The restoration of community assembly processes in degraded tropical dry forests

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Statement of originality

I declare that I performed and prepared all of the work in this thesis under the supervision of Dr Bonnie Waring and Dr Leland Werden. All sources of information are properly cited.

This work is my own, but it benefitted from invaluable contributions from collaborators and colleagues. I will publish Chapters 2, 3, and 4 in peer-reviewed journals, and so these chapters are written in the third person plural. Specific contributions by colleagues to each chapter are highlighted below.

Chapter 2

This chapter has been submitted to the Journal of Ecology, and the text shown here is a reproduction of that manuscript, for which I am the first author. This research was carried out under the supervision of Dr Bonnie Waring and Dr Leland Werden, who aided with the conception of the idea. I led the study design and data collection, which was aided by Oscar E. Verduzco-Salazar and Ruiming Nie (an MSc student under my co-supervision). I led the statistical analysis and writing, with advice and edits from Dr Waring and Dr Werden.

Chapter 3

Dr Bonnie Waring and Dr Leland Werden aided with the conception of the idea and advised on the methodology, analysis and writing of this chapter. I led the study design and data collection, aided by Oscar E. Verduzco-Salazar. I carried out all the chemical analyses and the statistical analysis and writing, with feedback and edits from my supervisors, Dr Waring and Dr Werden.

Chapter 4

I devised the idea for the research, designed the experiment and led data collection. Julie (Capito) Hernandez and Efren Sánchez Lopez aided with data collection. I performed the statistical analysis and wrote the chapter, with advice and input from my supervisors, Dr Waring and Dr Werden.

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Main Abstract

Secondary forests, which regrow following conversion to non-forest land use, form through secondary succession. Community assembly processes shape the trajectory of secondary succession, but our understanding of these mechanisms is mostly based on research in intact wet tropical forests. Tropical dry forests are relatively understudied but represent a widespread and vulnerable ecosystem type. We lack a clear understanding of the environmental gradients driving dry forest succession and their efects on species turnover. Furthermore, secondary forests grow within human-modified landscapes, but the impact of landscape context on successional trajectories is unclear. This thesis addresses these knowledge gaps using novel data from a successional tropical dry forest in Mexico, ofering insights into best practice for forest restoration. In Chapter 2 I examined functional and taxonomic changes in tree community composition at multiple ontogenetic stages along a successional chronosequence. I found that taxonomic composition appeared stochastic, but functional composition followed deterministic patterns, with key deterministic processes acting during tree recruitment. In Chapter 3 I characterised how variation in the abiotic environment responded to diferent forest restoration interventions and tested whether increased abiotic heterogeneity promoted greater tree diversity. I found that mean abiotic conditions, rather than heterogeneity, were more important for recruit diversity at multiple scales. To complement the observational research in Chapters 2 and 3, Chapter 4 describes a large-scale outplanting experiment in which I manipulated the abiotic and biotic conditions experienced by planted seedlings. This experiment demonstrated that abiotic processes alone determined seedling growth and survival early in succession but interacted with biotic processes later in succession. Overall, the results from my thesis reveal key diferences between dry and wet forest secondary succession. They suggest that widespread recovery of ecosystem functioning in tropical dry forests is possible and can be assisted through targeted interventions addressing the mechanisms involved in tree recruitment.

Table of Contents

Funding 2
Supervision 2
Statement of originality 3
Chapter 2 3
Chapter 3 3
Chapter 4 3
Copyright Declaration 4
Acknowledgements 5
Main Abstract 6
Table of Contents 7
List of Figures 10
List of Tables 13
Abbreviations 15
Chapter 1: Main Introduction 16
1.1 Community assembly and secondary succession 19
1.2 Dispersal limitation 21
Box 1.1 Functional traits 22
1.3 Establishment limitation 24
Box 1.2 Tree ontogeny 24
1.3.1 Establishment limitation due to abiotic filters (environmental filtering) 25
1.3.2 Establishment limitation due to biotic filters 27
1.4 Restoration ecology 29
1.5 Study site 30
Chapter 2: Secondary succession of a seasonally dry tropical forest is taxonomically stochastic but functionally deterministic 36
2.1 Introduction 36
2.2 Materials and Methods 39
2.3 Results 49
2.4 Discussion 58

2.5 Conclusions 65

Chapter 3: The role of small-scale environmental heterogeneity in the restoration of tropical dry forests 66

3.1 Introduction 66

3.2 Methods 71

3.3 Results 80

3.4 Discussion 87

3.5 Conclusion 93

Chapter 4: Interacting abiotic and biotic gradients during tropical dry forest succession: natural enemy pressure increases seedling mortality most in the low-resource environment of late succession 95

4.1 Introduction 95

4.2 Materials and methods 101

4.3 Results 109

4.4 Discussion 120

4.5 Conclusions 123

Chapter 5: Main Discussion 125

5.1 Overview 125

5.2 The balance of community assembly processes changes with: 126

a) Succession 126

b) Land use intensity 127

c) Spatial scale 128

d) Ontogenetic stage 129

5.3 Implications for TDF restoration 130

1. Define the target community by its functional composition, rather than its taxonomic composition 130

2. Identify and remove barriers to natural regeneration at the recruitment stage 131

3. Consider the phylogeographic context 132

4. Think at a landscape scale 134

5.4 Future work 134

Overcoming the limitations of large-scale observational plant surveys 134

Selection and measurement of relevant functional traits 136

5.5 Summary 137
6. References 138
7. SupplementaryMaterial 177
7.1 Main introduction 177
7.2 Chapter 2 178
7.3 Chapter 3 188
7.4 Chapter 4 192

List of Figures

Chapter 1. Main introduction

Figure1.1Hierarchical filteringframework of community assembly 20

Figure1.2 Location of study site 31

Figure1.3 Satellite images of study site in June2023 (wet season) with plot locations indicated 34

Chapter 2: Secondary succession of a seasonally dry tropical forest is taxonomically stochastic but functionally deterministic

Figure2.1 Schematic of sampling design 40

Figure2.2 Thetaxonomic and functional composition of the tree community changed with secondary succession 51

Figure 2.3 Community assembly was taxonomically stochastic but functionally deterministic for selected functional traits during secondary succession 53

Figure 2.4 Trajectories of taxonomic and functional composition were both directional with succession,but the majorshifts in functional composition tookplace during recruitment 55

Figure 2.5 Light availability decreased with succession, while water availability was lowest early in succession 56

Figure 2.6 ∂ recruitment limitation responded to abundance of conspecifics at the same ontogenetic stage 58

Chapter 3: The role of small-scale environmental heterogeneity in the restoration of tropical dry forests

Figure3.1 Designof one large circular plot 73

Figure 3.2 Mean and CV of environmental variables by intervention type and plot age 80

Figure 3.3 Partial regressions of species richness (ICE) against the mean and CV of environmental variables (canopy openness, soil carbon, soil nitrogen and soil pH) after correctingfor stem number 82

Figure3.4 Quadrats with higher canopy closure had higher species richness in natural regenerationplots 84

Figure 3.5 The proportion of variance in recruit community composition and environmental variables explained by the nested hierarchical factors of quadrat within plot within interventiontype 86

Chapter 4:Interactingabiotic and biotic gradientsduringtropical dry forest succession: natural enemy pressure increases seedling mortality most in the low-resource environment of late succession

Figure4.1 Designof the split-split-plot experiment 103

Figure4.2 Survival across the successional gradient was species-specific, such that speciessurvivalrankingschangedwith succession 111

Figure4.3RGRof all species and both drought strategy groups was highest in the early successional forest. The RGR of deciduous species decreased more over the successional gradient than the RGRof evergreenspecies, so that deciduous species had higher RGRearly in succession, but evergreenspecies had higher RGRin mid and late succession 113

Figure4.4 Leaf damage by natural enemies was universally high across successional environmentsand did not changewith natural enemyexclusion 115

Figure 4.5 Survival and growth rates increased significantly with natural enemy exclusion in the late successional environment, but not in early or mid successional environments 117

Figure 4.6 Leaf damage was highest on deciduous species across successional stages and levels of natural enemy treatment. Survival and growth rates of evergreen species were always higher than deciduous species but natural enemy exclusion reduced the magnitude of the diference 119

Supplementary Material

Chapter 2

Figure S2.1 $\partial_{establishment}$ limitation increased with seed mass in the late-successional plot, but not in the early or mid successionalplots.....187

Chapter 4

FigureS4.1 Most growth happened in the early successional treatment during the wet season (months 8 –12) 192

Figure S4.2 Observer accuracy for the percentage of leaves with natural enemy damage on each individual, and average area of leaf surface with natural enemy damage..... 193

Figure S4.3 The average area of leaf that was damaged by natural enemies was negativelycorrelated with RGR 194

List of Tables

Chapter 1: Main introduction

Table 1.1 Mean ± standard error of measured abiotic variables across the successional gradient in the study landscape 35

Chapter 2: Secondary succession of a seasonally dry tropical forest is taxonomically stochastic but functionally deterministic

Table 2.1 Functional traits used in the analyses..... 43

Chapter 3: The role of small-scale environmental heterogeneity in the restoration of tropical dry forests

Table 3.1 Definitions of terms used in Chapter 3 75

Table 3.2 Type III ANOVA results 81

Chapter 4: Interacting abiotic and biotic gradients during tropical dry forest succession: natural enemy pressure increases seedling mortality most in the low-resource environment of late succession

Table 4.1 Species used in the experiment 105

Table 4.2 Type III ANOVA Table for linear mixed-efects model of seedling survival 110

Table 4.3 Type III ANOVA Table for linear mixed-efects model of seedling RGR..... 112

Table 4.4 Type III ANOVA Table for linear mixed-efects model of leaf damage 114

Supplementary Material

Main Introduction

Table S1.1 Definitions of seedling, sapling and adult stages in tree ontogeny 177

Chapter 2

Table S2.1 Functional traits of woody plant species surveyed 178

Table S2.2 Observed and expected dispersal limitation 185

Table S2.3 Observed and expected establishment limitation 186

Table S2.4 Table of results for models of recruitment limitation 186

Chapter 3

Table S3.1 Intervention type and age of plots 188

Table S3.2 Within-plot partial Mantel tests of the correlation between compositional dissimilarity and environmental distance (all environmental variables), correcting for spatial autocorrelation 189

Table S3.3 Within-plot partial Mantel tests of the correlation between compositional dissimilarity and environmental distance (soil variables only), correcting for spatial autocorrelation 190

Table S3.4 Within-plot partial Mantel tests of the correlation between compositional dissimilarity and environmental distance (canopy openness only), correcting for spatial autocorrelation 191

Abbreviations

AIC	Akaike Information Criterion
ANOVA	Analysis of Variance
BCE	Before Common Era
BNF	Biological Nitrogen Fixation
CE	Common Era
CNDD	Conspecific Negative Density Dependence
CV	Coeficient of Variation
CWM	Community-Weighted Mean
DBH	Diameter at Breast Height
ETA	Ecological Trajectory Analysis
FLR	Forest Landscape Restoration
GLMM	Generalised Linear Mixed Model
HDR	Heterogeneity-Diversity Relationship
HSD	Honest Significant Diferences
ICE	Incidence-based Coverage Estimator
LDMC	Leaf Dry Matter Content
LES	Leaf Economics Spectrum
NDVI	Normalised Diference Vegetation Index
NMDS	Non-metric Multidimensional Scaling
PCoA	Principal Coordinates Analysis
PERMANOVA	Permutational Multivariate Analysis of Variance
RES	Resource Economics Spectrum
RGR	Relative Growth Rate
SER	Society for Ecological Restoration
SLA	Specific Leaf Area
SSQ	Sum of Squares
TDF	Tropical Dry Forests

Chapter 1: Main Introduction

A major goal in ecology is to describe and explain patterns of diversity in space and time. Since the earliest attempts to test theories about species distributions over a century ago (Grinnell, 1917), our understanding of these patterns has been improved and refined through theoretical and empirical approaches (e.g., Grime, 1973; Hubbell, 2001; Huston, 1979; Hutchinson, 1957; Tilman, 1982). However, the increasing dominance of human-modified ecosystems presents a novel challenge for the discipline. The vast majority of anthropogenic changes since the industrial revolution have been associated with a common suite of ecological outcomes, including the selective removal of trees (Lance et al., 2019), homogenisation of the biotic and abiotic environment (Newbold et al., 2018; Rodrigues et al., 2013), addition or depletion of soil nutrients (Smith et al., 2016), fragmentation (Haddad et al., 2015) and defaunation (Granados et al., 2017). Reductions in diversity following anthropogenic disturbances have been well documented (Gibson et al., 2011) but mostly describe static patterns, while there has been less research into long-term ecological dynamics. It is therefore crucial to determine whether and how the fundamental mechanisms that generate patterns of ecological diversity are changed by human activity (Wearn et al., 2019). To achieve this, the models describing these fundamental mechanisms, which have mostly been developed based on research in intact ecosystems, must be synthesised with the more recent literature on changes to diversity with human land use.

Secondary forests are those that regrow on land that was previously converted to a non-forest land use, a process known as secondary succession (Poorter et al., 2021). Secondary forests are increasingly widespread; between 1990–2020 the rate of net forest loss declined from 7.8 million hectares (ha) per year to 4.7 million ha per year, as deforestation rates declined in some countries and global forest cover expanded by an average of 7.5 million ha per year through natural regeneration and tree planting (FAO, 2020). Between 2001 and 2010, net changes in forest cover were positive for many Central American countries, including Mexico, Honduras, Costa Rica and El Salvador (Aide et al., 2013), and secondary forests covered 28% of the lowland Latin American tropics in 2008 (Chazdon et al., 2016). The

processes that determine the tree species composition in these secondary forests may be influenced by prior and ongoing human activities and so difer from those acting in old-growth forests (Jakovac et al., 2021). Therefore, secondary forests are an increasingly widespread and important forest type, but our understanding of the mechanisms that generate patterns of diversity in secondary forests lags behind that in old-growth forests.

In addition, another anthropogenic land use type is becoming increasingly prevalent: active forest restoration. 4% of forest area worldwide is forest that has been intentionally planted for purposes other than commercial timber production and since 1990 the area of planted forest has increased by 123 million ha (FAO, 2020). One of the drivers of this increase is large-scale tree planting promoted by international agreements such as the 2011 Bonn Challenge (www.bonnchallenge.org) and the 2014 New York Declaration on Forests (forestdeclaration.org) and carried out by governments, private organisations and charities worldwide. While most of the non-governmental organisations plant crop or timber trees for their economic and livelihood benefits (Martin et al., 2021), forest restoration projects can also have diverse aims related to carbon sequestration, biodiversity recovery and provisioning of ecosystem goods and services (Lamb, 2005, 2018). The potential advantages of applying ecological theory to help achieve the aims of such projects has given rise to the scientific field of restoration ecology (Gann et al., 2019; Wainwright et al., 2018).

The Society for Ecological Restoration (SER) defines ecological restoration as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Gann et al., 2019). Forest restoration can be thought of as the practice of intervening in secondary succession, with a scale of potential levels of human intervention (Chazdon et al., 2024). The field of restoration ecology aims to support the practice of ecosystem restoration with insights gained through fundamental ecological research. Importantly, community assembly theory can be used in the context of forest restoration to understand the processes that determine the composition of the tree community throughout secondary succession, and the efects of human intervention in these processes. The following sections give an overview of community assembly theory and its potential applicability to the practice of forest restoration in an understudied ecosystem: tropical dry forests (TDF).

TDF are forests found between the Tropics of Cancer and Capricorn that have lower annual precipitation than moist or wet forests and a multi-month dry period with little to no rainfall. There is no consensus on the exact amount of precipitation or length of dry season that defines a TDF, and TDF can be found all along a broad precipitation gradient from 250 mm to 2000 mm per year (Derroire, 2016). TDF are widespread, making up approximately 42% of tropical forests worldwide (Murphy & Lugo, 1986), but are also highly threatened and relatively under-examined (Janzen, 1988; Vieira & Scariot, 2006). Research into secondary succession in anthropogenic landscapes has mostly taken place in moist or wet tropical forests, and more research is needed in TDF to identify generalities and idiosyncrasies (Jakovac et al., 2021).

My research addressed this knowledge gap by assembling a large novel dataset on patterns of tree community composition in a regenerating TDF in Mexico. In Chapter 2, I surveyed tree seeds, seedlings, saplings and mature trees along a gradient of secondary succession to gain insights into the factors that determine which species take hold in a naturally regenerating forest. Analysis of these data revealed that, although the species composition of TDF tree communities appeared random, the trees present each stage of succession had a predictable set of functional traits. This suggested that aspects of the abiotic environment (e.g., light, water or soil nutrient availability) are important for driving succession, so in Chapter 3 I looked at how the mean and variance of such properties afected the diversity of seedling communities. This analysis suggested that seedling community composition was indeed determined by the abiotic environment at large spatial scales, but was mostly random at small spatial scales, though small-scale variation in the light environment was important for the establishment of rare shade-tolerant tree species. The research in Chapters 2 and 3 was observational, limiting my ability to pinpoint the specific mechanisms guiding community assembly in this ecosystem. Therefore, in Chapter 4 I experimentally planted trees with a range of functional traits along the successional gradient, and excluded natural enemies, thereby manipulating both abiotic and biotic filters to establishment. I found that the abiotic environment alone did not fully explain variation in seedling growth and survival with succession, but that it interacted with other living parts of the ecosystem,

specifically pests and pathogens, to determine successional species turnover. Overall, my research contributes to the mechanistic understanding of community reassembly through TDF succession.

