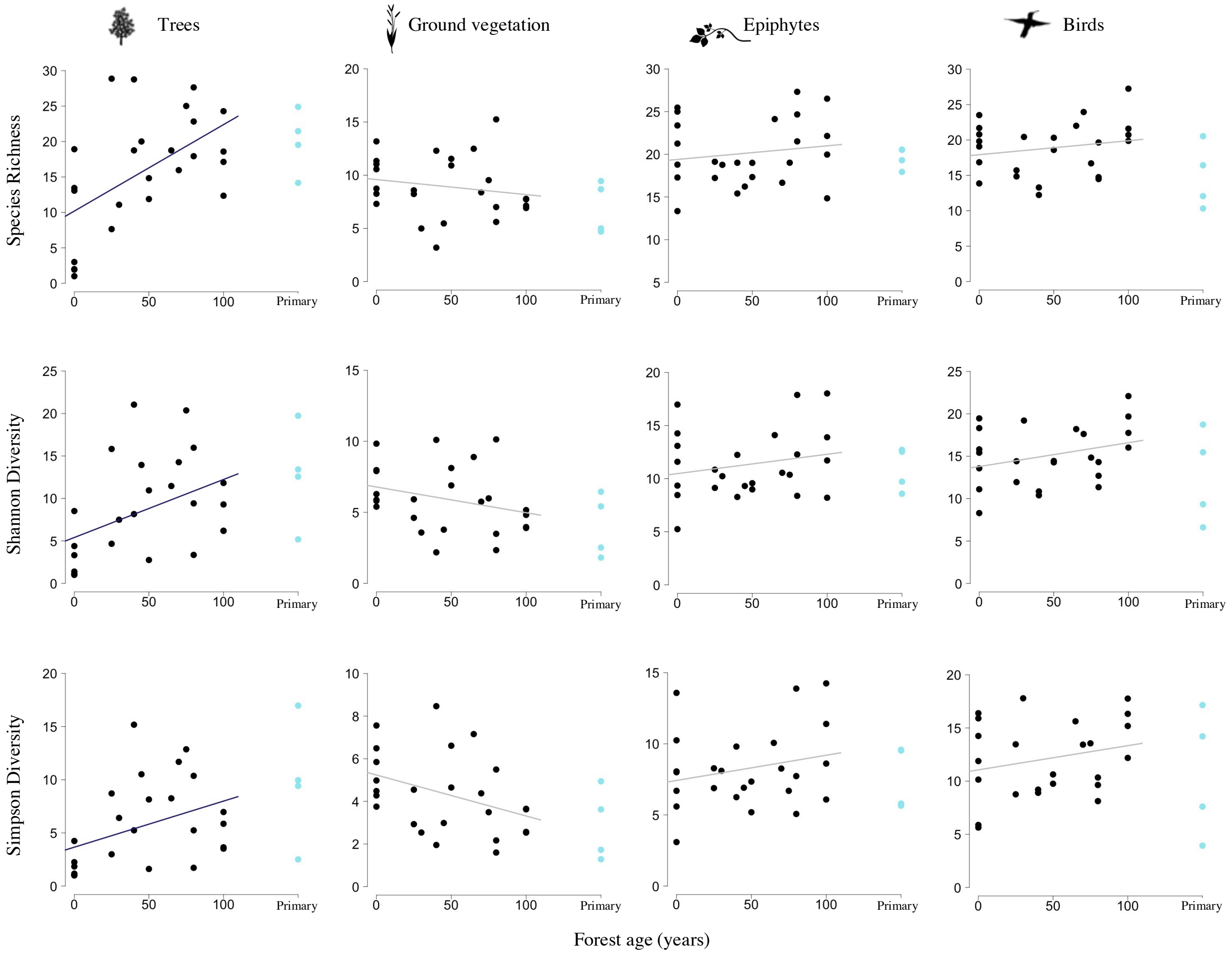


Figure 4.2.1. Species richness, Shannon diversity and Simpson diversity with forest age in tree, ground vegetation, epiphyte, and bird assemblages. The points represent the field sites, and blue lines indicate statistically significant trends (regression information is detailed in Table 4.1). Primary forest sites were not included in regressions but are shown in blue for comparison.

GLM linear regressions were used to test whether there were significant changes in taxonomic alpha-diversity over time, excluding primary forest sites. Tree species richness, Shannon diversity, and Simpson diversity increased significantly with forest age, but there was no significant change in ground vegetation, epiphyte, or bird assemblages. These results are in line with those including primary forest sites apart from ground vegetation. Ground vegetation Shannon and Simpson diversity decreased significantly when primary forest sites are included in analyses (Figure 4.5; Table 4.1).

Table 4.2.1 GLM linear regression results for alpha-diversity measures with forest age (without primary forest sites). Sites is the number of sites (n) included in each analysis.

Taxon	Model	df	Sites	adj R²	F value	P value
Trees	Richness ~ Forest age	1 on 23	25	0.26	9.82	<0.01
	Shannon ~ Forest age	1 on 23	25	0.15	5.13	0.03
	Simpson ~ Forest age	1 on 23	25	0.11	4.10	0.05
Birds	Richness ~ Forest age	1 on 22	24	0.04	0.90	0.35
	Shannon ~ Forest age	1 on 22	24	0.05	2.30	0.14
	Simpson ~ Forest age	1 on 22	24	0.02	1.36	0.26
Vegetation	Richness ~ Forest age	1 on 23	25	-0.01	0.81	0.38
	Shannon ~ Forest age	1 on 23	25	0.04	2.12	0.16
	Simpson ~ Forest age	1 on 23	25	0.11	3.98	0.06
Epiphytes	Richness ~ Forest age	1 on 23	25	-0.02	0.56	0.46
	Shannon ~ Forest age	1 on 23	25	<0.01	1.08	0.31
	Simpson ~ Forest age	1 on 23	25	0.01	1.35	0.26

Taxonomic beta-diversity

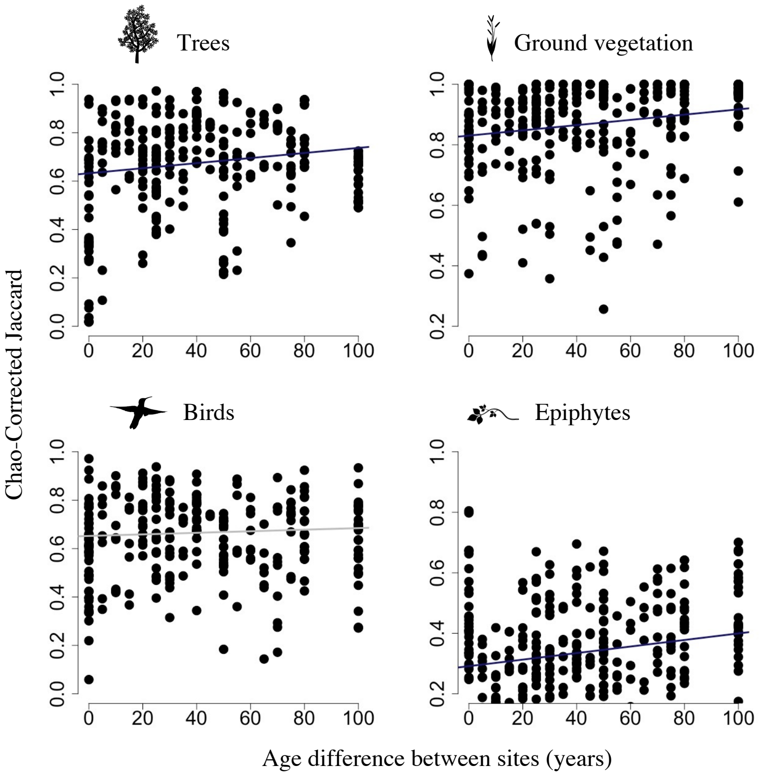


Figure 4.2.2. Species compositional change (Chao-Jaccard) with age difference between site pairs. 'Age difference' is the pairwise difference in age between sites. Blue lines indicate statistically significant change in species composition with increasing difference in forest age between sites from a 0.5 quantile regression (regression information is detailed in Table 4.2.2).

0.5 quantile regressions were used to assess whether there was a significant change in species composition (Chao-Jaccard) with age difference between sites (excluding primary forest sites). There was significant change in species composition with increasing age difference in tree, ground vegetation, and epiphyte assemblages. When these analyses were conducted including primary forest sites, there was also significant change in bird species composition.

Table 4.2.2 Results from 0.5 quantile regression of Chao-corrected Jaccard with age difference between site pairs (excluding primary forest sites). Sites is the number of sites (n) included in each analysis.

Taxon	Model	df	Sites	adj R^2	T value	P value
Trees	Chao-Jaccard ~ Age difference	1 on 298	25	0.02	2.73	<0.01
Birds	Chao-Jaccard ~ Age difference	1 on 274	24	0.03	0.75	0.46
Vegetation	Chao-Jaccard ~ Age difference	1 on 298	25	0.03	9.94	<0.01
Epiphytes	Chao-Jaccard ~ Age difference	1 on 298	25	0.02	6.72	<0.01

Functional alpha-diversity

GLM linear regressions were used to test for significant change in functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) with forest age in tree, ground vegetation, and bird assemblages (details in Chapter 3.3 and Chapter 5.2; Villéger, Mason and Mouillot, 2008). There was a significant increase in tree functional divergence with forest age. There was no significant change in functional alpha-diversity over time in the other taxa, however.

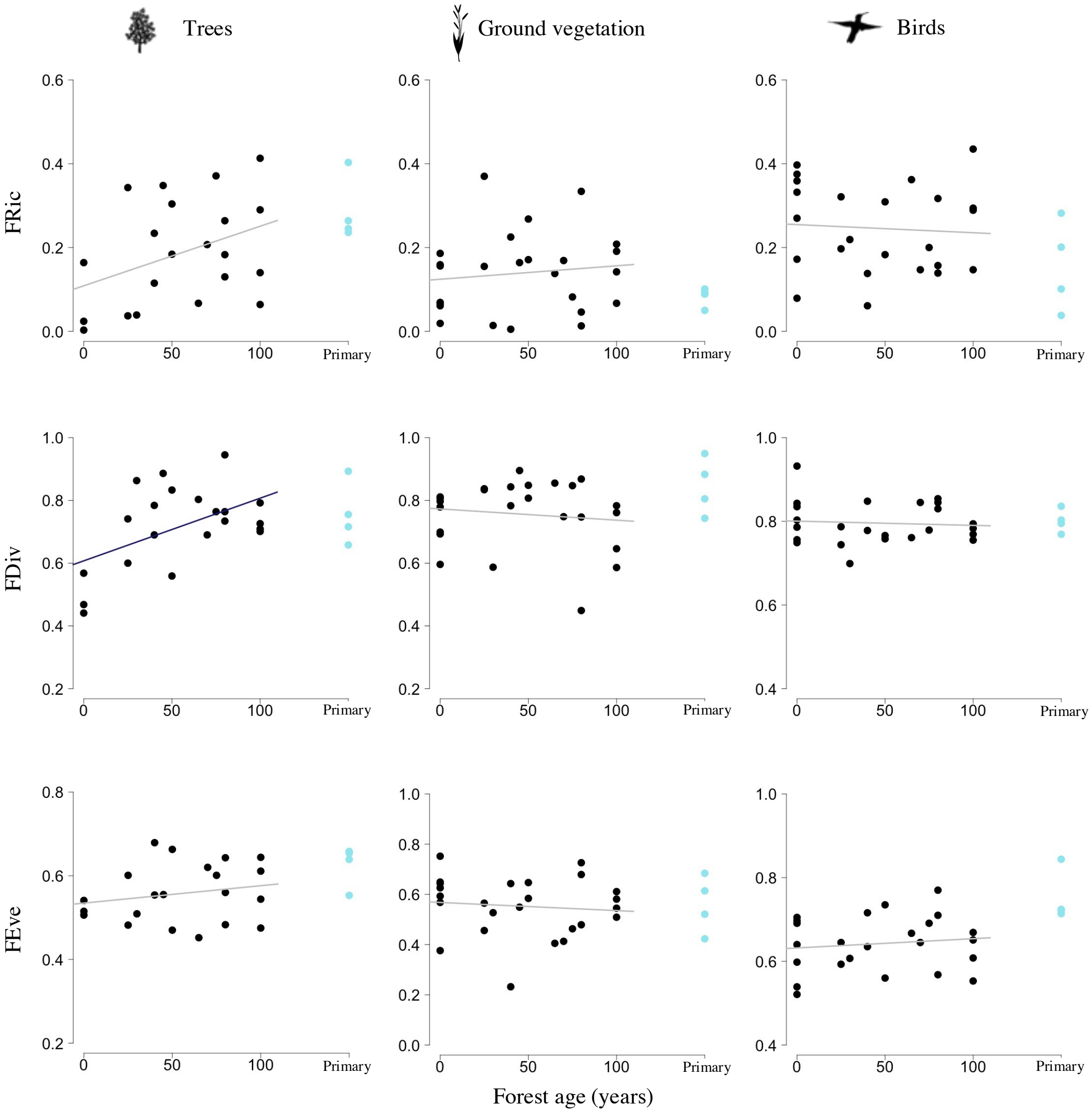


Figure 4.2.3. Functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve) with forest age in tree, ground vegetation and bird assemblages. Blue lines indicate statistically significant trends (information in Table 4.2.3). Primary forests were not included but are shown in blue for comparison.

Table 4.2.3 GLM regression results for functional alpha-diversity measures with forest age. Sites is the number of sites (n) included in each analysis.