1.1 Community assembly and secondary succession

Community assembly is frequently understood as a hierarchical series of filters that species must pass through to form the local site-level community (Fig. 1.1; Götzenberger et al., 2012). Processes of speciation, extinction and migration (phylogeographic assembly, sensu Götzenberger et al., 2012) define the regional species pool available to the subsequent filters, which are collectively known as ecological assembly filters. Ecological filters act sequentially on the regional species pool to define the local community at a site. Dispersal filtering is when propagules of a species fail to arrive at a site. If a species arrives at a site but then fails to germinate and establish as a seedling then it is limited by the establishment filter. Limitations to further growth and survival of established seedlings eventually determine the mature tree community. A species may fail to pass through each filter for deterministic reasons, i.e., a negative species-specific interaction with some aspect of its abiotic or biotic environment. A species may also fail to pass through each filter due to random chance, thus increasing the stochasticity of community assembly.

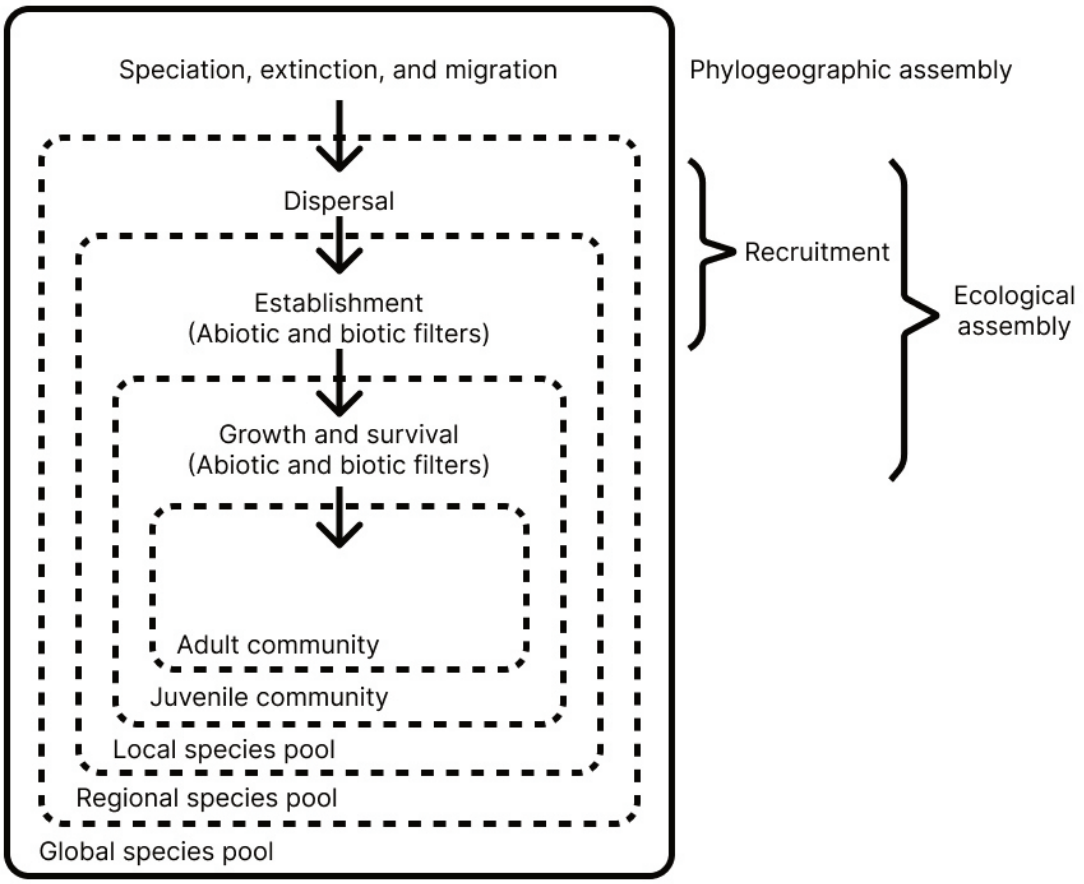


Figure 1.1 Hierarchical filtering framework of community assembly (adapted from Götzenberger et al., 2012). Each ecological assembly filter acts at a diferent ontogenetic stage. Dispersal acts at the seed stage, establishment acts at the seedling stage, and growth and survival act at the juvenile and adult stages.

Secondary forests are created through the process of secondary succession, which follows community assembly rules but takes place within a landscape context altered by historical and contemporary land use. Anthropogenic land use can influence any stage in the process of community assembly by afecting both site conditions and landscape composition. A comprehensive review of land use efects on community reassembly by Jakovac et al. (2021)

identified multiple ways in which human activities may afect the rate or trajectory of secondary succession. At the site level, management legacies are common, such as reduced soil nutrient availability, increased populations of generalist herbivores and the promotion of certain species. At the regional scale, land use afects propagule availability by changing the cover and composition of mature forest. However, despite such examples of anthropogenic efects on secondary succession, it is unclear how general these impacts are, as a continent-wide study found that the composition of early successional secondary forests is determined more by biogeography than anthropogenic disturbance (Jakovac et al., 2022). It is therefore important to develop a mechanistic understanding of secondary succession in diferent anthropogenic contexts. Integration of observed land use efects into the model of community assembly processes (Fig. 1.1) can help to predict the rate and/or trajectory of secondary succession following diferent anthropogenic land uses (Estrada-Villegas et al., 2020).

1.2 Dispersal limitation

Dispersal limitation refers to the failure of a species to arrive at a site as a seed, either due to limited seed abundance or non-uniform seed distribution. When dispersal limitation dominates community assembly, species relative abundances depend on which species arrive (or arrive first) at a site (Muller-Landau et al., 2002). Dispersal is therefore often considered to introduce stochasticity into community assembly (Hurtt & Pacala, 1995; Muller-Landau et al., 2002) but can also be determined by species-specific traits, such that the dispersal filter is diferentially permeable to diferent species (Vellend et al., 2007).

It has been proposed that dispersal limitation is weaker in TDF than in wet tropical forests, as TDF tend to have a higher proportion of species with wind-dispersed seeds or high resprouting ability (Derroire et al., 2016a; Jakovac et al., 2021; Lebrija-Trejos et al., 2010a; Wunderle, 1997). However, proximity to seed sources has been shown to determine tree species composition and diversity of TDF (Hernández-Stefanoni et al., 2011), suggesting dispersal limitation does influence the trajectory of TDF succession. I am only aware of two studies that have attempted to directly quantify dispersal limitation during TDF succession

(Martínez-Ramos et al., 2021; Werden et al., 2020b), and in both cases the authors found strong dispersal limitation during early succession, which persisted for over a decade of forest recovery. Unexpectedly, early-successional dispersal limitation in TDF does not appear to be determined by species functional traits (Box 1.1); the phylogenetic dispersion of seeds in an abandoned pasture was random (Martínez-Ramos et al., 2021), and seed size only explained interspecific variation in dispersal limitation under certain conditions (Werden et al., 2020b). Dispersal limitation may therefore play a greater role in the community assembly of TDF than previously thought, but our ability to predict the strength of dispersal limitation for different tree species is restricted.

Box 1.1 Functional traits

Deterministic community assembly processes assume that there are meaningful differences between species in their interactions with abiotic and biotic community assembly filters (i.e., niches; Lebrija-Trejos et al., 2010b). Such differences are likely to manifest in species' functional traits, defined by Violle et al. (2007) as "any morphological, physiological or phenological feature measurable at the individual level …which impacts fitness indirectly via its effects on growth, reproduction and survival". As such, functional trait distributions in communities have often been used to infer community assembly processes (e.g., Kraft & Ackerly, 2010). Generally, trait clustering is interpreted as resulting from environmental filtering (i.e., abiotic filters on community assembly), while overdispersion is interpreted as resulting from biotic interactions such as competition and conspecific negative density dependence (e.g., Ding et al., 2012). However, functional trait distributions must be interpreted with caution. The assumption that clustering implies environmental filtering while overdispersion implies biotic interactions can be misleading. Li et al. (2015) demonstrated that modification of the environment through succession promoted colonisation by more functionally dissimilar species to the existing residents, resulting in a pattern of trait overdispersion, but that this was not driven by competitive interactions.

Functional traits can also be used to infer specific drivers of community assembly. For example, environmental filtering may be caused by limitations in certain essential resources, which for plants are likely to be light, space, water and/or soil nutrients (Helbach et al., 2022). Multiple authors have attempted to infer the limiting resource based on the functional traits of the community (Muscarella et al., 2017). For example, Lohbeck et al. (2013) inferred that water availability was limiting in an early successional forest due to the high community-weighted mean (CWM) values of water-use traits like wood density and compound leaves.

Importantly, functional traits are not completely independent because they must be integrated within an individual. Functional traits trade-of against one another such that common multivariate trait syndromes can be defined (Bravo-Monzónet al., 2022). Such trade-ofs are the basis of the leaf economics spectrum (LES), a globally consistent trade-of between cheap productive leaves with short lifespans and expensive, tough leaves with longer lifespans (Bakker et al., 2011; Reich, 2014). The LES may be related to leaf phenological habit; deciduous species are considered to be resource-acquisitive, while evergreen species are resource-conservative (Méndez-Alonzo et al., 2012). Pineda-García et al. (2013) found a trade-of between the ability to maintain xylem functioning at low soil water potential (drought tolerance) and stem water storage and deciduous habit (drought avoidance), however Lohbeck et al. (2015) found that the deciduous-evergreen spectrum was independent of the LES.

It has been proposed that the LES is part of a broader resource economics spectrum (RES) due to the whole-plant integration of resource-capturing organs (leaves, stems, and roots). The evidence for a fully integrated RES is mixed, but within each organ there does appear to be an independent spectrum from cheap resource-acquisitive organs to expensive resource-conservative organs (Reich, 2014).

1.3 Establishment limitation

Establishment limitation refers to the failure of a species to germinate, grow, or survive at a site. There is no generally accepted definition of when a tree is considered to be established (Box 1.2), though the term generally refers to the earliest post-dispersal stages in tree ontogeny. When community assembly is dominated by establishment limitation, species relative abundances are determined by their regeneration niches and the availability of suitable microhabitats (Muller-Landau et al., 2002). Establishment limitation has been further decomposed into limitation imposed by the abiotic environment and limitation imposed by the biotic environment.

Box 1.2 Tree ontogeny

The traditional concept of the ecological community focuses on a single trophic level (Chesson, 2000; de Bello et al., 2021), but consideration of multiple life stages (ontogenetic stages) within that trophic level can be useful when exploring community assembly processes. This is because the diferent filters act at diferent ontogenetic stages. For example, the dispersal filter acts at the seed stage, the establishment filter acts across the seed-to-seedling transition, and later growth and survival occurs between the juvenile and adult stages (Fig. 1.1). This approach gave rise to the regeneration niche hypothesis (Grubb, 1977) that posits that abiotic and biotic conditions in the earliest stages of a plant's life cycle determine patterns of abundance when mature. Some authors have argued that later ontogenetic stages (i.e., growth and survival from seedling to sapling to adult stages) are also important (Marques & Burslem, 2015). Nevertheless, the earliest stages have consistently been identified as an important demographic bottleneck (Bagchi et al., 2010; Baldeck et al., 2013; Green et al., 2014; Umaña et al., 2016; Zhu et al., 2018).

However, there are no consistent definitions for each ontogenetic stage in a tree's life cycle. In tropical forest research alone, seedlings have been variously defined by

maximum height (from <10 cm (Saavedraet al., 2017; Walker, 2000) to <170 cm (Norden & Stevenson, 2015)), diameter at breast height (DBH; < 1 cm (Chang-Yanget al., 2021; Norden & Stevenson, 2015; Oliveira et al., 2021; Queenborough et al., 2009; Zhu et al., 2015), and/or diameter at base (< 2 mm (McLaren et al., 2005) to < 2 cm (Vieira et al., 2015)). Definitions of saplings are equally variable; an individual would be classed as a sapling by diferent authors if above 10 cm height (Walker, 2000), or only if above 160 cm height (Vieira et al., 2015), and with a maximum DBH from 2.5 cm (Vargas-Rodriguezet al., 2005) to 10 cm (Paine et al., 2009; Toledo-Aceves et al., 2009) or a maximum basal diameter from 2 cm (McLaren et al., 2005) to 8 cm (Vieira et al., 2015). The full range of definitions for ontogenetic categories are given in Table S1.1. The lack of a consistent definition for each ontogenetic stage reflects the variation in life history between species, though standardised definitions across demographically comparable species would be useful (Oliveira et al., 2019). For simplicity, I will refer to all stages between the seed and mature adult stages as juveniles.

1.3.1 Establishment limitation due to abiotic filters (environmental filtering)

Environmental filtering sensu stricto refers to conditions in the abiotic environment that some species are physiologically unable to tolerate, thus preventing their recruitment through establishment limitation at the seed-to-seedling transition (Box1.2) or through later mortality (Kraft et al., 2015). This is therefore the abiotic component of the establishment filter (Fig. 1.1). If there is heterogeneity in the abiotic environment, for example if diferent patches havediferent abiotic conditions, then diferent species will be excluded from these patches, resulting in increased diversity. This is known as the heterogeneity-diversity relationship (HDR; Lundholm, 2009). HDRs are a stabilising coexistence mechanism because niche diferences can cause species to limit conspecifics more than they limit heterospecifics (Levine & HilleRisLambers, 2009).

The specific environmental gradients that drive species turnover with succession in TDF are contested. Many authors have proposed that the most important environmental gradient with succession is whichever resource is most limiting. It has further been suggested that this resource is light in wet tropical forests, which becomes highly limiting as succession progresses (Lebrija-Trejos et al., 2011), but is water in TDF, which becomes less limiting with succession (Lohbeck et al., 2015). Tests of this theory have mostly examined functional trait distributions throughout succession (Box 1.1). In wet tropical forests, species shift along the resource economics spectrum with succession, as resource-acquisitive species dominate in the high-light environment of early succession and are replaced by resource-conservative species as light levels drop with succession. It has been assumed that TDF will show the opposite pattern in functional trait turnover, i.e., shift from conservative to acquisitive as water becomes less limiting with succession (Lohbeck et al., 2015). The expected shift has been found by Buzzard et al. (2016), Derroire et al. (2018), Poorter et al. (2019), and Werden et al. (2020a), though the opposite trend was found by Subedi et al. (2019) and changes to the community-weighted mean (CWM) of individual traits sometimes show unclear or opposing patterns. For example, the CWM of specific leaf area (SLA), an acquisitive trait, increased with succession and CWM of wood density, a conservative trait, did not change with succession in Becknell & Powers (2014), while both wood density and SLA decreased with succession in Lohbeck et al. (2013).

This could be due to the extreme seasonal variation in abiotic conditions that characterises TDF. Studies that directly characterised the abiotic environment found that abiotic variables were determined by an interaction between season and successional stage (Lebrija-Trejos et al., 2011; Werden et al., 2020a). Indeed, it has been proposed that water is the limiting resource during the dry season, but light is more limiting during the wet season (Derroire, 2016). Seasonality means that temporal variation is important for vegetation dynamics in TDF. For example, seasonal leaf-fall in TDF means that the spa; al pa<ern of light availability changes dras; cally throughout the year (Ceccon et al., 2003), and so an individual seedling must be able to tolerate a broad range of light levels (Brokaw & Busing, 2000), poten; ally precluding the narrow niche par; ; oning of the light environment that is suggested to occur in wet tropical

forests (Kobe, 1999). Diferences between studies may also be related to average precipitation; TDFare found along a steep precipitation gradient from 250 – 2000 mm per year, and the expected conservative to acquisitive successional shift has been found at the upper end of this gradient (Costa Rica, 1700 mm per year) but the opposite pattern was found towards the lower end of this gradient (Mexico, 900 mm per year; Derroire, 2016). A final explanation for the lack of consistency in resource economics turnover with succession is that trait turnover with TDFsuccession instead occurs along an axis from drought-avoiding deciduous species to drought-tolerant evergreenspecies, which is largely independent from the resource economics spectrum (Lohbeck et al., 2015). Such shifts in phenological habit have been widely documented in TDF (Arroyo-Mora et al., 2005; Derroire et al., 2018; Lohbeck et al., 2015), which are likely to be related to water availability but depend more on drought severity and length than mean annual precipitation. Indeed, Werden et al. (2020a) found that ecophysiological traits related to drought-strategy were better predictors of seedling growth and survival than resource economics. Therefore, species turnover with TDF succession is related to microclimatic gradients (Werden et al., 2018b), particularly those related to drought stress, but the relationship is non-linear due to seasonal variation in water availability.

1.3.2 Establishment limitation due to biotic filters

A species may fail to establish at a given site due to attack by herbivores and pathogens (together referred to as natural enemies). This can occur at multiple points throughout recruitment; seed predation is common (Dirzo et al., 2007), and juvenile trees are vulnerable to attack by herbivores and infection by fungal, bacterial or viral pathogens that can limit growth and/or cause increased mortality (Forrister et al., 2019). Natural enemy attack is often non-random, depending on a complex interplay of natural enemy populations and specialisation, host plant populations and defences, and environmental conditions (Aguilar-Peralta et al., 2020; Benítez et al., 2013; Krishnadas et al., 2018; Kulikowski et al., 2022). Non-random natural enemy pressure has been shown to reinforce species-habitat associations created by abiotic filtering (Fine et al., 2004) and promote diversity at multiple ontogenetic stages through conspecific negative density-dependence (CNDD; Forrister et

al., 2019; Krishnadas et al., 2018). One subcategory of CNDD is the Janzen-Connell hypothesis (Connell, 1971; Janzen, 1970), which posits that specialised natural enemies reduce recruitment close to conspecific adult trees (Downey et al., 2018; McCarthy-Neumann & Kobe, 2010), allowing recruitment of heterospecifics instead (Alvarez-Loayza& Terborgh, 2011). Overall, specialised natural enemies are expected to increase efective intraspecific competition relative to efective interspecific competition, and thus stabilise species coexistence.

The relative balance of abiotic and biotic filtering has been found to shift with TDF succession. Harsh abiotic conditions in early succession, resulting in physiological seedling failure, are thought to give way to biotic filtering (e.g., natural enemy pressure) later in succession (Hammond, 1995; Martínez-Ramos et al., 2021). Functional trait distributions have been used to explore this dynamic. Assuming phylogenetic trait conservation, Maza-Villalobos et al. (2020) interpreted a shift from phylogenetic clustering to random dispersion as supporting the hypothesised shift from abiotic to biotic filtering. However, patterns of trait dispersion with TDF succession are often unclear, and depend on the trait chosen (Bhaskar et al., 2014; Buzzard et al., 2016; Swenson & Enquist, 2009). Furthermore, common interpretations of functional trait distributions can be misleading (Box 1.1) and phylogenetic conservatism has been shown to occur for some ecological traits but not others, so cannot be assumed (Swenson & Enquist, 2009). The evidence for a shift from abiotic to biotic filtering with TDF succession is almost entirely derived from interpretations of functional or phylogenetic dispersion, and alternative methods are needed to confirm the mechanisms underlying the observed patterns.

Overall, community assembly in TDF succession difers from wet tropical forest succession due to the efects of seasonality, diferent limiting resources, and simpler forest structure. However, knowledge gaps remain regarding the balance of abiotic versus biotic filtering, the relative importance of diferent assembly filters (i.e., dispersal, establishment, growth, and mortality), and the complex dynamics of species turnover along the multiple non-linear environmental gradients associated with secondary succession.

1.4 Restoration ecology

Community assembly theory has clear applicability to the practice of forest restoration. For example, if the dispersal filter is most limiting, restoration practitioners and land managers may aim to increase propagule sources by ensuring landscape connectivity (Brokaw & Busing, 2000) or overcome the dispersal filter through direct seeding or planting (Jakovacet al., 2021). On the other hand, if establishment is limited by abiotic filtering, local management actions designed to ameliorate inappropriate abiotic conditions may be more appropriate (Jakovacet al., 2021). The relevant ecological theory may depend on the goals of the restoration project. Many restoration projects define success by the survival rates of planted trees (Banin et al., 2022; Schubert et al., 2024), but community assembly theory suggests that this must be balanced against the need to restore processes that generate diversity through random and non-random filtering so that restored forests are diverse and able to self-propagate this diversity (Oliveira et al., 2019). The relationship between restoration practice and ecological theory is complementary; restoration can act as an "acid test" of ecological theories (Bradshaw, 1987), allowing for large-scale empirical tests of our understanding of community assembly and species coexistence (e.g., Werden et al., 2020a).

My research was designed to answer questions about applied restoration practice, as well as fundamental ecological processes. Chapter 2 characterised the shifts in the taxonomic and functional composition of the tree community throughout secondary succession, which can inform species selection for restoration. These data were also separated by ontogenetic stage to identify the most limiting community assembly filters for restoration practitioners to target. In Chapter 3, I explored the hypothesis that the diversity of naturally recruited trees in restored forests can be increased by enhancing environmental heterogeneity. The experiment presented in Chapter 4 provided data on the growth and survival of ten native tree species in diferent successional environments and quantified the potential magnitude of tree mortality caused by natural enemies. In addition to the direct utility of these data for short-term planning, Chapters 3 and 4 both emphasised the importance of long-term thinking in forest restoration, as both explored the processes of non-random filtering that may help to promote the self-propagation of diversity in restored forests.

1.5 Study site

The research presented in this thesis was conducted at a site in the state of Campeche on the Yucatán Peninsula in south-western Mexico (Fig. 1.2; 18°40'46.2"N, 90°08'24.4"W). The climate is warm and sub-humid (Aw, Köppen classification), with a mean annual temperature of 24 – 28°C and a total annual precipitation of 1200 – 1500 mm (García Gil et al., 2002; Pablo-Rodríguez et al., 2023). It therefore represents a mid-point on the precipitation gradient that TDF span, thus addressing an important research gap as the majority of research into community assembly during TDF secondary succession has taken place in drier sites elsewhere in Mexico (e.g., Almazán-Núñez et al., 2012; Bravo-Monzón et al., 2022; Ceccon et al., 2004; Lebrija-Trejos et al., 2008, 2010a, 2011; Martínez-Ramos et al., 2021) or wetter sites in Costa Rica (e.g., Becknell & Powers, 2014; Buzzard et al., 2016; Werden et al., 2018b, 2020a) and Panama (e.g., Estrada-Villegas et al., 2020). During the period from 1982 to 2016, precipitation in the region became more intense and more unevenly distributed throughout the year (Mardero et al., 2020).

The Yucatán Peninsula has a limestone karst geology with little topographic variation, ranging from about 100 to 360 m above mean sea level. However, even within this limited topographic range, vegetation varies significantly between the upland areas and low-lying bajos (Mardero et al., 2020; Vester et al., 2007). This research was conducted in bajo sites, which are characterised by seasonally flooding Vertisols that have a high clay content, causing them to undergo shrink-swell cycles (Werden et al., 2018a). The vegetation is seasonally dry semi-evergreen tropical forest; approximately 25% of the vegetation sheds its leaves during a pronounced dry season between November and May (Pablo-Rodríguez et al., 2023). Forests are further categorised in Spanish based on their stature and the seasonal inundation typical of the bajos, such that the forest in the study site is best described as selva baja inundable due to its short stature (8 – 15 m high; Pablo-Rodríguez et al., 2023; Vester et al., 2007). In addition to wet season flooding, forest fires are common in the dry season (Hernández-Stefanoni et al., 2011, pers. obs.).

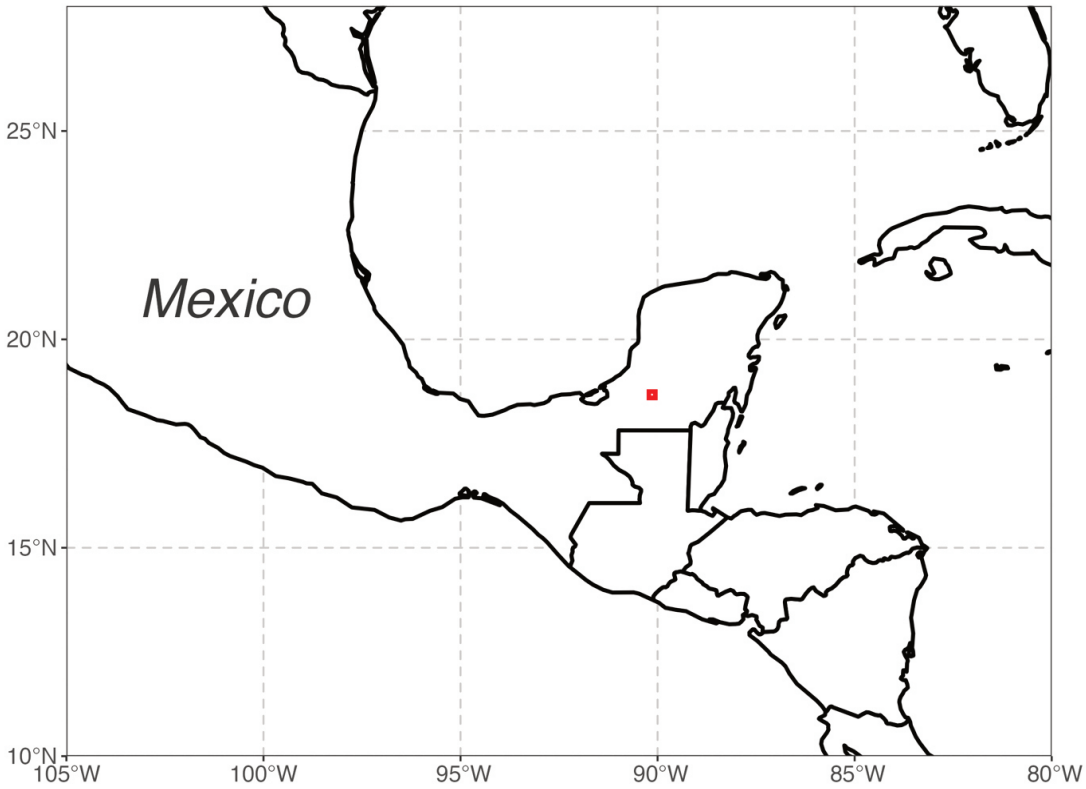


Figure 1.2 Location of study site (red square).

The site is adjacent to the Calakmul Biosphere Reserve, part of the second largest continuous area of tropical forest in the Americas and the largest protected tropical area in Mexico (Bohn et al., 2014; Pablo-Rodríguez et al., 2023). The Ancient Mayan civilisation existed in the region for 3,000 years (~2,000 BCE to ~900 CE) practicing traditional swidden agriculture with alternate vegetation removal using slash-and-burn techniques and fallow periods that allowed the natural process of secondary succession to proceed (Bohn et al., 2014; Vester et al., 2007). Furthermore, hurricanes regularly flatten large areas of the forest (Boege, 1995). All forest on the peninsula is therefore secondary (Ceccon et al., 2004; Sorensen, 2006), though some is old-growth. The precise age of the old-growth forest has

not been estimated, but some patches may have been undisturbed by human activity for nearly 1000 years (Vester et al., 2007). A drastic increase in immigration to the region that began in the 1960s saw an rise in more intensive agricultural practices and cattle ranching (Bohn et al., 2014; Vester et al., 2007). However, in more recent years further agricultural intensification and declining rural populations have also led to some land abandonment, a trend that is being seen across the tropics (Wright & Muller-Landau, 2006). The current landscape is therefore a mosaic of patches with difering intensity and duration of human land use and time since abandonment.

The research site has been owned by a forest restoration organisation, Plant-for-the-Planet Mexico A.C., since 2021. According to historical Google Earth satellite imagery, the western section of the site has remained closed-canopy forest for at least the past 30 years, though some selective logging has taken place (pers. obs.). This site is similar in structure and composition to old-growth forest found in the Calakmul Biosphere Reserve (Bohn et al., 2014). A central section of the site was partially cleared of vegetation in 2017 but was not used further and has been naturally regeneratingsince that time. The eastern section of the site was used for rice farming and, later, cattle ranching until 2021 (O. E. Verduzco-Salazar, pers. comm.). From 2021 to present, parts of this eastern section have been planted with a mix of up to 41 native tree species (see https://www.plant-for-the-planet.org/yucatan/ for more details), while other regions have been left to regeneratenaturally. Cattle are excluded from the whole site by wire fencing, though this is not completely efective (pers. obs.). Where trees were planted, the ground was prepared using a tractor-mounted mechanical rototiller. Grasses growing around the planted trees are periodically removed using machetes for 5 years after planting.

Diferent parts of this site were used for Chapters 2, 3, and 4. For Chapter 2, 1-hectare plots (100 m ´100 m) were established in each of the three sites described above (old-growth, abandoned 2017, and abandoned 2021). These plots therefore represent three stages of secondary succession: late, mid, and early respectively and are indicated by large squares in Figure 1.3. For Chapter 3, 20 circular plots were established across all three sites (indicated by stars in Fig. 1.3). Seven plots were randomly located within the old-growth

forest, six were randomly located in areas that had regenerated naturally (in both areas abandoned in 2017 and in 2021), and six plots were randomly located in areas that had undergone restoration tree plantings since 2021. These plots therefore represent two diferent restoration interventions (natural regeneration and tree planting), as well as an old-growth forest to act as a reference ecosystem, but are also confounded with the successional gradient. Finally, for Chapter 4, nine 4 ´10 m plots were established for an outplanting experiment in random locations in the same three successional stages as Chapter 2 (indicated by yellow triangles in Fig. 1.3). These experimental plots were close to the three 1-ha plots, but their exact locations were generated randomly so they were treated as independent replicates. In all cases, successional stage is confounded with previous land use intensity. This is a common challenge for studies of secondary succession, as less productive and intensively used sites are more likely to be abandoned (Chazdon & Guariguata, 2016; Jakovac et al., 2021). All sites are selva baja inundable growing on Vertisols.

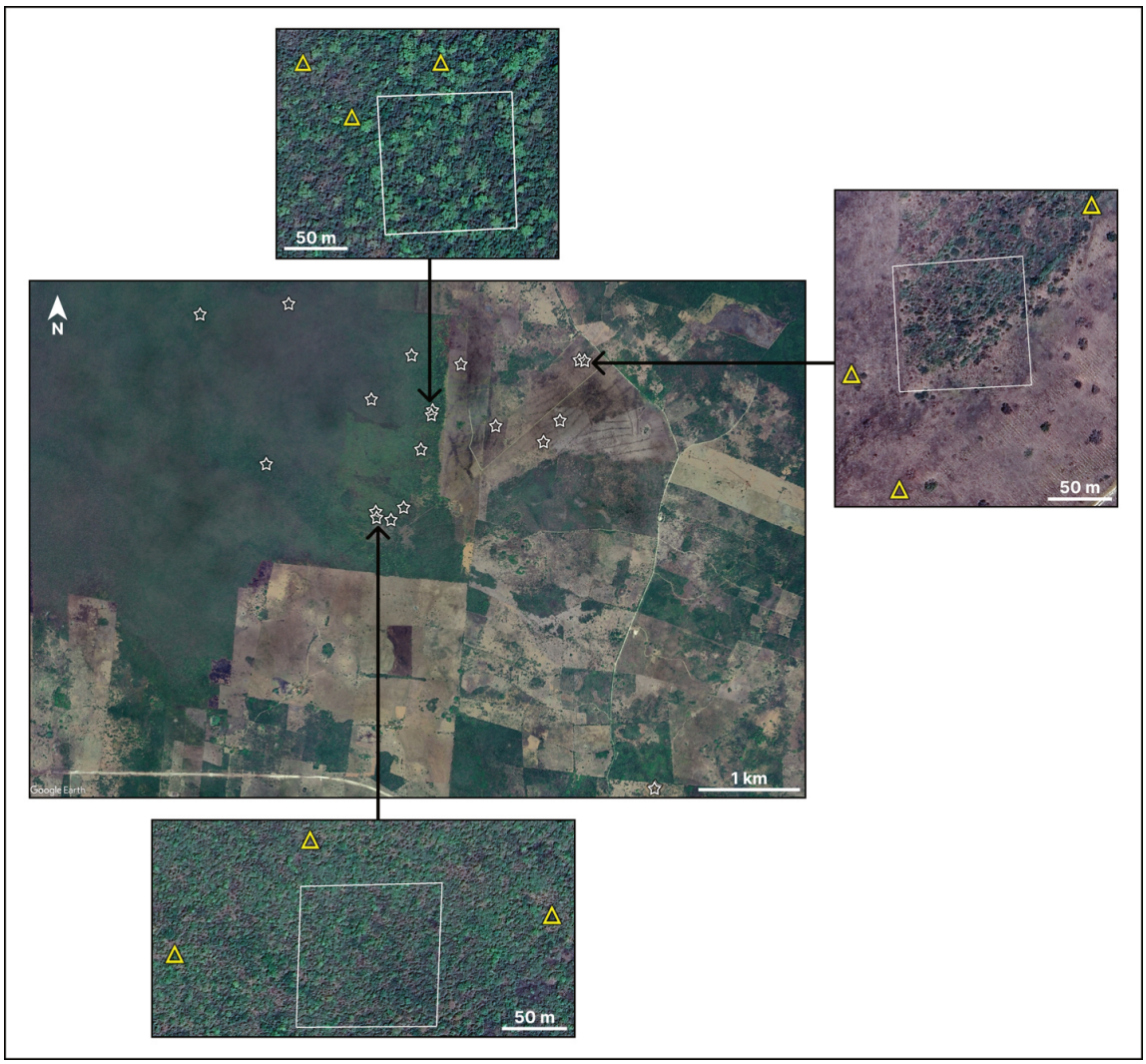


Figure 1.3 Satellite images of study site in June 2023 (wet season) with plot locations indicated. Centre: Locations of circular plots used in Chapter 3 (stars); top: late successional forest; right: early successional naturally regenerated forest; bottom: mid successional naturallyregenerated forest. Largesquaresindicate location of 1-haplots used in Chapter 2; yellow triangles indicate locations of plots used in Chapter 4. Images from Google Earth, Ó2025 CNES/ Airbus.