Taxon	Model	df	Sites	adj R²	F value	P value
Trees	FRic ~ Forest age	1 on 19	21	0.15	3.27	0.09
	FDiv ~ Forest age	1 on 19	21	0.23	6.96	0.02
	FEve ~ Forest age	1 on 19	21	-0.01	0.82	0.38
Vegetation	FRic ~ Forest age	1 on 23	25	-0.03	0.35	0.56
	FDiv ~ Forest age	1 on 23	25	-0.03	0.34	0.56
	FEve ~ Forest age	1 on 23	25	-0.03	0.24	0.63
Birds	FRic ~ Forest age	1 on 22	24	-0.04	0.11	0.75
	FDiv ~ Forest age	1 on 22	24	-0.04	0.13	0.72
	FEve ~ Forest age	1 on 22	24	-0.03	0.36	0.55

Functional beta-diversity

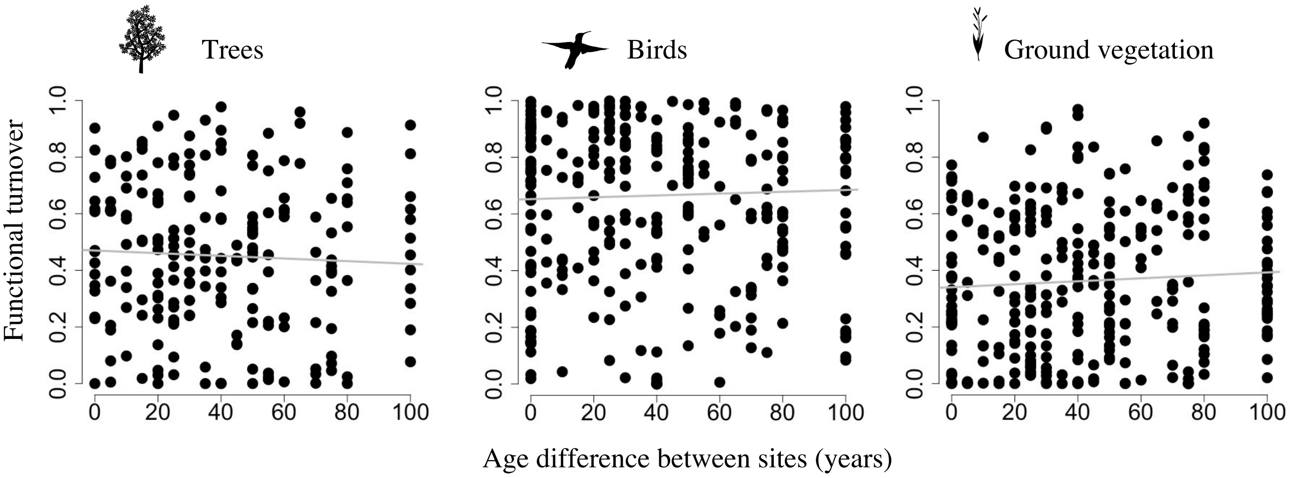


Figure 4.2.4. Functional trait turnover with age difference between site pairs. Age difference is the pairwise difference in age between sites. Grey lines indicate no statistically significant change in functional trait composition with forest age from a 0.5 quantile regression (details in Table 4.2.4).

0.5 quantile regressions were again used to assess whether there was a significant change in functional trait composition (functional turnover) with age difference between sites (excluding primary forest sites). There was no significant change in functional composition with increasing age difference in tree, ground vegetation, and epiphyte assemblages. When these analyses were conducted including primary forest sites, there was significant change in tree and ground vegetation functional composition.

Table 4.2.4 Results from 0.5 quantile regression of functional turnover (FTurn) with age difference between site pairs. Sites is the number of sites (n) included in each analysis.

Taxon	Model	df	Sites	adj R^2	F value	P value A
Trees	FTurn ~ Age difference	1 on 208	21	-0.02	0.61	0.43
Vegetation	FTurn ~ Age difference	1 on 298	25	<0.01	1.19	0.28
Birds	FTurn ~ Age difference	1 on 274	24	-0.003	0.12	0.09

Appendix 5.1 Functional trait information

The plant traits used to quantify functional diversity for the tree and ground vegetation assemblages in Trinidad were: maximum height at maturity (m), average leaf length (cm), primary dispersal mode, and dominant flower colour (Appendix 5.1; Trait data compiled from: Hendrix and Marquis, 1983; Little and Skolmen, 1989; Anderson, 1990; Sheridan, 1994; Scariot, Lleras and Hay, 1995; Milliken and Ratter, 1998; Quesnel and Farrell, 2000; Hewitt, 2005; Plowman, 2012; Ramirez, Jhala and Singh, 2012; Kuete, 2014; Kachhiyapatel, Patel and Rajput, 2016; Aximoff, Soares and Bernadello, 2020; Kattge *et al.*, 2020; CABI, 2021; EOL, 2021; Fern, 2021; GBIF.org, 2021; Kew, 2021; NC State University, 2021; Nparks, 2021; Piertro and Beltramini, 2021; Smithsonian, 2021; University of Florida, 2021).

The bird traits used were: primary trophic guild, body length (cm), generation time (years), average number of eggs per clutch, sexual dimorphism, forest dependence, and the forest strata (ground, canopy, aerial, etc) which a species predominantly occupies (trait data compiled from: ffrench, 1973; Kenefick, Restall and Hayes, 2013; Wilman *et al.*, 2014; Acevedo-Charry and Aide, 2019; BirdLife International, 2020).

Categorical traits were transformed onto a numeric scale in order to avoid generating negative eigenvalues in functional diversity analyses as follows. The primary dispersal modes of tree and ground vegetation plants were ordered according to the level of specialisation: (1) autochory, (2) anemochory, (3) hydrochory, (4) zoochory. The dominant flower colours (according to human vision) were ordered by conspicuousness: (1) green, (2) brown, (3) white, (4) yellow, (5) pink, (6) purple, (7) blue, (8) orange, and (9) red. Bird trophic guilds were also ordered according to the general level of specialisation: (1) omnivore, (2) predator / scavenger, (3) granivore, (4) disperser / pollinator, and (5) insectivore. Forest strata was ordered according to strata height from low (ground) to high up (aerial). Forest dependence in birds was ordered as: (1) low, (2) medium, and (3) high.

Appendix 5.2 Change in bird traits over succession

Violin plots were used to visually assess changes in body mass over succession for the bird assemblages (ggplot2 in R statistical software; Figure 5.9; Wickham *et al*., 2021). For these plots, the width of the line represents the number of individual birds with a given body mass in an assemblage. The results show that there was no consistent change in bird body mass through time.