I directly characterised abiotic conditions across the successional/land use intensity gradient (Table 1.1). Mean canopy openness decreased by approximately 80% with succession. In contrast, edaphic properties showed very little variation across the landscape. Soil carbon and nitrogen content were highly correlated (Pearson'sr = 0.90) and were lowest in the mid successional environment. Soil pH varied independently to soil carbon (r = -0.06) and nitrogen (r = 0.18) and decreased along the successional gradient. Soil texture was determined with thewidely usedUSDASoil TextureTrianglebased on the relative percentages of sand, silt, and clay (Groenendyk et al., 2015). The early successional environment had sandy clay loam soils, with a higher sand content, while the mid and late successional environments had sandy clay soils, with a higher clay content.

	Successional environment		
	Early	Mid	Late
Canopy openness	0.92 ± 0.03	0.26 ± 0.01	0.18 ± 0.005
Soil carbon (%)	3.49 ± 0.21	3.05 ± 0.14	4.66 ± 0.24
Soil nitrogen (%)	0.33 ± 0.02	0.20 ± 0.01	0.35 ± 0.02
Soil pH	7.78 ± 0.02	6.75 ± 0.04	6.70 ± 0.03
Soil % sand	56.58 ± 1.53	46.97 ± 0.46	49.34 ± 0.35
Soil % clay	29.33 ± 2.51	45.49 ± 0.55	43.86 ± 0.34
Soil % silt	14.09 ± 1.25	7.54 ± 0.36	6.79 ± 0.27

Table 1.1 Mean ± standard error of measured abiotic variables across the successional gradient in the study landscape.

Chapter 2: Secondary succession of a seasonally dry tropical forest is taxonomically stochastic but functionally deterministic

2.1 Introduction

Approximately 72% (2.96 billion ha) of forest area globally has been disturbed, degraded or otherwise significantly changed by human activities (FAO,2020). Many of these forests are now recovering, whether through natural regeneration or active restoration efforts, such that secondary forests are an increasingly important ecosystem type. Over 28% of lowland forest in the Latin American tropics is secondary forest (Chazdon et al., 2016), and these forests are recognised as important sources of ecosystem goods and services such as biodiversity habitat, carbon sequestration, and provision of timber and non-timber forest products (Chazdon, 2008; Chazdon et al., 2016). Patterns of tree species diversity and composition in these secondary forests, vital for ensuring their functioning and resilience, are generated by community assembly processes throughout secondary succession (Chazdon & Guariguata, 2016; Norden et al., 2009b).

One framework for understanding community assembly is that species in the global species pool must pass through a hierarchical series of filters to form the local site-level community (Götzenberger et al., 2012). In this framework, ecological filters act at diferent stages of tree ontogeny: dispersal, establishment and persistence (Marques & Burslem, 2015). The dispersal filter removes species that do not arrive at the site. The establishment filter removes species that arrive as propagules but are unable to germinate and establish as seedlings. Subsequent filters act by limiting growth and survival of established seedlings. A species may fail to pass through each filter for deterministic reasons, i.e., the functional traits of that species interact with the filter in such a way that prevents it from passing through (Lebrija-Trejos et al., 2010b). This may be due to abiotic processes, such as environmental filtering, and/or biotic processes, which can include competition, facilitation

and attack by pests, pathogens, or predators (Kraft et al., 2015). A species may also fail to pass through a filter by random chance, introducing an important stochastic component into community assembly (Norden et al., 2015).

There is ongoing research into the relative importance of abiotic versus biotic filters, and how important their deterministic interactions with species identity and/or functional traits are relative to stochastic processes. This maps on to the classic niche versus neutral debate in community assembly (Chase & Leibold, 2003; Hubbell, 2001). As with the move away from a strict niche-neutral dichotomy, it is generally accepted that both abiotic and biotic deterministic filters, as well as stochastic processes, are important (Shoo & Catterall, 2013), but each may play a relatively greater or lesser role in determining community composition under diferent conditions. It is vital to understand which filters are limiting community assembly in secondary forest succession because these can prevent natural regeneration, which is often the most cost-efective approach to the restoration of resilient forest ecosystems (Chazdon & Guariguata, 2016; Gilroy et al., 2014).

Community assembly processes may also change along a successional gradient. Both dispersal and establishment are highly limited in early successional forests (Holl, 1999; Holl et al., 2017; Martínez-Ramos et al., 2021). Werden et al. (2020b) found that dispersal limitation decreased with succession, while establishment limitation increased, possibly due to increased negative density-dependence or deeper leaf litter. Furthermore, multiple authors have hypothesised that abiotic processes such as habitat filtering dominate early in succession while biotic processes become increasingly important as succession progresses (Lohbeck et al., 2014; Martínez-Ramos et al., 2021). However, the evidence for this is mostly based on analyses of the dispersion of functional trait or phylogenetic distributions, a method that has been criticised as the same distribution can result from diferent processes (Kraft et al., 2015; Li et al., 2015). Understanding how the balance of stochastic, deterministic, biotic, and abiotic community assembly processes change throughout succession can help to predict how secondary forest community composition and patterns of diversity will change through time.

Conclusions about the relative importance of diferent community assembly processes also depend on the spatial scale of sampling (Cottenie, 2005). In a meta-analysis of community assembly studies on woody plants, Götzenberger et al. (2012) found that the proportion of tests suggesting biotic assembly increased with the spatial extent of sampling. This was unexpected; larger spatial scales encompass more environmental heterogeneity, so it is generally thought that abiotic filtering is more likely to be observed (Davies et al., 2005; Nishizawa et al., 2022; Townsend et al., 2008). In contrast, biotic processes, such as conspecific negative density dependence (CNDD), require individuals to be physically close to each other, and so biotic processes are generally considered to occur at small spatial scales (Comita & Hubbell, 2009; Kraft & Ackerly, 2010).

We used large-scale, spatially explicit surveys of tree communities across three ontogenetic stages (seed, juvenile, and adult) and three stages of secondary succession (early, mid, and late) to explore the changes in the taxonomic and functional composition of these communities within a tropical dry forest ecosystem. The majority of research into community assembly has taken place in intact wet tropical forests (Sunderland et al., 2015). However, 42% of tropical forests are tropical dry forests (TDF; Murphy & Lugo, 1986) and there is growing evidence that the balance of assembly processes is changed by the climatic diferences between these two forest types (Cottenie, 2005). The most important diference that relates to secondary succession is that the limiting resource in wet tropical forest succession is often light, while multiple studies have found that water limitation defines the successional gradient in TDF (Ceccon et al., 2006; Lohbeck et al., 2015). Therefore, while late successional species in wet tropical forest need conservative traits to survive in the light-limited understory, in TDF conservative traits are required in the water-stressed environment of early successional forest. Consistent with this model, Buzzard et al. (2016) and Poorter et al. (2019) found a shift from conservative to acquisitive trait syndromes with TDF succession, though the picture is complicated as the same individual can have both conservative and acquisitive traits (Werden et al., 2018a, 2022a) and the selection and measurement of functional traits most relevant to robustly categorise the community remains challenging (de Bello et al., 2021; Werden et al., 2020a). As such, there have been

multiple calls for more research in TDF ecosystems to identify ways in which they difer from wetter ecosystems, and gain a fuller picture of how plant communities develop in regenerating tropical forests (Jakovac et al., 2021; Werden et al., 2020a).

Our investigation aimed to address four questions in this seasonally dry forest landscape. Firstly, we investigated how the taxonomic and functional composition of juvenile and adult tree communities changes along a successional gradient. Secondly, we asked whether these changes move deterministically through successional stages towards a “climax” community (Derroire et al., 2016a; Powers et al., 2009; Rozendaal et al., 2019) or are stochastic and unpredictable (Chazdon et al., 2007; Norden et al., 2015; Poorter et al., 2021). Third, to explore the drivers of these changes, we assessed whether the abiotic environment also exhibits predictable changes across the plots, and, fourth, how community composition might be shaped by abiotic or biotic limitation during juvenile recruitment (Marques & Burslem, 2015; Muller-Landau et al., 2002; Norden et al., 2009a; Werden et al., 2020b), when the processes causing non-random mortality are strongest (Green et al., 2014).

2.2 Materials and Methods

2.2.1 Study system

The study was carried out in a mosaic TDF landscape in Mexico (18°40'46.2"N, 90°08'24.4"W), described in detail in section 1.5 (Main introduction). We established three 1-ha (100´100 m) plots across this landscape. Potential plots were initially identified based on a map of Normalised Diference Vegetation Index (NDVI) across the site (Hartter et al., 2008), followed by field visits and examination of satellite images to verify successional stage. The early successional plot had been used for rice cultivation and, later, cattle pasture for over 30 years, up until abandonment 2 years before the study took place (O. E. Verduzco-Salazar, pers. obs.). Based on satellite photography, the mid successional plot was cleared of forest 5 years before the study took place. Occasional larger trees were left standing, and the site was not used further and has been naturally regenerating since that time. The late

successional plot has continuously remained closed-canopy forest for at least the past 30 years, and only a few trees have been removed.

2.2.2 Tree census

Within each 1-ha plot, we censused the woody plant community (93 tree species, 1 palm species and 4 liana species, so we will refer to this as the "tree community") at three ontogenetic stages: seeds; seedlings and saplings (henceforth "juveniles", 10 – 200 cm tall); and adults (> 200 cm tall and > 5 cm diameter at breast height (DBH)). Seeds were sampled using 0.5 ´ 0.5 m seed traps consisting of a 40 cm deep mesh bag suspended 1 m above the ground. Juveniles were sampled in 2 ´ 2 m quadrats, and adults were sampled in 10 ´ 10 m quadrats to account for the diferent sizes of the individuals. Each 1-ha plot was divided into 100 subplots, and a juvenile quadrat was placed in a random location in every other subplot and at the four corners of the plot (Fig. 2.1). Half of these quadrats were randomly selected to also receive a seed trap and adult quadrat, so that 25 of the 54 sampling stations in each plot had nested adult, juvenile and seed surveys used to track community reassembly across ontogenetic stages (Fig. 2.1).

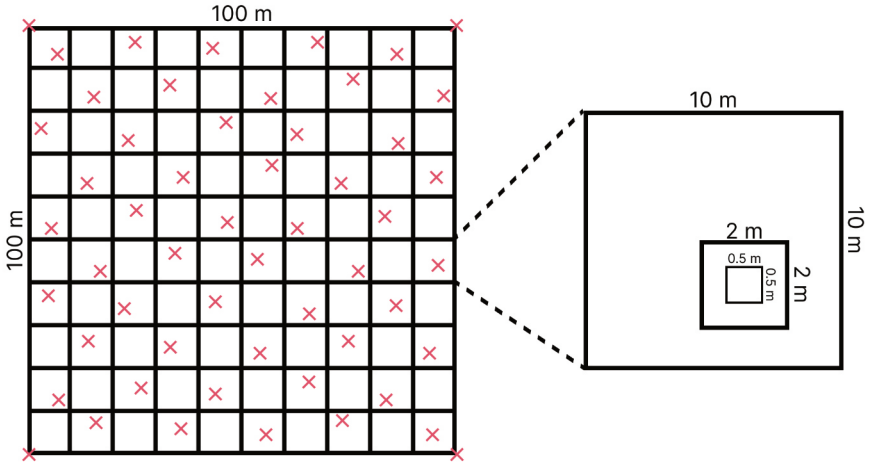


Figure 2.1 Schematic of sampling design. 54 sampling stations were established in each of three 100 ´ 100 m plots, each of which were divided into 10 ´ 10 m subplots. A station was

established within every other subplot, centred on a random location (indicated by a red cross) and on each of the plot corners. Each station consisted of a 2 ´2 m quadrat within which all woody plants between 10 and 200 cm in height were censused. 25 stations in each plot were randomly selected to also receive a seed trap (0.5 ´0.5 m) and an adult tree quadrat (10´10 m).

Individual juveniles and adults were identified to species in the field. Where identification in the field was not possible, leaves and stems were saved in a plant press and identified after the census using published local guides. The seed traps were deployed for 11 full months from May 2022 until March 2023 and were emptied every 2 weeks (every 4 weeks during the dry season). Due to sampling limitations, we did not collect seed rain in the month of April, and so may be missing species that only disperse during this month. If any species are missing these are likely to be those species that fruit during the rainy season, which tend to be fleshy-fruited zoochorous species (Derroire, 2016). Seeds were counted and identified to species where possible using published local guides and the seed bank at the Regional Laboratory for the Study and Conservation of Germplasm, CICY, Mérida. All seeds with > 15 individuals were identified to genus or species, except for one morphospecies with 430 individuals and one morphospecies with 60 individuals where we lacked a clear ID. The majority of unidentified morphospecies were only represented by one or two individuals. In total, 84.3% of all individual seeds were identified to genus or species. Where species could not be identified, they were given a unique morphospecies identity. In all cases, taxonomic names follow the World Flora Online (WFO) Plant List as of 20/11/2024.

2.2.3 Abiotic variables within plots

All abiotic measurements were taken during the dry season between February – May 2022, the leaf-of period for deciduous species. In the centre of each 2 ´2 m quadrat we took a 360° hemispherical photosphere (N = 162) using the Google Street View app (Google LLC) and a smartphone camera on a 1 m high tripod. Raw canopy photos were processed using the Python-3 and scikit-image tool Cano.py (Waring et al., 2024) to calculate percent canopy

openness. In brief, images were converted to hemispherical through polar projection, then automatically binarised with a threshold of 0.8. To ensure the binarisation step was completed correctly, we checked each image for clouds that were misclassified as canopy and manually brightened them. Canopy openness is the area of the sky hemisphere that is not canopy and was calculated following ter Steege(2018).

We also took 3 soil cores to 15 cm depth as close as possible to the centre of each quadrat and combined the three cores into one sample (N = 162). Soil samples were air-dried and sieved (2 mm). Soil pH was measured on a 1:5 solution of soil: deionised water using a Hanna HI5222 bench pH meter. Soil samples were then ground to fine powder, acidified with addition of 6% H_2SO_3 to remove carbonates, oven-dried at 65°C, and analysed for total organic carbon and nitrogen content (%) on a ThermoFlash EA1112 Elemental Analyser. Soil particle size distribution (sand, silt and clay percentages) was measured using the hydrometer method (Gavlak et al., 2005) on bulked soil samples from three adjacent quadrats (to ensure suficient soil weight (60 g) for the protocol).

2.2.4 Functional traits of tree recruits

Functional trait data for all species were compiled from publicly available TRY data (Kattge et al., 2020), data tables in the relevant literature, and field measurements following Pérez-Harguindeguy et al. (2013). Sources of all functional trait data are given in Table S2.1. Where sources gave diferent values, the value obtained from the most geographically proximate site was given preference. Field measurements were taken for 10 focal species chosen using a stratified method to represent each leaf phenological group and are highlighted in Table S2.1. Traits were chosen that were hypothesised to be relevant to species' responses to the expected major resource gradients with secondary succession: light and water availability. Where species-level trait coverage was < 60% of species and/or individuals (which was the case for seed mass, petiole length and specific leaf area (SLA)), we included the genus-level average value where available to increase the trait coverage. The final set of functional traits used in the study and their coverage is shown in Table 2.1. Where analyses of adult and juvenile functional community composition required abundance-weighted trait data (i.e.,

community-weighted mean; CWM), trait coverage was calculated as a percentage of all individuals in the dataset. The recruitment limitation analysis required species-level trait data for selected species present as seeds and/or juveniles (see section 2.2.5.4 for further details of species selection), so trait coverage was calculated as a percentage of all species in the recruitment limitation dataset.

Trait	Biological interpretation	Trait coverage: juvenile individuals	Trait coverage: adult individuals	Trait coverage of species in recruitment limitation dataset
Maximum height (m)	Associated with rapid growth for light acquisition	91%	91%	88%
Seed mass (mg)	Represents a trade-oA between fecundity/dispersal and establishment	89%	87%	88%
Petiole length (mm)	Longer petioles maximise light capture	87%	76%	76%
Specific Leaf Area (SLA) (mm^2mg^{-1})	Indicates light uptake as a function of investment in leaf production	74%	77%	80%
Leaf phenological habit	Deciduous trees are drought-avoidant, evergreen trees are drought-tolerant	98%	100%	92%
Leaf type	Compound leaves are associated with desiccation avoidance and fine-tuning the drought response	100%	100%	96%

Nitrogen fixation	Species that form symbioses with bacteria that do biological nitrogen fixation	99%	99%	96%

Table 2.1 Functional traits used in the analyses.