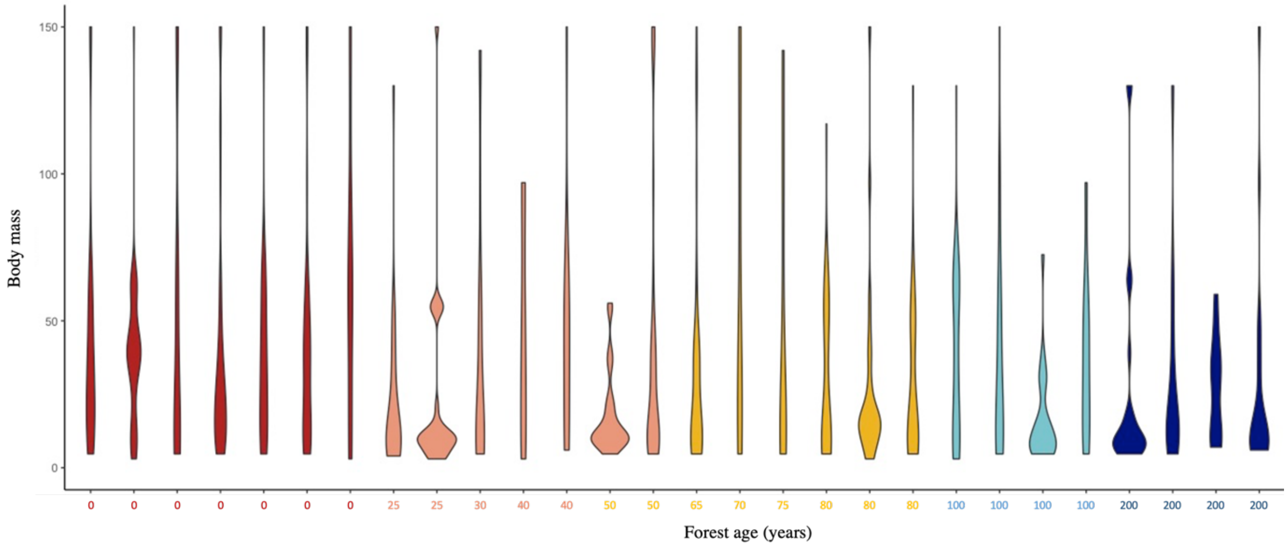


Figure 5.2.1 Violin plots of bird body mass over succession. The width of the line corresponds with the abundance of birds with a given body mass and assemblage. Red plots are active sites, pink plots are 25–50 yo secondary forest sites, yellow plots are 60–80 yo secondary forests, light blue plots are >100 yo secondary forests, and dark blue plots are primary forest sites.

Bird assemblages were further analysed by looking at changes in the average number of eggs per clutch (Figure 5.2.1). Violin plots were used to illustrate the density of individual birds which lay a certain average number of eggs per clutch in each site (Figure 5.2.2; Wickham *et al*., 2021). For these violin plots, the width of the lines indicates the abundance of birds which lay a certain average number of eggs per clutch in each site. There was overall little variation in the number of eggs per clutch birds lay on average between sites.

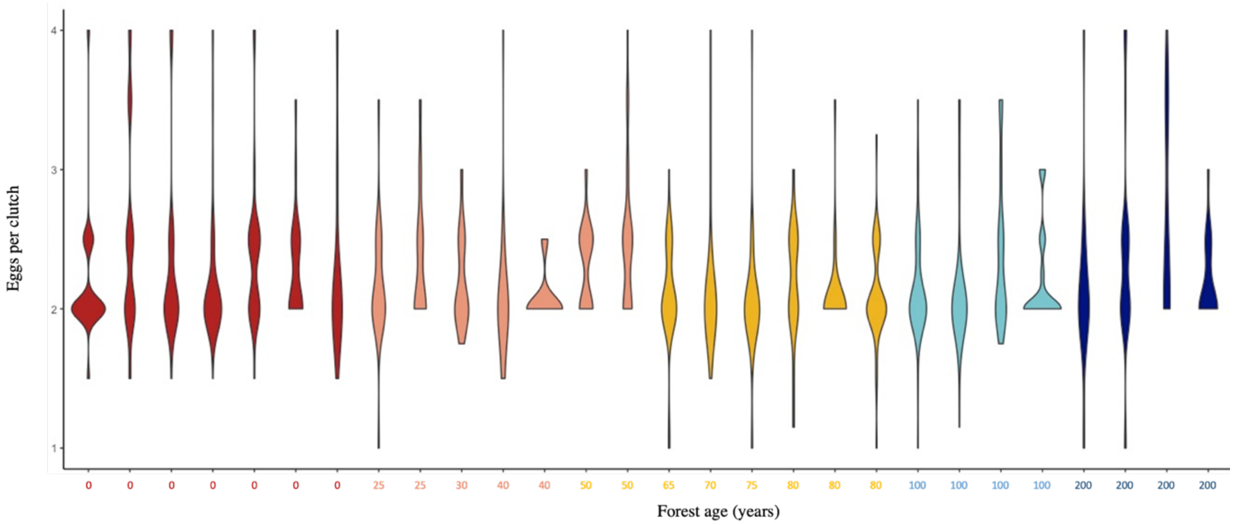


Figure 5.2.2 Violin plots of average number of eggs per clutch over succession. The width of the line corresponds with the abundance of birds which lay a given number of eggs per clutch in an assemblage. Red plots are active sites, pink plots are 25–50 yo secondary forest sites, yellow plots are 60–80 yo secondary forests, light blue plots are >100 yo secondary forests, and dark blue plots are primary forest sites.

Lastly, changes in the average generation time (the average length of time between the birth of an individual and the birth of that individual's offspring) of birds over succession were also analysed using a violin plot (Figure 5.1.3). Again, there was little consistent change in the generation time of birds with forest age.

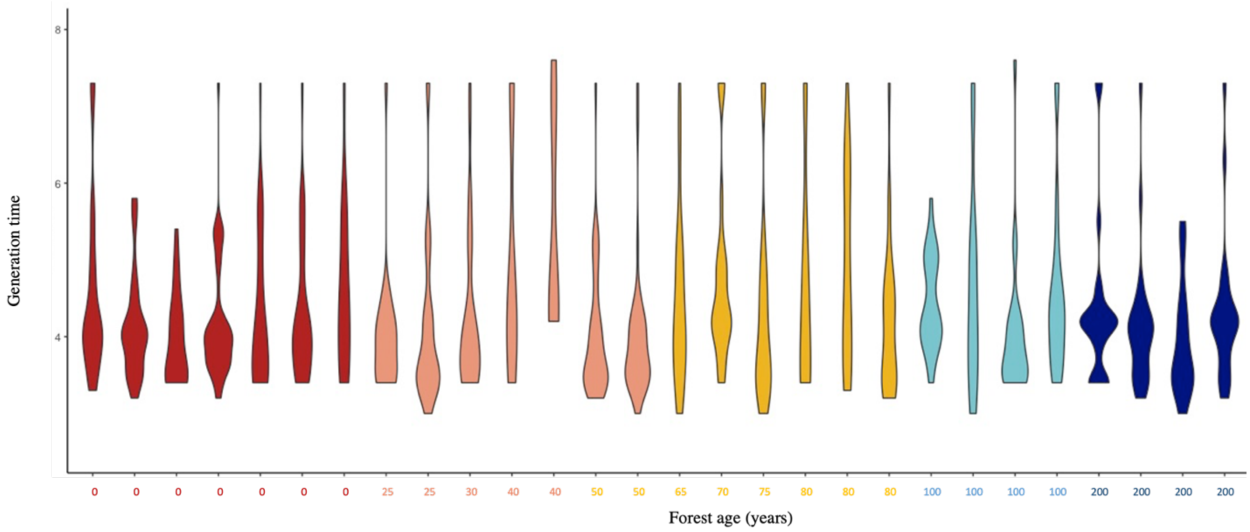


Figure 5.2.3 Violin plots of bird generation time (years) over succession. The width of the line corresponds with the density of birds with a certain generation time in an assemblage. Red plots are active sites, pink plots are 25–50 yo secondary forest sites, yellow plots are 60–80 yo secondary forests, light blue plots are >100 yo secondary forests, and dark blue plots are primary forest sites.