2.2.5 Statistical analysis

All statistical analysis was done using R version 4.2.3 (R Core Team, 2023) and the vegan package (Oksanen et al., 2024) was used for all analyses unless otherwise noted. We used ordination-based methods to address our first question, whether the composition of plant communities varied among plots (i.e., through a successional/land use gradient). We explored our second question, whether changes in composition are deterministic or stochastic, through analyses of the trajectory of the taxonomic and functional composition of the tree community along the successional chronosequence. To explore the potential drivers of determinism, we also directly measured how the abiotic environment changed across the plots. We then used spatially explicit recruitment limitation analysis to explore how changes in juvenile recruitment responded to the abiotic and biotic changes associated with secondary succession.

2.2.5.1 Exploring changes to taxonomic and functional community composition with secondary succession.

We first examined how the diversity and community composition of seeds, juveniles, and adults varied across successional stages. We tested for variation in observed species richness between plots using ANOVA, treating each station as an independent replicate (N seeds = 75; N juveniles = 162; N adults = 75). Rarefaction and extrapolation of species richness in each plot was performed using the iNEXT package (Hsieh et al., 2016). Species richness at the curve asymptote was estimated by extrapolation.

We tested whether communities difered significantly across stages of secondary succession (i.e., among plots) using permutational multivariate analysis of variation (PERMANOVA). Pairwise comparisons between all pairs of successional stages were tested and p-values Bonferroni corrected for multiple comparisons. The assumption of equal within-group variance was tested using distance-based tests for homogeneity of multivariate dispersions (Anderson, 2006) and diferences between the mean distance-to-centroid of the successional stage groups and 95% confidence intervals were calculated using Tukey's Honest Significant Diference (HSD) method. The assumption of equal variance within each group was violated in some cases (see Box S2.1 for details). PERMANOVA is robust to violations of the assumption of homogeneity of variances, but any diferences in community composition may be driven by heterogenous within-group variation, diferences in the group mean values, or both.

To visualise how the juvenile and adult tree communities varied in their taxonomic and functional composition across the successional gradient, we used non-metric multidimensional scaling (NMDS) to produce unconstrained ordinations of the communities in all 2 ´2 m quadrats (for juveniles) or 10 ´10 m quadrats (for adults). For the taxonomic composition, the NMDS was performed on a Chao dissimilarity matrix (Chao et al., 2005). A Bray-Curtis dissimilarity matrix (Bray & Curtis, 1957) was also used and gave visually similar results. For the functional composition, the NMDS was performed using Gower's distance based on the CWM values for traits. Functional trait variables were additionally fit to the trait-based ordination to show the correlation of individual functional traits with overall functional dissimilarity.

2.2.5.2 Are the changes to taxonomic and functional community composition with secondary succession stochastic or deterministic?

To explore the changes in the composition of plant communities through secondary succession, we considered each combination of successional and ontogenetic stage to represent a unique stage in a successional chronosequence and looked for taxonomic/functional similarities among them. This is essentially an extension of the classic

space-for-time substitution (chronosequence) approach commonly used to study successional dynamics. During succession, the adult trees modify the abiotic and biotic environment such that the juveniles that recruit under them experience diferent conditions to those experienced by the adult trees when they were recruited (Derroire et al., 2016c). We therefore assume that the juveniles of one successional stage are experiencing conditions closer to that experienced by the adults of the subsequent successional stage. For example, the present-day adult trees in the mid successional plot have regenerated following forest clearance ~5 years earlier. Therefore, as juveniles, these plants would have experienced a similar environment to those currently growing in the early successional (~2 years abandoned) plot. As such, the order of the successional chronosequence is: juveniles in the early successional plot (there were no adults recorded in this plot), adults in the mid successional plot, juveniles in the mid successional plot, adults in the late successional plot, and juveniles in the late successional plot.

We then performed the following analyses on the dataset, each time grouping individuals in four diferent ways: by species (taxonomic composition), or by three categorical functional traits: leaf phenological habit (deciduous, brevi-deciduous or evergreen), leaf type (compound or simple) and biological nitrogen fixation ability (nitrogen-fixer or non-fixer) We calculated the relative abundance of each group within each community. To explore whether the changes in taxonomic and functional composition followed a stochastic or deterministic pattern at each stage in the successional chronosequence, we compared each community to the communities directly preceding and directly following it. If communities had a similar composition, we considered this to be evidence for deterministic processes in the assembly of those communities. This is because the communities are not actually related (e.g., the mid successional adults have not actually grown from the early successional juveniles), so compositional similarity would suggest that similar processes have assembled both communities despite assembling at diferent times and in diferent locations.

For each pair of communities, the null hypothesis of no diference in the distribution of individuals between the taxonomic (species) and functional groups was tested using Fisher's Exact Test, as the assumptions of the c^2 test of independence were violated. P-

values were computed by Monte Carlo simulation with 9,999 replicates. The relative abundance of each group in each community was visualised using an alluvial plot, where each stratum represented a taxonomic (species) or functional group, and each point on the x-axis represented a stage in the successional chronosequence. Flows were included from one stage to the next where the species identity was the same.

We then used ecological trajectory analysis (ETA; De Cáceres et al., 2019) to explore the pattern of taxonomic and functional composition with succession in a way that enabled us to include the multidimensionality of the community data. Taxonomic and functional dissimilarity was calculated as in section 2.2.5.1. Following this we performed Principal Coordinates Analysis (PCoA) on the dissimilarity matrices and the trajectories in the ordination space were drawn onto the PCoA plots. The PCoA plot is a two-dimensional representation of a multidimensional dissimilarity matrix, so the lengths of the drawn trajectory segments may not correlate linearly with the true distance between two communities. Likewise, the lengths of the taxonomic and functional trajectories cannot be directly compared because the dissimilarity matrices were calculated using diferent metrics (Chao for taxonomic dissimilarity and Gower for functional dissimilarity). We therefore calculated the length of each segment as a percentage of total trajectory length.

2.2.5.3 Do changes to functional community composition reflect a resource availability gradient?

To determine whether abiotic variables influenced observed community patterns across the successional gradient, we tested for variation in abiotic variables (canopy openness, soil pH and soil particle size distribution) among plots using ANOVA followed by Tukey's HSD test. If the variable was markedly non-normal, we used the non-parametric Kruskal Wallis test followed by the Pairwise Wilcox Test instead. P-values of pairwise tests were Bonferroni corrected for multiple comparisons.

2.2.5.4 Are changes to functional composition occurring at the stage of juvenile recruitment driven by abiotic or biotic limitations to recruitment?

We calculated observed versus expected dispersal and establishment limitation for for each unqiue combination of species´plot (i.e., for each species at each successional stage), to assess how abiotic filtering and density-dependent dynamics might play out over our successional/land-use gradient. Recruitment limitation calculations follow Muller-Landau et al. (2002). For each species in each plot, dispersal limitation refers to the proportion of seed traps that did not receive seeds, and establishment limitation refers to the proportion of stations that received seeds but that did not have a juvenile. Thus, dispersal limitation for species ! was calculated as

$$1 - \frac{\$stationsreachedbyseedsofspecies!}{totalnumberofstationsinplot}$$

Establishment limitation was calculated as

$$1 - \frac{\$stationswithbothseedsandjuvenilesofspecies!}{\$stationswithseedsofspecies!}$$

To further decompose recruitment limitation into that arising from limited numbers of seeds/juveniles and that arising from the limited distribution of available seeds/juveniles (Muller-Landau et al., 2002), we compared observed recruitment limitation to expected recruitment limitation under a stochastic uniform distribution of seeds/juveniles. Expected limitation was calculated as the mean recruitment limitation of 1000 simulated distributions of seeds and juveniles at stations based on a Poisson distribution with an equal expectation at all stations that is equal to the mean abundance of that species in the plot (following Norden, et al. (2009b), further details given in Box S2.2). The diference between observed and expected limitation is given as ∂ recruitment limitation. ∂ recruitment limitation varies from -1 to 1; positive values indicate a species is more limited than expected, and vice versa for negative values.

To assess whether deviations from expected dispersal, and establishment limitation were linked to species' traits and/or driven by density dependent processes, $\partial_{dispersal}$ limitation and $\partial_{establishment}$ limitation were modelled as a function of functional traits and conspecific abundance (of seeds, juveniles and adults). Abundance data were corrected for diferences

in the sampled area to scale counts of seeds, juveniles and adults to one hectare (Marques & Burslem, 2015). Only biologically relevant a priori hypotheses were tested. For example, only maximum height and seed mass were used as predictor traits for $\partial_{dispersal}$ limitation, as leaf traits like SLA and phenological habit were not expected to impact dispersal. Response variables were bounded between 0 and 1 and so were modelled using generalised linear mixed models (GLMM) with a zero-inflated beta error distribution, with species as a random efect. Where the random efect had a variance of 0, it was removed from the model to avoid a singular model fit. The marginal and conditional R^2 for mixed models were calculated following Nakagawa & Schielzeth (2013). We first tested for interactions between plot and predictor variables in modelling $\partial_{dispersal}$ and $\partial_{establishment}$ limitation values with mixed-efects two-way ANOVAs (Type-III). We then tested for diferences in $\partial_{dispersal}$ and $\partial_{establishment}$ limitation values with mixed-efects one-way ANOVAs (Type-II to account for the unbalanced number of species in each plot) for each predictor variable.

2.3 Results

2.3.1 Species identification and diversity.

We recorded 15,665 seeds of 65 morphospecies, of which 23 were identified to species (35.4%) and two were identified to genus (3.1%), representing 96.2% of all seeds collected. No unidentified morphospecies were used in the analyses except in the estimation of species richness. We recorded 2,610 juveniles of 65 morphospecies, of which 61 were identified to species (93.8%) and one was identified to genus (1.5%), together representing 98.7% of individuals. We recorded 531 adults of 35 morphospecies, of which 31 were identified to species (88.6%), with one identified to genus (2.9%), representing 99.1% of individuals.

Observed species richness was significantly diferent among plots for all three ontogenetic stages (seed $F_{2,72} = 23.7$, $p < 0.001$; juvenile $F_{2,159} = 99.14$, $p < 0.001$; adult $F_{2,72} = 259.2$, $p < 0.001$). Rarefied seed species richness was estimated to be intermediate (mean: 40; 95% CI: 23 – 80) in the early successional plot, lowest (32; 20 – 52) in the mid successional plot and highest (45; 37 – 61) in the late successional plot. Rarefied juvenile species richness

increased almost six-fold on averageacross the successional gradient: it was estimated to be lowest (17; 13 – 26) in the early successional plot, intermediate (60; 35 – 98) in the mid successional plot, and highest (99; 43 – 168) in the late successional plot. Similarly, estimated adult species richness increased over three-fold from 10 (9 – 16) in the mid successional plot to 36 (30 – 52) in the late successional plot. Therewere no adult trees in the sampling stations in the early successional plot.

2.3.2The taxonomic and functional composition of both adult and juvenile tree communities changed with secondary succession.

Thejuvenile (Fig. 2.2A & C) and adult (Fig. 2.2B & D) communities associated with early, mid, and late-successional plots form clearly distinct groups (Juvenilecommunity PERMANOVA: taxonomic $F_{2,130}$ = 42.76, p = 0.001; functional $F_{2,130}$ = 46.27, p = 0.001; p = 0.003 for all pairwise comparisons. Adult PERMANOVA:taxonomic$F_{1,42}$= 23.65, p = 0.001; functional $F_{1,40}$ = 68.52, p = 0.001). Earlier successional communities are more dispersed in taxonomic and functional space than late successional communities (Box S2.1). Both taxonomic and functional composition change directionally along the NMDSaxeswith succession, and this is particularly apparent for the juvenile community (Fig. 2.2A). The correlation of specific functional traits with the overall functional ordinations (arrows, Fig. 2.2C & D) suggeststhat, with succession, the juvenile community becomes increasingly dominated by evergreen species with greater maximum height and larger seeds. Species with greater maximum height also become increasingly important in the adult community, as well as species with simple leaves, and no ability to fix nitrogen.

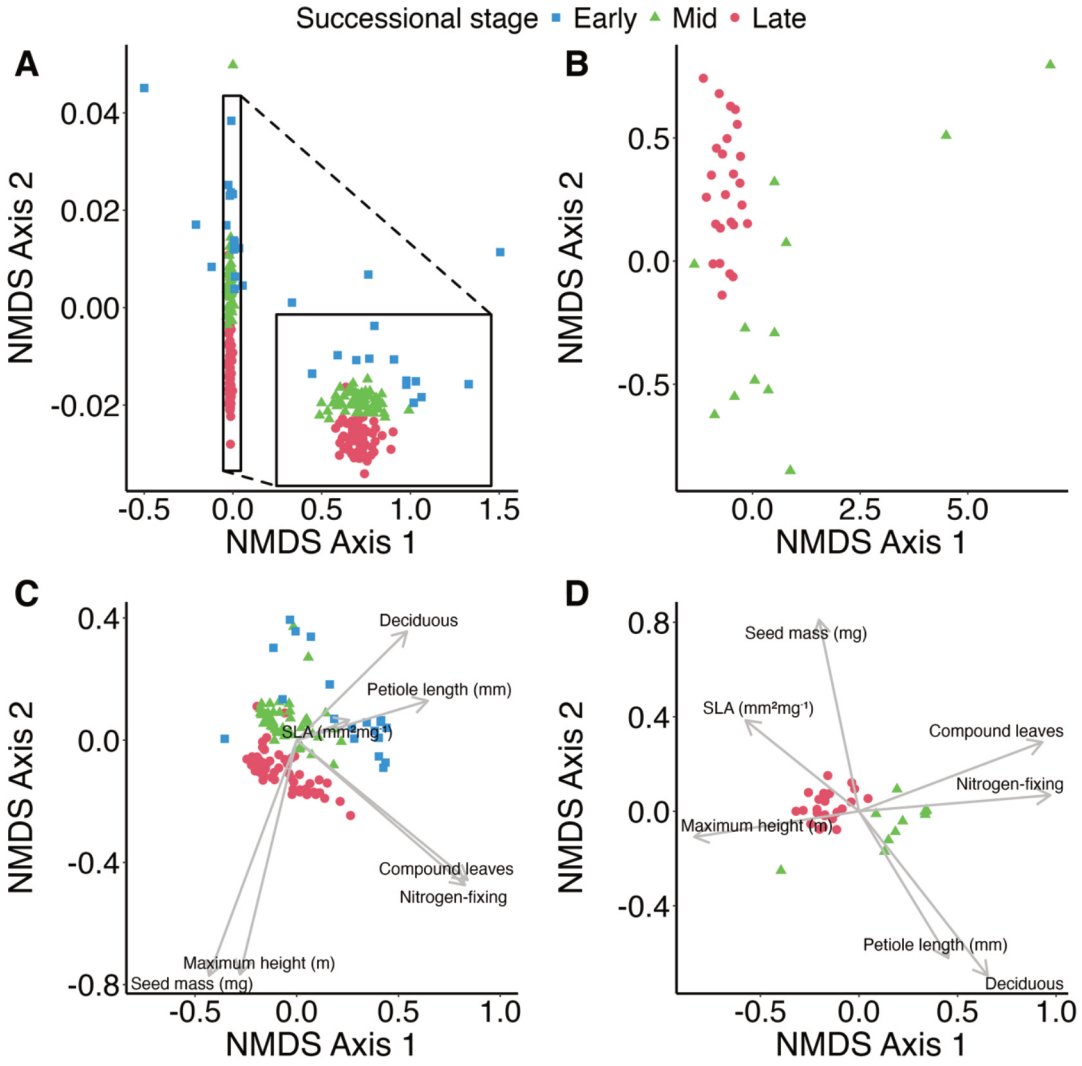


Figure 2.2 The taxonomic (A juveniles; B adults) and functional (C juveniles; D adults) composition of the tree community changed with secondary succession. Non-metric multidimensional scaling (NMDS) of (A & B) species composition based on the Chao dissimilarity index (Chao et al., 2005); (C & D) functional composition based on the Gower dissimilarity index. Stress of the unconstrained ordinations was A = 0.06, B = 0.08, C = 0.11, D = 0.05. Blue squares are early successional quadrats, green triangles are mid-successional quadrats, red circles are late successional quadrats. The cluster of points was magnified in A for clarity. Covariation of individual functional traits with overall functional

dissimilarity is indicated by arrows in C & D, where longer arrows indicate a stronger association.

2.3.3 Juvenile tree community composition appeared to be taxonomically stochastic but functionally deterministic.

There were no clear patterns in the taxonomic composition of plant assemblages over the successional chronosequence. The proportion of individuals in each taxonomic (species) group was significantly diferent between each pair of communities. (Fig. 2.3A). However, when exploring functional groups defined by species' traits, a clear pattern emerged. The juveniles of a plot belonging one successional stage showed diferent functional composition to the adult community preceding them but very similar functional composition to the adult community following them (Fig. 2.3B – D).

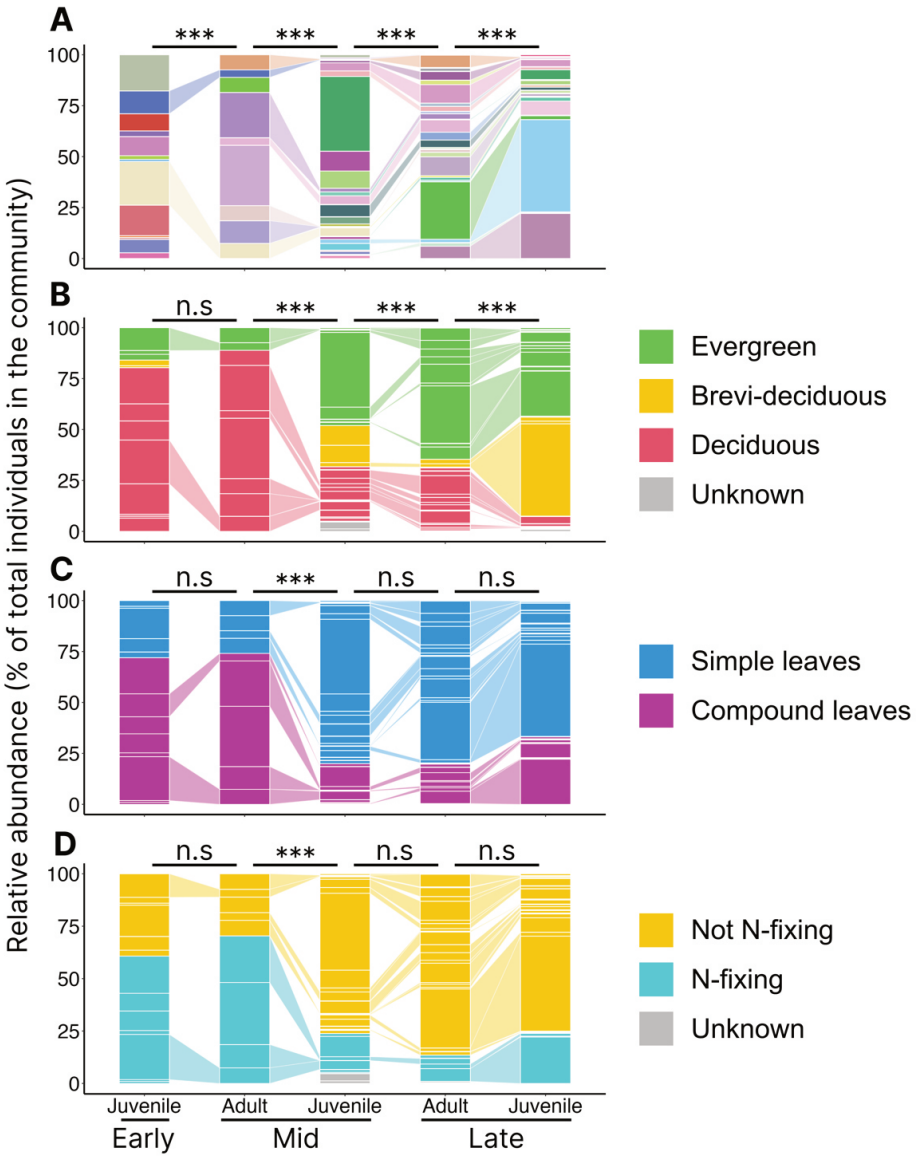


Figure 2.3 Community assembly was (A) taxonomically stochastic but (B – D) functionally deterministic for selected functional traits during secondary succession. Each community contained a diferent number of total individuals, so the relative abundance of each species within each community was calculated to make composition comparable between communities. Species are grouped and coloured by (A) species-level taxonomic identity, (B) leaf phenological habit, (C) leaf type, and (D) biological nitrogen

fixation ability. Within a community (defined by the unique combination of ontogenetic and successional stage), species are separated by white lines, and where the same species is found in two adjacent communities, this is indicated by a flow between them. Fisher's Exact Test was used to test the null hypothesis that the proportion of individuals in each group was the same between the juvenile and adult communities along the successional gradient. Significance of Fisher's Exact Test for each pair of communities is indicated in the figure: $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***.

In ecological trajectory analyses (ETA), both the taxonomic and functional trajectories moved consistently in one direction along the first PCoA axis with succession (Figure 2.4), suggesting a deterministic successional trajectory. The first two PCoA axes captured 77% of the variation in taxonomic composition (Fig. 2.4A) and 92% of the variation in functional composition (Fig. 2.4B). The taxonomic trajectory was composed of three compositional shifts of roughly equal magnitude between the early juvenile, mid adult, mid juvenile and late adult communities (Fig. 2.4A; 33.4%, 30.8% and 29.2% respectively of the total trajectory length). The compositional change between late successional adults and late successional juveniles (the presumed ofspring of those adults) only represented 6.6% of the total trajectory length, reflecting the higher number of shared species between these two communities (Fig. 2.4A). By contrast, the magnitude of the shifts in functional composition varied along the trajectory (Fig. 2.4B). The shift from the early juvenile community to the mid adult community formed only 9.4% of the total trajectory length. In contrast, the shift from the mid adult community to the mid juvenile community represented 43.5% of the total trajectory length. This result for overall functional dissimilarity is consistent with the pattern observed for leaf phenological habit, leaf type and nitrogen fixation ability (Fig. 2.3B-D), whereby adult communities are more functionally similar to the juvenile community preceding them than the juvenile community following them, indicating that the major changes in functional composition occur during recruitment. However, the pattern was not observed later in succession, where the shifts between the mid juvenile community, late

adult community and late juvenile community are of a similar magnitude (23.2% and 23.9% of total trajectory length respectively).

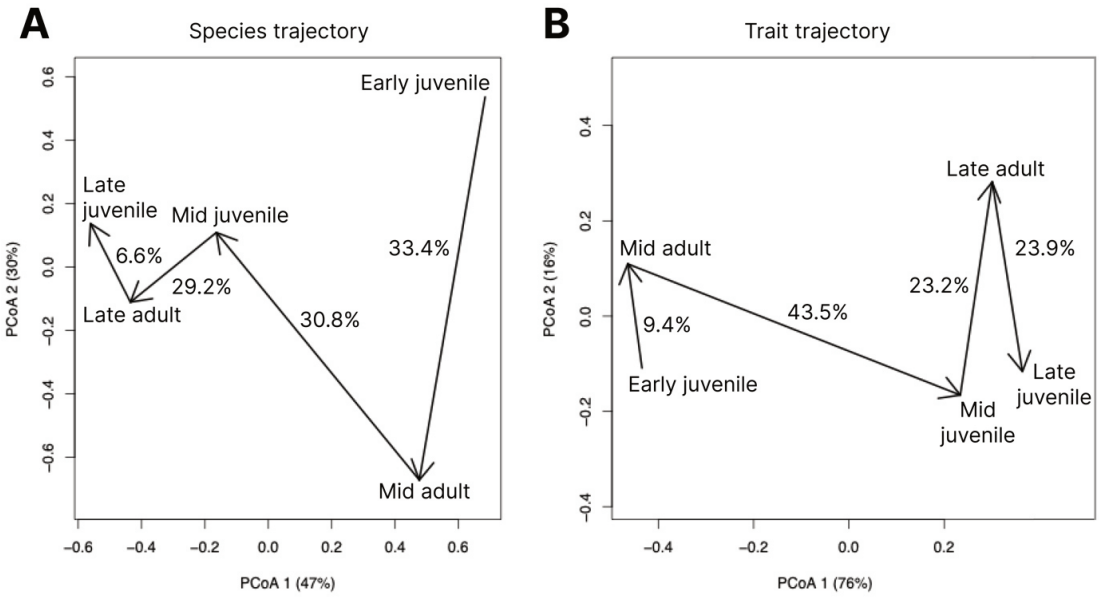


Figure 2.4 Trajectories of (A) taxonomic and (B) functional composition were both directional with succession, but the major shifts in functional composition took place during recruitment. The length of each segment as a percentage of total trajectory length is shown, as taxonomic and functional trajectories were based on Chao and Gower dissimilarity matrices respectively, and as such the lengths are not directly comparable. Communities are ordered by their position within the successional chronosequence: it begins with juveniles in the earliest successional plot (where there are no adults) and ends with the juveniles of the late-successional plots (presumed to be the ofspring of the adults currently growing there).

2.3.4 Plant communities spanned a strong resource availability gradient

Canopy openness was significantly diferent between all successional stages and decreased as succession progressed (Fig. 2.5A). Soil texture and pH did not difer between mid and late succession, but in early succession soil pH (Fig. 2.5B) and sand and silt content

(Fig. 2.5E & G) was higher, while clay content (Fig. 2.5F) was significantly lower. Soil carbon content was higher in late succession than in early or mid succession (Fig. 2.5C) and soil nitrogen content was lower in mid succession than in early or late succession (Fig. 2.5 D).

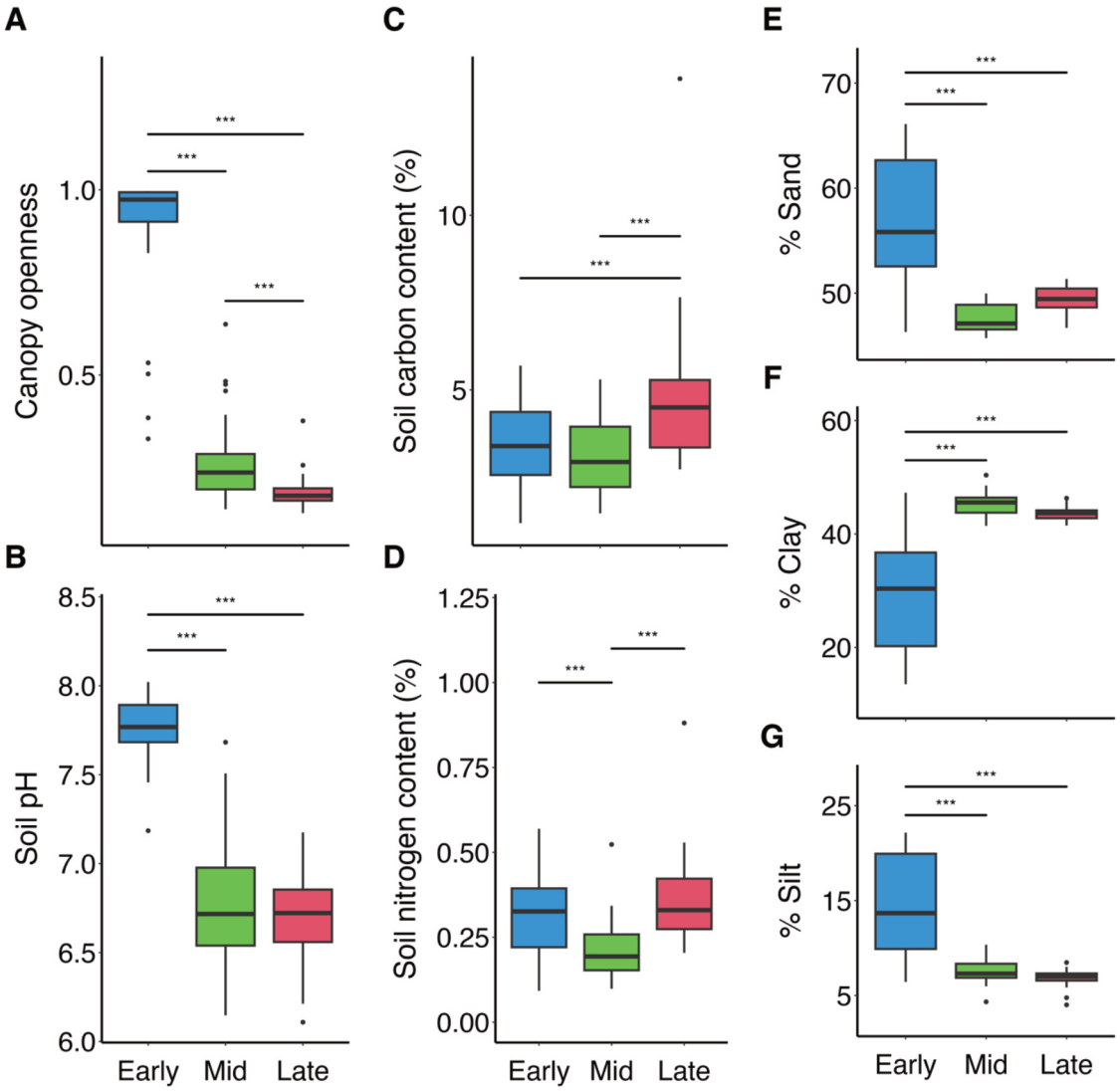


Figure 2.5 Light availability decreased with succession, while water availability was lowest early in succession. All measured abiotic variables difered significantly across the successional gradient (ANOVA: canopy openness $F_{2,159} = 824.30$, $p < 0.001$; pH $F_{2,159} = 303.20$, $p < 0.001$; % carbon $F_{2,159} = 28.51$, $p < 0.001$; % nitrogen $F_{2,159} = 28.51$, $p < 0.001$; % sand $F_{2,48}$

= 28.17, $p < 0.001$; % clay $F_{2,48} = 35.41$, $p < 0.001$; % silt $F_{2,48} = 27.25$, $p < 0.001$). Significance of pairwise comparisons is indicated in figure: $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***.

2.3.5 Changes to functional composition occurring at the stage of juvenile recruitment showed evidence of biotic drivers

The unit of analysis in our analysis of recruitment limitation was the unique combination of species identity and successional stage, i.e., 'Croton arboreus in the early successional plot'. Recruitment limitation was widespread among identified species, and this was consistent across successional stages. For 21 of the 37 cases for which dispersal limitation was calculated, species were significantly more dispersal limited than the null expectation (Table S2.2). In the remaining instances, dispersal limitation did not difer from the null expectation and $\partial_{dispersal}$ limitation was not negative in any instance. Establishment limitation, which was consistently high across species and successional stage (³0.77 across all instances), was significantly greater than expected for 9 of the 22 cases for which it was calculated, and did not difer from the null cases in the remaining instances (Table S2.3).

Surprisingly, variation in $\partial_{dispersal}$ limitation and $\partial_{establishment}$ limitation was not explained by successional stage, selected functional traits, or any interaction between the two (Table S2.4). $\partial_{establishment}$ limitation was influenced by the interaction between seed mass and successional stage, where $\partial_{establishment}$ limitation increased with seed mass in the late successional plot but not in the early or mid successional plots (Fig. S2.1). However, this interaction was not significant when a potential outlier species (Gymnopodium floribundum) was removed and therefore was not considered robust.

In contrast to the weak impacts of functional traits, variation in ∂ recruitment limitation was well-explained by the abundance of conspecifics in the same ontogenetic stage. $\partial_{dispersal}$ limitation was best explained as a quadratic function of log-transformed conspecific seed abundance (Fig. 2.6A; $c^2_{df = 1} = 33.87$, $p < 0.001$), indicating that $\partial_{dispersal}$ limitation peaked at

intermediate conspecific seed abundances. $\partial_{establishment}$ limitation increased linearly with log-transformed conspecific juvenile abundance (Fig. 2.6B; $c^2_{df=1} = 101.85$, $p < 0.001$).

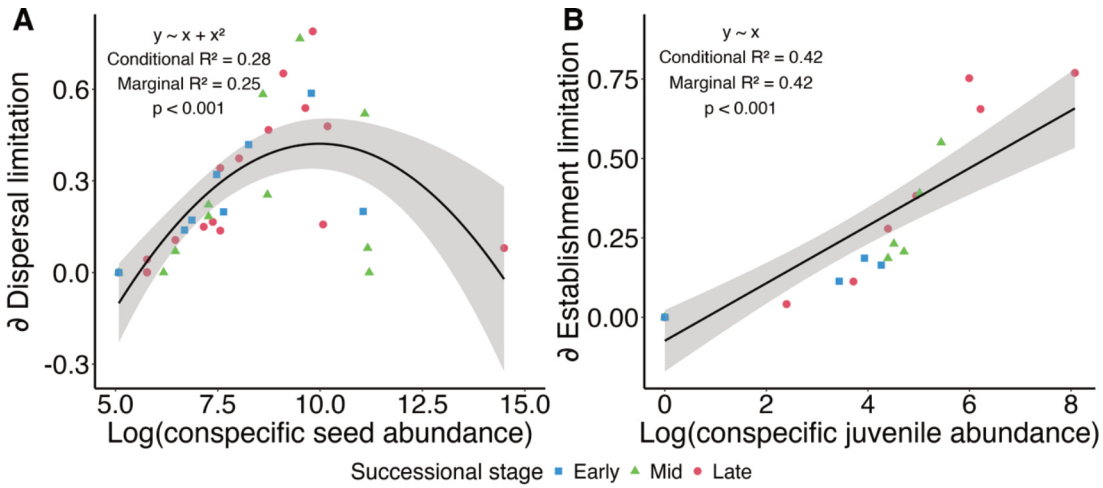


Figure 2.6 ∂ recruitment limitation responded to abundance of conspecifics at the same ontogenetic stage. (A) $\partial_{dispersal}$ limitation increased with conspecific seed abundance up to an abundance of approximately 2,600 seeds per hectare, after which $\partial_{dispersal}$ limitation decreased with increasing conspecific seed abundance. (B) $\partial_{establishment}$ limitation increased linearly with conspecific juvenile abundance. Shaded area indicates 95% confidence interval.