Appendix 6.1 Tanglegram null models

Null models were used to test if the alignment of each tanglegram. In this model, the site names for one of the two assemblages being compared was randomly reshuffled and a new dendrogram was produces. The cophenetic correlation between this and the dendrogram produced by the other, unshuffled assemblage was then computed. This process was repeated 200 times to generate a null distribution of the cophenetic correlation coefficients against which the observed alignment value could be compared (Galili, 2015; Gotelli & Entsminger, 2003).

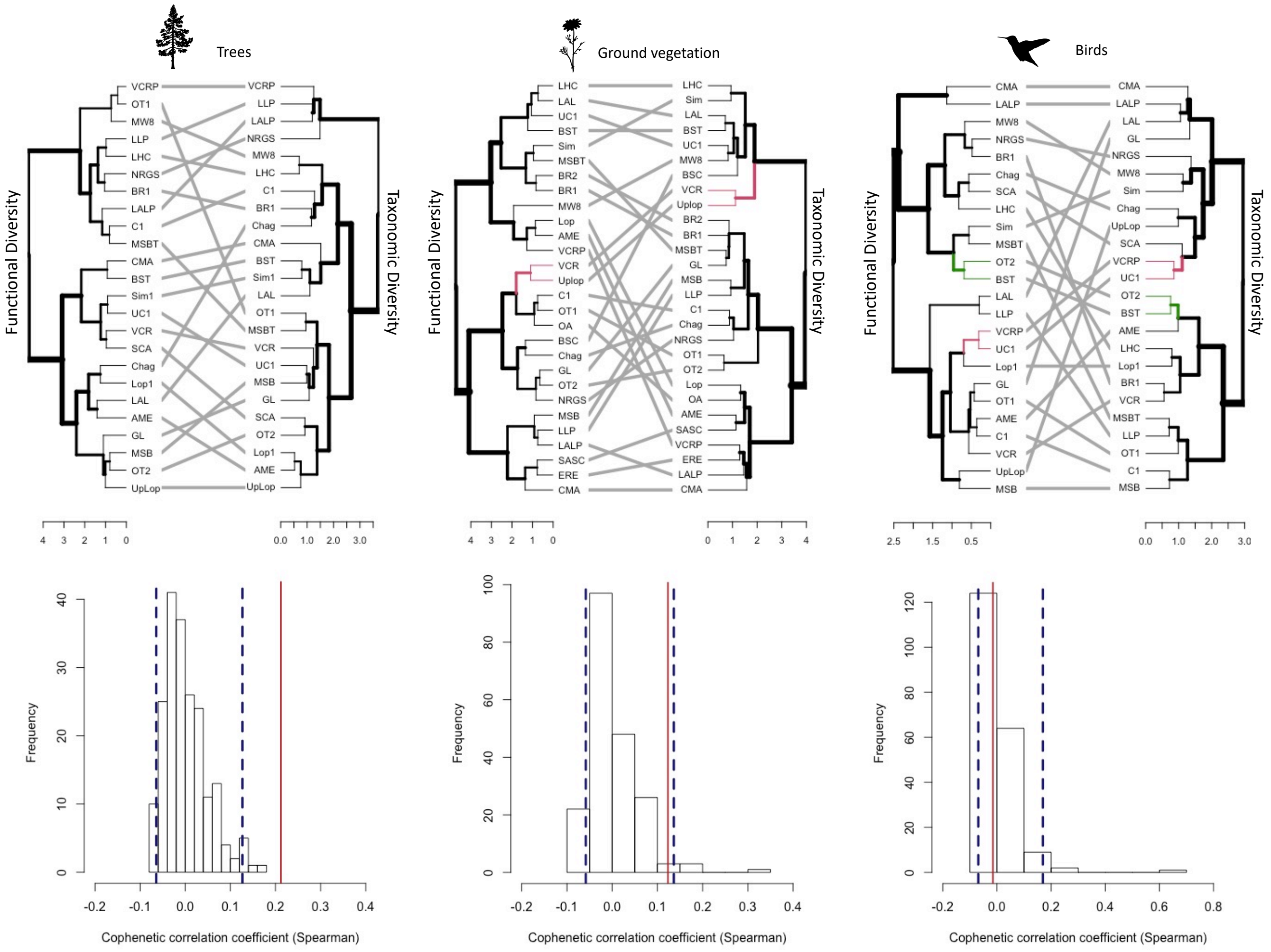
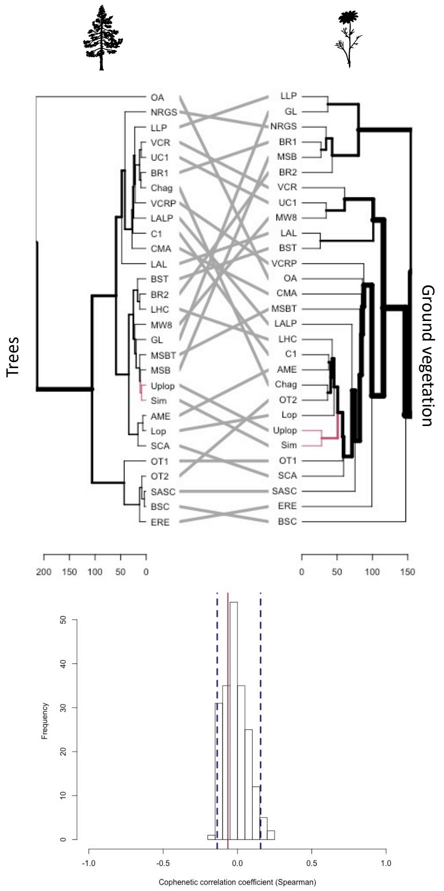


Figure 6.1.1 Tanglegrams comparing the hierarchical clustering of sites based on tree, ground vegetation and bird species and functional trait composition from Chapter 6. Red and green lines indicate common branches between the two dendrograms.

Null models test whether the cophenetic correlation coefficient between taxa differed from what would be expected by chance. Null plots show the observed correlation coefficient (red) in relation to the null distribution. The correlation coefficient represents how similarly sites are grouped according to species composition between taxa. Values closer to zero indicate less correlation between two taxa. The 2.5% and 95.7% quantiles are shown in blue as dashed lines.

The null model analyses between taxonomic and functional diversity within each taxon found that tree species and functional compositional change are more aligned than would be expected by chance (Figure 6.1.1). Null model analyses between taxa further found that the dendrograms based on tree and epiphyte assemblages, and on tree and bird species compositional change are more aligned than would be expected by chance (Figure 6.1.2).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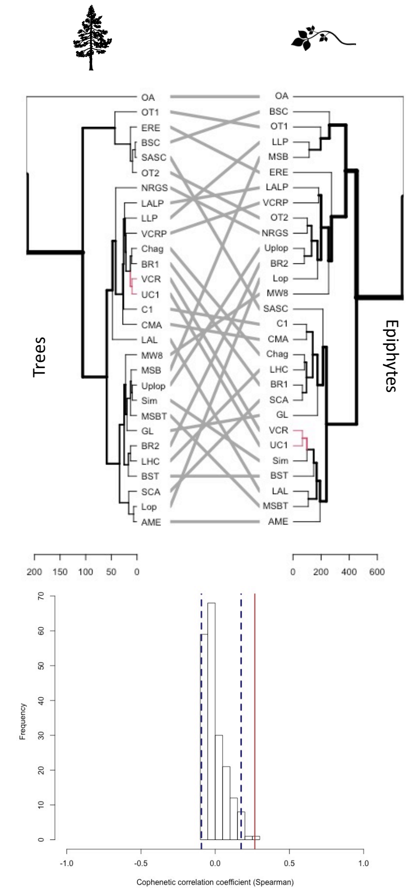
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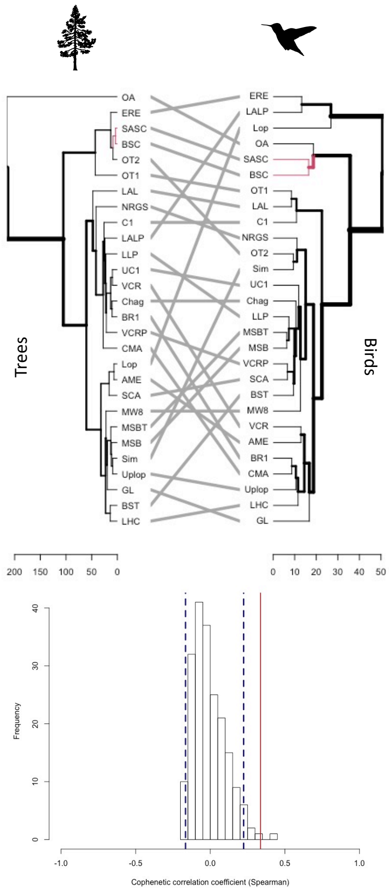
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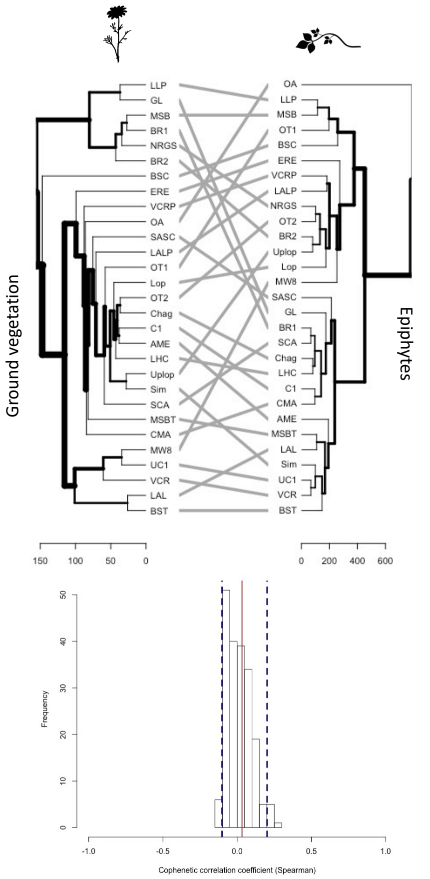
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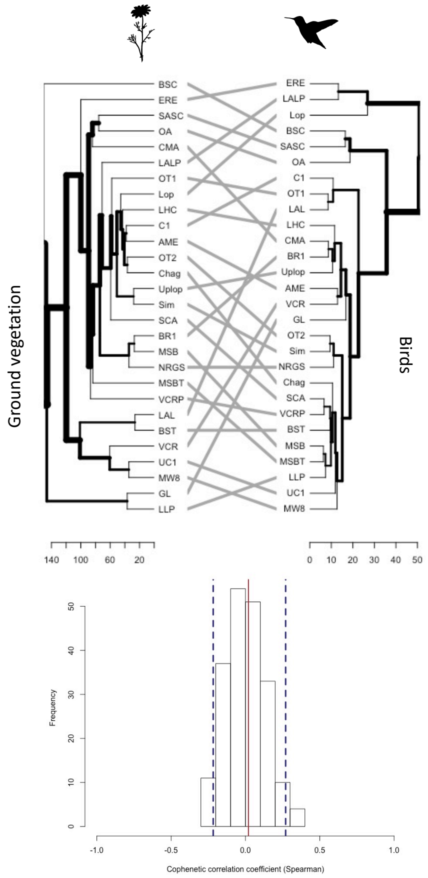
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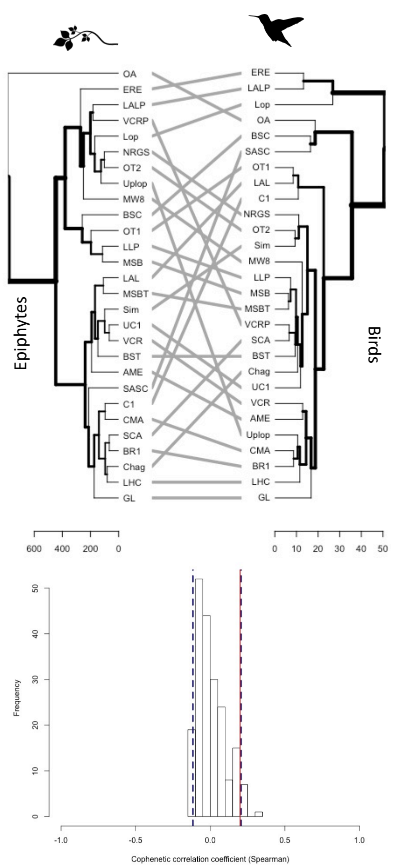
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Cophenetic correlation coefficient (Spearman)

Figure 6.1.2 Tanglegrams comparing the hierarchical clustering of sites based on tree, ground vegetation, epiphyte, and bird composition from Chapter 6. Red and green lines indicate common branches between the two dendrograms. Null models test whether the cophenetic correlation coefficient between taxa differed from what would be expected by chance. Null plots show the observed correlation coefficient (red) in relation to the null distribution. The correlation coefficient represents how similarly sites are grouped according to species composition between taxa. Values closer to zero indicate less correlation between two taxa. The 2.5% and 95.7% quantiles are shown in blue as dashed lines.

References

Aide, T.M. *et al.* (1995) 'Forest recovery in abandoned tropical pastures in Puerto Rico', *Forest Ecology and Management*, 77(1), pp. 77–86. doi:10.1016/0378-1127(95)03576-V.

Arroyo-Rodríguez, V. *et al.* (2017) 'Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research', *Biological Reviews*, 92(1), pp. 326–340. doi:https://doi.org/10.1111/brv.12231.

Becknell, J.M., Kissing Kucek, L. and Powers, J.S. (2012) 'Aboveground biomass in mature and secondary seasonally dry tropical forests: A literature review and global synthesis', *Forest Ecology and Management*, 276, pp. 88–95. doi:10.1016/j.foreco.2012.03.033.