2.4 Discussion

We have demonstrated that the composition of juvenile and adult tree communities changes both taxonomically and functionally with secondary succession. We further explored the assembly processes that have generated these compositional changes and assessed whether the same processes drive the changes in both taxonomic and functional composition. Below, we discuss how both abiotic and density-dependent processes influence plant communities in regenerating tropical dry forest, and how these patterns might shed light on the best ways to restore this vulnerable ecosystem.

2.4.1 Secondary succession was taxonomically stochastic but functionally deterministic

Moving along a successional gradient from a recently abandoned pasture to a >30-year-old forest stand, both juvenile and adult tree communities became markedly more diverse. The taxonomic composition of both juvenile and adult tree communities also exhibited pronounced diferences among plots, and the magnitude of the change in taxonomic composition was roughly equal between each stage in our chronosequence. Despite this high species turnover, we found a clear pattern in functional composition. Early in succession, communities were dominated by deciduous, nitrogen-fixing species with compound leaves, which were replaced throughout succession by simple-leaved evergreen and brevi-deciduous species with large seeds and a high maximum height, consistent with other studies in this forest type (Lohbeck et al., 2015). There was a striking similarity in functional composition between each adult community and the juvenile community in the prior successional stage. This suggests that these adult and juvenile communities, though temporally and spatially distinct, were likely recruited under similar abiotic conditions that deterministically shaped their functional composition. Following a similar logic, Norden et al., (2009b) found that the taxonomic composition of adult trees in old stands of tropical rainforests was similar to that of young trees in secondary forests, which the authors also interpreted as deterministic taxonomic succession. In contrast to the functional similarity we observed between juveniles and adults across plots, the juvenile and adult tree communities within the same plot always exhibited a clearly diferent functional composition. This pattern is consistent with a model of succession in which adult trees modify abiotic conditions, and those conditions deterministically create a diferent functional composition in the juvenile trees that recruit under them (Werden et al., 2020a). These results also suggest that processes acting during the recruitment of juveniles, as opposed to those acting on growth and survival as juveniles become adults, have the greatest impact on the functional trajectory of a regenerating forest stand.

The functional similarity between each adult community and the preceding juvenile community, despite the diferent land use histories of each plot, suggests that deterministic secondary succession can overcome land use legacies. This remains a controversial topic

in the literature; for example, Jakovac et al. (2021) describe several cases in which land use legacies lead to alternative successional pathways that can persist for decades, due to feedbacks between the initial species composition and the abiotic environment it creates. Although we found that the functional composition of the community was largely determined by successional stage, the species identities of individuals in each adult community were mostly diferent from the preceding juvenile community, potentially reflecting ecological contingencies.

The successional pattern we observed – where species composition is variable, yet functional trait composition is predictable – has been found in other ecosystems. For example, Capers et al. (2005) observed taxonomically distinct tree communities in four secondary forests 13 – 26 years post abandonment that did not converge over 5 years of sampling, while the functional composition, in terms of the proportion of trees, shrubs, palms, and lianas, did. We do, however, note an apparent contradiction in our results relating to the level of determinism in taxonomic succession. The taxonomic composition appeared to follow a deterministic ecological trajectory with succession in the ecological trajectory analysis (ETA), despite the taxonomic composition of each community appearing unrelated in Figure 2.3A. The highly multidimensional nature of community data means that such patterns can be dificult to distinguish visually but are revealed by analyses such as ETA that are designed to summarise such data. It remains an open question whether taxonomic composition follows a stochastic trajectory with secondary succession, as found by Capers et al. (2005) and Chazdon et al. (2007), or whether taxonomic composition is also deterministic (Lebrija-Trejos et al., 2010a; Norden et al., 2009b). Nonetheless, our finding of deterministic functional traits assembly along the successional gradient is significant because the functional composition of a forest community is more important for the provision of ecosystem goods and services than the particular taxonomic identity of its components (Cadotte et al., 2011).

2.4.2 Abiotic resource gradients occurred with succession, but abiotic filtering during recruitment was not explained by light or water-related functional traits

The shifts in plant community functional traits across the successional gradient may be driven by the availability of water, light, and soil nutrients, which also change over the course of succession. Direct measurements of the abiotic environment revealed two resource gradients: light availability decreased with succession, while water may be most limited early in succession in this seasonally dry system. We infer a gradient of water availability as the sandier soils found in the early successional plot have higher hydraulic conductivity, meaning water is more easily lost from the soil, and water availability is lower (Suganumaet al., 2018). These results are consistent with previous research in tropical dry forests that have found that the important resource gradient in TDF secondary succession is the increasing availability of water, as opposed to decreasing light availability with succession in wet tropical forests (Borchert, 1994; Lohbeck et al., 2015; Werden et al., 2020a, though the latter identified a more complex relationship between water availability and succession due to interseasonal diferences).

It is important to note that in our study area, successional stage was confounded with intensity of previous land use. This is a common phenomenon across the tropics, as more intensively used lands are presumably more productive and less likely to be abandoned (Chazdon & Guariguata, 2016; Jakovacet al., 2021). Therefore, the abiotic conditions are a product of both successional stage and land use history. As such, several factors may have caused the diference in the state of soil properties: the intensity of previous land use, the impact of successional vegetation, or geological diferences between the plots. Equally, the degree of canopy closure can reflect a balance between previous removal of trees by humans and recovery through secondary succession. It is not possible to distinguish between these factors with the low plot-level replication of this study.

If the changes in functional community composition observed during recruitment of the juvenile community do reflect an abiotic resource gradient, we would expect relevant functional traits to predict changes to recruitment limitation along the resource gradient. Surprisingly, no single functional trait showed a significant interaction with successional stage in any of our models of $\partial_{dispersal}$ or $\partial_{establishment}$ limitation (Table S2.4; see below for exceptions). This was unexpected because such interactions have been found by previous

studies. For example, Werden et al. (2020b) found that establishment limitation was highest in reference forests for small-seeded and early successional species and Muscarella et al. (2013) found a negative relationship between seed mass and $\partial_{establishment}$ limitation but not $\partial_{dispersal}$ limitation. We also found that $\partial_{establishment}$ limitation increased with seed mass only in the late successional plot (Table S2.4), but that this relationship was dependant on one species (Gymnopodium floribundum) and the interaction disappeared when it was removed. Such interactions suggest that the relationship between seed size, successional stage and ∂ recruitment limitation is context-specific, and further investigation would be required to determine when ∂recruitment limitation is predictable.

The apparent contradiction between the recruitment limitation analysis (which suggests limited importance of species' traits) and our other results (which suggest abiotic filtering based on traits) may be related to the scale of the analysis. While our plot-level measurements indicate a gradient of abiotic conditions with succession that determined the functional composition of the recruited community at the hectare scale, the recruitment limitation analysis instead focused on the spatial dynamics of recruitment within a plot. It is possible that there was not enough variation in abiotic conditions within each plot to afect recruitment limitation dynamics at this scale. Indeed, many studies have found that habitat filtering only emerges at larger spatial scales that encompass more environmental heterogeneity (Chase, 2014; Davies et al., 2005; Gómez-Aparicio et al., 2005; Nishizawa et al., 2022; Townsend et al., 2008 but see Götzenberger et al., 2012; Lundholm, 2009). At our study site, functional shifts from deciduous nitrogen-fixers to evergreen species occurred along the landscape-scale successional gradient, supporting the hypothesis that resource availability shaped trait distributions at this scale. For example, legumes are likely very abundant in early successional TDF because their small leaflets and high tissue nitrogen content enable them to tolerate drought stress (Gei et al., 2018). In our system this was most pronounced in the recently abandoned pasture. Thus, our recruitment limitation analyses reiterate the finding that community assembly was relatively predictable at the functional guild level and at large spatial grains, but more stochastic at the individual species level and at smaller spatial scales.

2.4.3 Evidence for density-dependent processes as drivers of community assembly during succession

We found the level of ∂ recruitment limitation was significantly predicted by the abundance of conspecifics in the same ontogenetic stage. The increase in $\partial_{establishment}$ limitation with increasing conspecific juvenile abundance suggests conspecific negative density dependence (CNDD) is acting during establishment, consistent with the finding that seedling mortality is higher in sites with high conspecific seedling density (Norden et al., 2009a). Similarly, $\partial_{dispersal}$ limitation peaked with conspecific seed abundance of approximately 2,600 seeds per hectare, after which it appeared to decrease. It is unclear why seed abundance would afect the spatial distribution of seed dispersal in this way. One potential explanation is that the more abundant seeds are those that have a mother tree in the plot, so dispersal was highly spatially clustered around the mother tree. We did not survey all adult trees in the plot, so it was not possible to test this hypothesis. It is interesting that these relationships between conspecific abundance and recruitment limitation held for all successional stages, as previous studies have suggested that the strength of CNDD may either decrease (Wang et al., 2016) or increase (Kulikowski et al., 2022) with succession. CNDD is dependent on the biotic neighbourhood of individuals (Comita & Hubbell, 2009), and its importance for within-plot recruitment limitation dynamics is consistent with the argument that biotic processes play a greater role in community assembly at smaller spatial scales. We have therefore found that both abiotic and biotic processes were important during the assembly of recruiting tree communities, but that the spatial scale of the analysis may determine which is given more weight.

CNDD processes may have a greater impact on taxonomic community composition, while habitat filtering is more closely linked to functional community composition. Schweizer et al. (2013) found that whether a neighbouring adult was a conspecific or not was the main predictor of seedling growth and survival, while the degree of phylogenetic relatedness of the heterospecific neighbour did not otherwise have a significant efect. The authors predicted that closely related species would also cause negative density dependence (NDD) due to phylogenetic conservatism of traits and natural enemies, but did not find this.

Furthermore, Sorensen, (2006) found that the level of NDD experienced by seedlings was not related to their functional trait grouping (based on shade tolerance). CNDD may therefore act in a trait-blind way to prevent any one species from excluding all others (but see Zhu et al. (2018) for an interaction between CNDD and functional traits), leading to the stochastic taxonomic turnover at small within-plot spatial scales, while the species pool at the plot level is determined by abiotic conditions, leading to the functional determinism we observed at the larger spatial scale.

2.4.4 Implications for restoration practitioners

Our results have implications for the management of forest restoration projects in tropical dry forest ecosystems. Many projects define a target state by its taxonomic composition, often based on a reference forest. However, natural secondary succession can follow multiple successional trajectories in terms of taxonomic community composition, and the chosen reference forest represents just one possible outcome of that process (Norden et al., 2015; Rodrigues et al., 2011). Our results indicate that functional composition is more deterministic during secondary succession and we therefore concur with Brancalion & Holl (2016) in suggesting that the functional composition of old-growth forests may represent a more appropriate target state for restoration projects than species composition.

Our results also suggest a potential method of achieving such a target. The functional composition of the adult tree community appeared to be mostly determined by processes acting during recruitment of the juvenile community, so management activities are likely to be most efective if implemented at the dispersal and establishment stages of community assembly. Such actions could include, for example, planting trees with large fleshy fruit to attract the animal dispersers of zoochorous species, or planting nurse trees to create a suitable microclimate for the seedlings and saplings of target species. Consistent with these arguments, both Li et al. (2018) and Werden et al. (2022b) found that active restoration interventions such as tree planting accelerated the recovery of functional diversity in recruiting tree communities. Li et al. (2018) further demonstrated taxonomic stochasticity in that the taxonomic composition of recruits was not related to the taxonomic composition of

the planted trees, indicating that recruits grew from seeds in the soil seed bank or dispersed from mother trees outside of planted plots. In other words, rather than attempting to recreate mature or "climax" tree communities by directly planting late successional species, our data and that of Li et al. (2018) and Werden et al. (2022b) suggest that restoration practitioners should focus on facilitating the natural processes that drive the early stages of TDF succession.

2.5 Conclusions

Our results demonstrated that secondary succession in a tropical dry forest ecosystem has created successional communities with a predictable functional composition through deterministic community assembly processes that took place during recruitment. While land use history may lead to diferences in secondary forests in terms of their taxonomic composition, we argue that the reassembly of functional community composition without further human intervention is promising for the recovery of ecological functions and processes. We have also highlighted that abiotic filtering was an important determinant of functional composition at a landscape scale, while biotic assembly processes played a greater role at smaller spatial scales. Therefore, practitioners and land managers should aim to promote both types of diversity-generating processes within restoration projects.

Chapter 3: The role of small-scale environmental heterogeneityin the restoration of tropical dry forests

3.1 Introduction

Large-scale forest restoration targets have been set at regional, national and international levels (e.g., the Bonn Challenge, https://www.bonnchallenge.org/) to mitigate land degradation, biodiversity loss and climate change. Achieving these goals requires restored forests to have both longevity and resilience over multiple centuries (Mackey et al., 2013; Mori et al., 2017), which depends on the successful recruitment of a diverse tree seedling community following diferent restoration interventions (Holl et al., 2017; Oliveira et al., 2019; Trevor Caughlin et al., 2019). Tree diversity is often associated with improved ecosystem multifunctionality, productivity and resilience (Lohbeck et al., 2016; Messier et al., 2019, 2021; Rodrigues et al., 2011; Steur et al., 2020). It has been suggested that one potential way to increase the diversity of tree seedling recruitment during forest restoration is through the promotion of environmental heterogeneity (Helbach et al., 2022; Holl et al., 2013, 2022). Thehypothesis that plant diversity is increased by environmental heterogeneity has its roots in well-established ecological concepts, including niche and coexistence theory, but the empirical evidence is mixed and very few projects to date have attempted to leverageenvironmental heterogeneity in forest restoration.

3.1.1 Why does theory predict positive heterogeneity-diversity relationships (HDRs)?

Environmental heterogeneity refers here to spatial variation in the abiotic environment. Based on the classical theory of species coexistence (Chesson, 2000), Hutchinson (1957) proposed that an increase in the niche space hypervolume (either an increased number or length of niche axes) will increase the number of species that can coexist (Ben-Hur & Kadmon, 2020; Stein et al., 2014). In other words, environmental heterogeneity is expected to increase species richness by increasing the number of available niches for species to sort

into (Lundholm, 2009; Wilson, 2000), creating a positive heterogeneity-diversity relationship (HDR).

When assessing whether an HDR exists, the impacts of heterogeneity must be separated from those of mean resource availability (i.e., resource levels integrated over the discrete patches that generate heterogeneity). The average quantity of a given resource available for plant uptake can itself impact diversity via several mechanisms. Firstly, some species are better able to exploit resources when they are supplied in excess, leading to competitive exclusion and reducing diversity (Balvanera & Aguirre, 2006). Second, increasing resource availability has been shown to increase species richness entirely through the increase in the number of stems that can be supported (the "density efect" sensu Denslow, 1995). A consensus is beginning to form around a hump-shaped relationship between resource availability and diversity (Reich et al., 2012) that arises from the density efect at lower absolute resource levels and competitive exclusion at higher absolute resource levels (Balvanera & Aguirre, 2006). However, it is unclear what relationship would be expected when stem number (i.e., plant density) is controlled for. These findings suggest that both the mean availability of resources and their spatial variation can afect species diversity, so empirical tests of HDRs must separate the two mechanisms.

3.1.2 Empirical evidence for and against HDRs

In a review and meta-analysis of the evidence for and against HDRs in plant communities, Lundholm (2009) found that positive HDRs were often found in observational studies but not in experimental studies, and that most studies of HDRs have been done in grasslands. Plants utilise a limited number of resources (water, soil nutrients, light and space), so some authors have questioned whether these resources could be partitioned into suficient discrete niches to support the high plant diversity of ecosystems like tropical forests (Helbach et al., 2022; Huston, 1979; Silvertown, 2004). In our study we focus on two of these resources: soil and light.

Many studies have described significant soil-plant associations that can be interpreted as species sorting along edaphic gradients (Condit et al., 2013; John et al., 2007; Peña-Claros

et al., 2012; Powers et al., 2009; Sorensen, 2006; Werden et al., 2018b), which is a possible driver of the HDR. In contrast, experimental manipulations of soil heterogeneity have had positive (Baer et al., 2020; Gundale et al., 2006; Williams & Houseman, 2014), neutral (Gazol et al., 2013; Reynolds et al., 2007), and negative (Baer et al., 2004, 2005; Gazol et al., 2013) impacts on plant diversity. Positive relationships are found more frequently at large spatial scales (Davies et al., 2005; Lundholm, 2009; Powers et al., 2009), though soil can show a high amount of variation even at very small spatial scales (Waring et al., 2016, 2021), so small-scale soil-plant HDRs are plausible.