Boucher, D.H. *et al.* (2001) 'Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest', *Plant Ecology*, 156(2), pp. 131–137. doi:10.1023/A:1012672005360.

Burslem, D.F.R.P., Whitmore, T.C. and Brown, G.C. (2000) 'Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands', *Journal of Ecology*, 88(6), pp. 1063–1078. doi:10.1046/j.1365-2745.2000.00517.x.

Cannon, null, Peart, null and Leighton, null (1998) 'Tree species diversity in commercially logged bornean rainforest', *Science (New York, N.Y.)*, 281(5381), pp. 1366–1368. doi:10.1126/science.281.5381.1366.

Chazdon, R.L. (2003) 'Tropical forest recovery: legacies of human impact and natural disturbances', *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1), pp. 51–71. doi:10.1078/1433-8319-00042.

Chazdon, R.L. (2014) *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*. University of Chicago Press.

Chinea, J.D. (2002) 'Tropical forest succession on abandoned farms in the Humacao Municipality of eastern Puerto Rico', *Forest Ecology and Management*, 167(1), pp. 195–207. doi:10.1016/S0378-1127(01)00693-4.

Chinea, J.D. and Helmer, E.H. (2003) 'Diversity and composition of tropical secondary forests recovering from large-scale clearing: results from the 1990 inventory in Puerto Rico', *Forest ecology and management. Vol. 180 (2003): Pages 227-240* [Preprint]. Available at: https://www.fs.usda.gov/treesearch/pubs/9024 (Accessed: 30 September 2021).

Cochrane, M.A. and Schulze, M.D. (1999) 'Fire as a Recurrent Event in Tropical Forests of the Eastern Amazon: Effects on Forest Structure, Biomass, and Species Composition', *Biotropica*, 31(1), pp. 2–16. doi:10.2307/2663955.

Cole, J., Lovett, G. and Findlay, S. (2012) *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*. Springer Science & Business Media.

Cubiña, A. and Aide, T.M. (2001) ‘The Effect of Distance from Forest Edge on Seed Rain and Soil Seed Bank in a Tropical Pasture’, *Biotropica*, 33(2), pp. 260–267. doi:https://doi.org/10.1111/j.1744-7429.2001.tb00177.x.

Derroire, G. *et al*. (2016) ‘Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession’, *Oikos*, 125(10), pp. 1386–1397. doi:https://doi.org/10.1111/oik.03229.

Donohue, K., Foster, D.R. and Motzkin, G. (2000) ‘Effects of the past and the present on species distribution: land-use history and demography of wintergreen’, *Journal of Ecology*, 88(2), pp. 303–316. doi:10.1046/j.1365-2745.2000.00441.x.

Dupouey, J.L. *et al*. (2002) ‘Irreversible Impact of past Land Use on Forest Soils and Biodiversity’, *Ecology*, 83(11), pp. 2978–2984. doi:10.2307/3071833.

Everham, E.M. and Brokaw, N.V.L. (1996) ‘Forest Damage and Recovery from Catastrophic Wind’, *Botanical Review*, 62(2), pp. 113–185.

Fernandes, D.N. and Sanford Jr., R.L. (1995) ‘Effects of Recent Land-Use Practices on Soil Nutrients and Succession under Tropical Wet Forest in Costa Rica’, *Conservation Biology*, 9(4), pp. 915–922. doi:10.1046/j.1523-1739.1995.09040915.x.

Ferry Slik, J.W., Verburg, R.W. and Keßler, P.J.A. (2002) ‘Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in East Kalimantan, Indonesia’, *Biodiversity & Conservation*, 11(1), pp. 85–98. doi:10.1023/A:1014036129075.

Finegan, B. (1996) ‘Pattern and process in neotropical secondary rain forests: the first 100 years of succession’, *Trends in Ecology & Evolution*, 11(3), pp. 119–124. doi:10.1016/0169-5347(96)81090-1.

Finegan, B. and Delgado, D. (2000) ‘Structural and Floristic Heterogeneity in a 30-Year-Old Costa Rican Rain Forest Restored on Pasture Through Natural Secondary Succession’, *Restoration Ecology*, 8(4), pp. 380–393. doi:10.1046/j.1526-100x.2000.80053.x.

Franklin, J.F. *et al*. (2002) ‘Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example’, *Forest Ecology and Management*, 155(1), pp. 399–423. doi:10.1016/S0378-1127(01)00575-8.

García-Montiel, D.C. and Scatena, F.N. (1994) ‘The effect of human activity on the structure and composition of a tropical forest in Puerto Rico’, *Forest Ecology and Management*, 63(1), pp. 57–78. doi:10.1016/0378-1127(94)90246-1.

Gehring, C., Denich, M. and Vlek, P.L.G. (2005) ‘Resilience of Secondary Forest Regrowth after Slash-and-Burn Agriculture in Central Amazonia’, *Journal of Tropical Ecology*, 21(5), pp. 519–527.

Gibson, L. *et al*. (2011) ‘Primary forests are irreplaceable for sustaining tropical biodiversity’, *Nature*, 478(7369), pp. 378–381. doi:10.1038/nature10425.

Glenn-Lewin, D.C., Peet, R.K. and Veblen, T.T. (1992) *Plant Succession: Theory and prediction*. Springer Science & Business Media.

Guariguata, M.R. *et al*. (1997) ‘Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica’, *Plant Ecology*, 132(1), pp. 107–120. doi:10.1023/A:1009726421352.

Guariguata, M.R. and Ostertag, R. (2001) ‘Neotropical secondary forest succession: changes in structural and functional characteristics’, *Forest Ecology and Management*, 148(1), pp. 185–206. doi:10.1016/S0378-1127(00)00535-1.

Herbert, D.A., Fownes, J.H. and Vitousek, P.M. (1999) ‘Hurricane Damage to a Hawaiian Forest: Nutrient Supply Rate Affects Resistance and Resilience’, *Ecology*, 80(3), pp. 908–920. doi:10.1890/0012-9658(1999)080[0908:HDTAHF]2.0.CO;2.

Holdsworth, A.R. and Uhl, C. (1997) ‘Fire in Amazonian Selectively Logged Rain Forest and the Potential for Fire Reduction’, *Ecological Applications*, 7(2), pp. 713–725. doi:10.2307/2269533.

Hooper, E.R., Legendre, P. and Condit, R. (2004) ‘Factors Affecting Community Composition of Forest Regeneration in Deforested, Abandoned Land in Panama’, *Ecology*, 85(12), pp. 3313–3326. doi:https://doi.org/10.1890/03-0655.

Hyatt, L.A. and Casper, B.B. (2000) ‘Seed bank formation during early secondary succession in a temperate deciduous forest’, *Journal of Ecology*, 88(3), pp. 516–527. doi:https://doi.org/10.1046/j.1365-2745.2000.00465.x.

Ingle, N.R. (2003) ‘Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation’, *Oecologia*, 134(2), pp. 251–261. doi:10.1007/s00442-002-1081-7.

Kennard, D.K. (2002) ‘Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia’, *Journal of Tropical Ecology*, 18(1), pp. 53–66. doi:10.1017/S0266467402002031.

Lambin, E.F. *et al*. (2001) ‘The causes of land-use and land-cover change: moving beyond the myths’, *Global Environmental Change*, 11(4), pp. 261–269. doi:10.1016/S0959-3780(01)00007-3.

Lawrence, D. (2005) ‘Biomass Accumulation after 10-200 Years of Shifting Cultivation in Bornean Rain Forest’, *Ecology*, 86(1), pp. 26–33.

Lebrija-Trejos, E. *et al*. (2008) ‘Successional Change and Resilience of a Very Dry Tropical Deciduous Forest Following Shifting Agriculture’, *Biotropica*, 40(4), pp. 422–431. doi:https://doi.org/10.1111/j.1744-7429.2008.00398.x.

Lebrija-Trejos, E. *et al*. (2010) ‘Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession’, *Perspectives in Plant Ecology, Evolution and Systematics*, 12(4), pp. 267–275. doi:10.1016/j.ppees.2010.09.002.

Lohbeck, M. *et al*. (2013) ‘Successional changes in functional composition contrast for dry and wet tropical forest’, *Ecology*, 94(6), pp. 1211–1216. doi:10.1890/12-1850.1.

Lugo, A.E. and Brown, S. (1991) ‘Comparing Tropical and Temperate Forests’, in Cole, J., Lovett, G., and Findlay, S. (eds) *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*. New York, NY: Springer, pp. 319–330. doi:10.1007/978-1-4612-3122-6_16.

Molino, J.F. and Sabatier, D. (2001) ‘Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis’, *Science (New York, N.Y.)*, 294(5547), pp. 1702–1704. doi:10.1126/science.1060284.

Mora, F. *et al*. (2015) ‘Testing Chronosequences through Dynamic Approaches: Time and Site Effects on Tropical Dry Forest Succession’, *Biotropica*, 47(1), pp. 38–48. doi:https://doi.org/10.1111/btp.12187.

Moran, E.F. *et al*. (2000) ‘Effects of soil fertility and land-use on forest succession in Amazônia’, *Forest Ecology and Management*, 139(1), pp. 93–108. doi:10.1016/S0378-1127(99)00337-0.

Nepstad, D.C. *et al*. (1996) ‘A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia’, *Oikos*, 76(1), pp. 25–39. doi:10.2307/3545745.

Norden, N. *et al*. (2015) ‘Successional dynamics in Neotropical forests are as uncertain as they are predictable’, *Proceedings of the National Academy of Sciences*, 112(26), pp. 8013–8018. doi:10.1073/pnas.1500403112.

Reiners, W.A. *et al*. (1994) ‘Tropical Rain Forest Conversion to Pasture: Changes in Vegetation and Soil Properties’, *Ecological Applications*, 4(2), pp. 363–377. doi:10.2307/1941940.

Rolim, S.G., Machado, R.E. and Pillar, V.D. (2017) ‘Divergence in a Neotropical forest during 33 years of succession following clear-cutting’, *Journal of Vegetation Science*, 28(3), pp. 495–503. doi:https://doi.org/10.1111/jvs.12502.

Rozendaal, D.M.A. *et al*. (2017) ‘Demographic Drivers of Aboveground Biomass Dynamics During Secondary Succession in Neotropical Dry and Wet Forests’, *Ecosystems*, 20(2), pp. 340–353. doi:10.1007/s10021-016-0029-4.

Sanaphre-Villanueva, L. *et al*. (2017) ‘Patterns of Plant Functional Variation and Specialization Along Secondary Succession and Topography in a Tropical Dry Forest’, *Environmental Research Letters*, 12, p. 055004. doi:10.1088/1748-9326/aa6baa.

Sandor, M.E. and Chazdon, R.L. (2014) ‘Remnant Trees Affect Species Composition but Not Structure of Tropical Second-Growth Forest’, *PLOS ONE*, 9(1), p. e83284. doi:10.1371/journal.pone.0083284.

Seedial, M. (2009) ‘Cocoa production a producer’s manual’. Edited by M. of A.L. and M. Resources. Trinidad and Tobago.

Seedial, M. (2013) ‘Shade management in cocoa production’. Edited by E.T. and I.S.D.M. of F. Production. Trinidad and Tobago.

Silver, W.L., Ostertag, R. and Lugo, A.E. (2000) ‘The Potential for Carbon Sequestration Through Reforestation of Abandoned Tropical Agricultural and Pasture Lands’, *Restoration Ecology*, 8(4), pp. 394–407. doi:10.1046/j.1526-100x.2000.80054.x.

Sitters, H. *et al.* (2016) ‘Opposing Responses of Bird Functional Diversity to Vegetation Structural Diversity in Wet and Dry Forest’, *PLOS ONE*, 11(10), p. e0164917. doi:10.1371/journal.pone.0164917.

Sovu *et al.* (2009) ‘Recovery of secondary forests on swidden cultivation fallows in Laos’, *Forest Ecology and Management*, 258(12), pp. 2666–2675. doi:10.1016/j.foreco.2009.09.030.

Uhl, C., Buschbacher, R. and Serrao, E.A.S. (1988) ‘Abandoned Pastures in Eastern Amazonia. I. Patterns of Plant Succession’, *Journal of Ecology*, 76(3), pp. 663–681. doi:10.2307/2260566.

Uhl, C. and Kauffman, J.B. (1990) ‘Deforestation, Fire Susceptibility, and Potential Tree Responses to Fire in the Eastern Amazon’, *Ecology*, 71(2), pp. 437–449. doi:10.2307/1940299.

Vandermeer, J. *et al.* (2000) ‘Hurricane Disturbance and Tropical Tree Species Diversity’, *Science*, 290(5492), pp. 788–791. doi:10.1126/science.290.5492.788.

Vázquez-Yanes, C. and Orozco-Segovia, A. (1993) ‘Patterns of Seed Longevity and Germination in the Tropical Rainforest’, *Annual Review of Ecology and Systematics*, 24(1), pp. 69–87. doi:10.1146/annurev.es.24.110193.000441.

West, D.C., Shugart, H.H. and Botkin, D.B. (eds) (1981) *Forest Succession: Concepts and Application*. New York, NY: Springer (Springer Advanced Texts in Life Sciences). doi:10.1007/978-1-4612-5950-3.

Wickham, H. *et al.* (2021) *ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics*. Available at: https://CRAN.R-project.org/package=ggplot2 (Accessed: 30 January 2022).

Wijdeven, S.M.J. and Kuzee, M.E. (2000) ‘Seed Availability as a Limiting Factor in Forest Recovery Processes in Costa Rica’, *Restoration Ecology*, 8(4), pp. 414–424. doi:10.1046/j.1526-100x.2000.80056.x.

Woods, P. (1989) ‘Effects of Logging, Drought, and Fire on Structure and Composition of Tropical Forests in Sabah, Malaysia’, *Biotropica*, 21(4), pp. 290–298. doi:10.2307/2388278.

Zimmerman, J.K. *et al.* (1995) ‘Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico’, *Forest Ecology and Management*, 77(1), pp. 65–76. doi:10.1016/0378-1127(95)03575-U.