The evidence for an efect of light heterogeneity on plant diversity is weaker. Many studies have found that diferent plant species cannot partition gradients of light availability (Beckage & Clark, 2003; Brokaw & Busing, 2000; Dalling & Hubbell, 2002; Denslow & Guzman G., 2000) and in one study where light heterogeneity was experimentally induced, it did not increase recruit diversity (Holl et al., 2013). It has been suggested that partitioning of light gradients is possible if relative species performance rankings change (Kobe, 1999), but this mechanism has only been empirically demonstrated for guilds segregating over a very broad light gradient (Balderrama & Chazdon, 2005; Clark et al., 1993; Kobe, 1999; Markesteijn et al., 2007; though see Sorensen (2006) for within-guild segregation). Furthermore, in dry tropical forests, deciduous tree species lose their leaves during the dry season, so most recruits need to be able to survive in a wide range of light levels (Ceccon et al., 2003), further reducing the plausibility of species sorting based on light levels.

Four explanations have been suggested for the failure of many studies to detect an HDR. Firstly, an HDR requires that all species are able to reach all available patches (Lundholm, 2009), so dispersal limitation can preclude an HDR. This mechanism has been invoked by Holl et al. (2013) to explain the lack of HDRs early in tropical forest succession. Secondly, mass efects can maintain populations of a species in unsuitable sites through continued dispersal from a source population (Lundholm, 2009). Thirdly, it has been suggested by multiple authors that experimental manipulations of environmental heterogeneity may not be experienced as heterogeneous by the focal organism, either because the wrong resources have been manipulated, the environmental gradient created is not extensive

enough, or the scale of the patches created is not suitable (Baer et al., 2016; Williams & Houseman, 2014). Finally, it has been widely agreed that spatial scale is crucially important for HDRs, and at very small scales stochastic demographic processes such as ecological drift may obscure HDRs (Nishizawa et al., 2022). It is therefore important to carefully consider the appropriate spatial scale (or scales) at which environmental heterogeneity should be promoted in forest restoration.

3.1.3 The role of HDRs and beta diversity in forest restoration

It is critical to accurately assess the importance of HDRs in maintaining plant diversity, as land use and land use intensity alter the magnitude and spatial scale of soil and light variation (Nicotra et al., 1999; Powers, 2006). It has been suggested that forest restoration activities may in fact risk reducing the environmental heterogeneity of landscapes due to similarities in the species planted and interventions implemented at different sites (biotic homogenisation, sensu Holl et al., 2022). This would result in reductions in beta diversity. Beta diversity has two distinct components that can occur simultaneously and/or independently (Graco-Roza et al., 2021). The first, species turnover, refers to changes in species composition from site to site. This component of beta diversity is expected to arise under the HDR hypothesis, as species sort into the different niches created by environmental conditions in each patch. The second, nestedness, refers to beta diversity that arises through changes in species richness, where the species in one patch are a subset of the species in another patch. At landscape scales, beta diversity may be increased by promoting large-scale environmental heterogeneity through landscape-wide land use planning that allows multiple land uses and forest management approaches to coexist, an approach known as Forest Landscape Restoration (FLR; Sayer et al., 2013).

While the concept of beta diversity is generally applied to landscapes or regions, it is also useful for assessing the possibility of leveraging HDR theory at smaller spatial scales (Balvanera et al., 2002). Restoration sites often lack small-scale environmental heterogeneity due to previous homogenising disturbances (Holl et al., 2022; Robertson et al., 1993) and even-aged stands of planted trees may not be effective at recovering small-

scale heterogeneity (Oliveira et al., 2019). At these scales, the promotion of site-level recruit alpha diversity by increasing environmental heterogeneity would also be expected to increase within-site species turnover and nestedness (i.e., beta diversity) if species sort into smaller within-site patches defined by, for example, high soil nutrient availability or a canopy gap. Few practitioners have explicitly attempted to manipulate small-scale environmental heterogeneity to increase tree recruit diversity in their forest restoration projects. One exception to this is Holl et al. (2013), who attempted to increase environmental heterogeneity by planting trees in clusters (the applied nucleation method). This successfully increased variation in canopy openness and soil base saturation, but did not increase the richness of tree recruits over that of a conventional spatially uniform planting design. Alternatively, many authors have advocated for a high number of native tree species to be included in traditional restoration plantations (Messier et al., 2021; Rodrigues et al., 2011), sometimes explicitly invoking the impact this is expected to have on environmental heterogeneity in the understorey and therefore recruit diversity (de la Peña-Domene et al., 2013). Finally, it has also been suggested that heterogeneity can be better achieved by allowing natural forest regeneration, as the stochastic assembly processes of secondary succession create spatial and temporal heterogeneity (Chazdon & Guariguata, 2016).

We used two restoration interventions implemented across a mosaic tropical dry forest landscape to address three questions: 1) How does the type of restoration intervention (conventional tree plantation versus natural regeneration) impact the recovery of small-scale environmental heterogeneity? We expected natural regeneration to generate more environmental heterogeneity than tree plantations due to the greater influence of stochastic processes (Chazdon & Guariguata, 2016). 2) Does small-scale environmental heterogeneity increase tree recruit diversity at the restoration plot level? We predicted that small-scale soil heterogeneity would have a positive relationship with the diversity of tree recruits, as the magnitude of variation in soil variables can be large even at small spatial scales (Waring et al., 2016, 2021), but that light heterogeneity would not, as light patches are transient (Ceccon et al., 2003). 3) Does large-scale environmental heterogeneity increase tree recruit diversity at the landscape level? We predicted that the implementation of a range of

restoration interventions across the landscape would increase compositional turnover among recruited tree communities, and therefore result in higher landscape-level beta diversity (Holl et al., 2022).

3.2 Methods

3.2.1 Study site

The study was conducted in a tropical dry forest landscape adjacent to the Calakmul Biosphere Reserve in Campeche, Mexico (18°40'46.2"N, 90°08'24.4"W), described in detail in section 1.5 (Main introduction).

The site covers an area of approximately 1,800 hectares (ha) and has been used for large-scale forest restoration by Plant-for-the-Planet Mexico A.C. since 2021. The landscape is a mosaic of areas historically used to graze cattle that have either 1) been left to regenerate naturally without any intervention (hereafter 'natural regeneration') or 2) have been subject to assisted recovery in the form of planting native tree species (hereafter 'planted'). Restoration interventions have not been randomly applied to the landscape due to the practical considerations of restoration practice; natural regeneration was more likely to be applied to areas that had been used less intensively and that had more remnant vegetation, while the plantation approach was more likely to be applied to intensively used areas. All areas are naturally short-statured semi-evergreen forest (selva baja inundable) growing on Vertisols with high clay content, which swells during the rainy season, resulting in flooding (Werden et al., 2018a). We used a stratified random approach to place a roughly equal number of plots (planted N = 6, natural regeneration N = 7) at random locations within each restoration intervention.

To select reference forest sites, we used historical satellite imagery to identify areas of forest that had continuous closed canopy cover for at least 30 years. In a study in the adjacent Calakmul Biosphere Reserve, the largest protected tropical area in Mexico, adult tree species richness in "primary" forest was reported as 211 – 244 species ha^{-1} (Bohn et al., 2014). In our "reference" site we reported 270 species ha^{-1} from surveys of juvenile trees and

120 species ha^{-1} from surveys of adult trees (Gee et al., 2025; all aforementioned values assume a linear species-area relationship; Bohn et al. censused 900 m^2 and we censused 2500 m^2). Our reference forest also hosted species such as Manilkara zapota, which was identified as typical of primary forest in Bohn et al. (2014). We therefore considered the identified forests to be appropriate reference sites for this landscape, though we acknowledge that both the undisturbed forests in our study site and the "primary" forest in Calakmul Biosphere Reserve likely have a history of Ancient Mayan influence (Sorensen, 2006). Plots were also placed at random locations within these reference forests (N = 7).

Plot age was defined as time since abandonment for the natural regeneration plots, and time since planting for the planted plots. Time since abandonment was estimated from Google Earth historical satellite imagery and verified by field staf at Plant-for-the-Planet México. Time since planting was sourced from data kept by restoration mangers at Plant-for-the-Planet México. The mean age of natural regeneration plots was 4.6 years (range 2.0 – 5.7), while the mean age of planted plots was 1 year (0.2 – 1.5; Table S3.1).

3.2.2 Vegetation survey design

All data was collected during two dry season survey periods in March – April 2022 and January – March 2023.

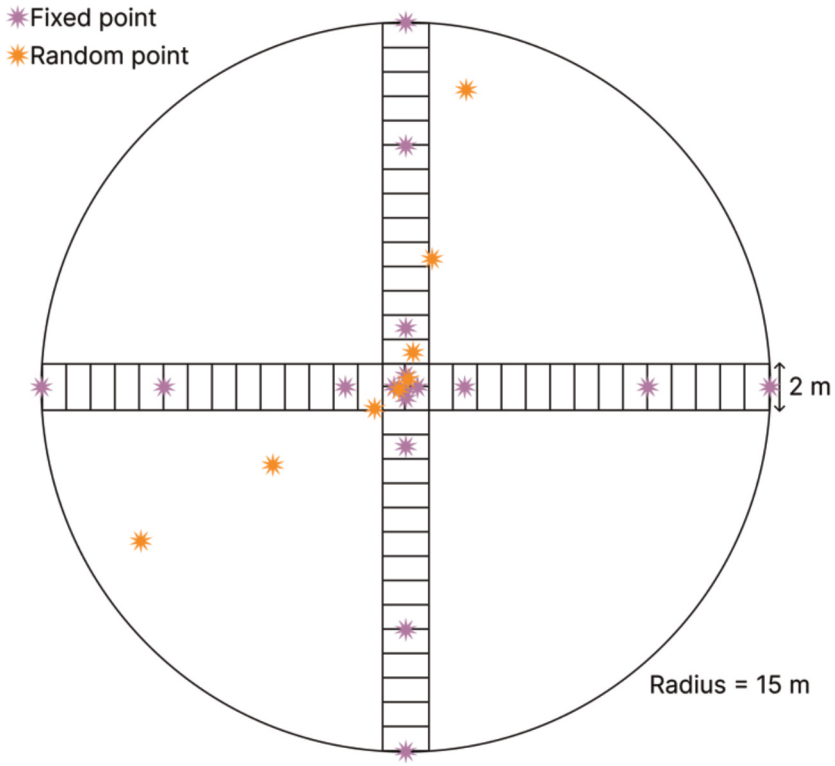


Figure 3.1 Design of one large circular plot. Tree recruits were surveyed in quadrats, indicated by rectangles. Sampling points for environmental variables are indicated by stars; 17 points along the four cardinal directions were fixed and consistent across plots, 8 points were along bearings that were randomly generated for each plot.

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20 circular plots (radius = 15 m) were established across the landscape, at a minimum distance of 15 m from one another (median pairwise distance was 1.81 km). Each plot contained four 15 m ´2 m transects, and each transect was divided up into fifteen 1 m ´2 m quadrats which were the units of analysis for seedling diversity surveys. Each plot also contained 25 samplingpoints at defined distances alongthe four cardinal directions and two random bearings (Fig. 3.1), at which environmental parameters were measured to estimate

their mean and variance within the plot. The plots were designed to allow us to investigate diversity and environmental heterogeneity at two spatial scales: small-scale (< 30 m; between quadrats, N = 1,200, and between sampling points, N = 500) and large-scale (0.5 – 6 km; between plots, N = 20).

The tree recruit community was surveyed along the four 15 m transects in the four cardinal directions from the centre of each plot. Four plots did not contain any recruits and so could not be included in analyses of species richness and composition. As described above, each transect was separated into 1 m increments to give fifteen 1 ´2 m quadrats per transect with a known bearing and distance from the plot centre. Within each quadrat, we censused all woody plants 1 – 200 cm in height, surveying 16,855 recruits in total. In this ecosystem we were able to identify most of the very small recruits (< 5 cm) as the dominant species had distinctive leaves from germination (36 very small individuals that could not be identified or assigned to morphospecies were removed from the analysis). Individuals were identified to species in the field. Where identification in the field was not possible, leaves and stems were saved in a plant press and identified after the census using published local guides. We identified 4 liana species, 1 palm species, and 71 tree species, but henceforth refer to all woody plants as "trees" for brevity. Where species could not be identified they were given a unique morphospecies identity. This included 23 unidentified morphospecies (159 individuals), which made up 0.9% of all individuals. Morphospecies were included in all analyses. We repeated the analyses with unidentified morphospecies removed, which did not afect any of our conclusions. In all cases, taxonomic names follow the World Flora Online (WFO) Plant List as of 20/11/2024.

Importantly, in the planted plots we only censused natural recruits, and did not include the trees that had been planted. The diversity and composition of planted trees in these plots is entirely determined by restoration managers and is not expected to respond to environmental heterogeneity.

3.2.3 Environmental variables

In each plot, soil samples and hemispherical photos were taken at the 25 sampling points (17 fixed points at 0.5, 2.5, 10 and 15 m along the transects, and 8 points at 0.25, 1.5, 6 and 12.5 m along two random bearings). At each sampling point we took a 360° hemispherical photosphere using the Google Street View app (Google LLC) and a smartphone camera on a 1 m high tripod. Raw canopy photos were processed using the Python-3 and scikit-image tool Cano.py (Waring et al., 2024) to calculate percent canopy openness. In brief, images were converted to hemispherical through polar projection, then automatically binarised with a threshold of 0.8. To ensure the binarisation step was completed correctly, we checked each image for clouds that were misclassified as canopy and manually brightened them. Canopy openness is the area of the sky hemisphere that is not canopy and was calculated following ter Steege (2018).

We also took 3 soil cores to 15 cm depth as close as possible to each sampling point and combined the three cores into one sample. Soil samples were air-dried and sieved (2 mm). Soil pH was measured on a 1:5 solution of soil: deionised water using a Hanna HI5222 bench pH meter. Soil samples were then ground to fine powder, acidified with addition of 6% H_2SO_3 to remove carbonates, oven-dried at 65°C, and analysed for total organic carbon and nitrogen content (%) on a ThermoFlash EA1112 Elemental Analyser.

3.2.4 Statistical analysis

All statistical analysis was done using R version 4.2.3 (R Core Team, 2023) and the vegan package (Oksanen et al., 2024) was used for all analyses unless otherwise noted. For ease of reference, Table 3.1 defines the terms used in our statistical analyses.

Term	Definition	Analyses
Small-scale heterogeneity	Heterogeneity within a large circular plot (radius = 15 m). Each quadrat (seedling survey) or sampling point (environmental survey) is considered a 'patch'.	Mean and CV of environmental variables, partial regressions, small-

		scale (partial) Mantel tests and PERMANOVA
Large-scale heterogeneity	Heterogeneity across the study landscape (~ 3 ´6 km). At this scale, each large circular plot represents a 'patch'.	Large scale (partial) Mantel tests and PERMANOVA
Incidence-based Coverage Estimator (ICE)	A metric of alpha diversity which uses the incidences of infrequent species to predict species richness. It is therefore highly sensitive to the presence of rare species.	Partial regressions
Community dissimilarity	A measure of the species turnover component of beta diversity; nestedness is the other component. Calculated as Bray-Curtis dissimilarity between communities of tree recruits. This metric is less sensitive to the presence of rare speciesbecause shared common species contribute more to compositional similarity.	(Partial) Mantel tests, PERMANOVA and variance partitioning

Table 3.1 Definitions of terms used in Chapter 3.

3.2.4.1 Does restoration intervention impact the level of small-scale environmental heterogeneity?

To find the magnitude ofsmall-scale (i.e.,within-plot)heterogeneity, we calculated the mean and coeficient of variation (CV) for canopy openness and soil variables for each plot. We modelled the mean and CV of each environmental variable as a linear function of intervention type and plot age. We took this approach (rather than comparing treatment-level means) because restoration treatment is confounded with plot age, as natural regeneration plots were 2 – 6 years old, while planted plots were 0 – 2 years old (Table S3.1). We then performed Type III ANOVAon these models to account for the non-independence of the two explanatory variables (car package; Fox et al., 2024). Reference forests were not

included in this analysis as their age is unknown, but their mean and CV is included in Figure 3.2 for comparison. Diagnostic plots were inspected to check that model assumptions (normality of residuals and homogeneity of variance) were met.

3.2.4.2 Does small-scale environmental heterogeneity increase recruit diversity at the plot level?

We used two diferent measures of diversity that are diferentially sensitive to rare species to explore how patterns of small-scale alpha and beta diversity are driven by species turnover and nestedness (Table 3.1). As a metric of species richness (alpha diversity) we used the Incidence-based Coverage Estimator (ICE) as recommended by Chazdon et al. (1998) for seedling communities in tropical forests. Species richness metrics are highly sensitive to rare species, as all species contribute equally to species richness regardless of their abundance, and the ICE metric is particularly sensitive to the incidence of rare species, which it weighs more strongly in its estimation of species richness. Species turnover (one component of beta diversity) was measured as community dissimilarity, calculated using the Bray-Curtis dissimilarity index (Bray & Curtis, 1957). This index is less sensitive to rare species than more modern indices (e.g., the Chao dissimilarity index; Chao et al., 2005), but we chose to use Bray-Curtis to emphasise the diference between the species richness and compositional dissimilarity indices, thereby exploring the efect that rare species have on the diversity patterns observed.

We tested for HDRs by modelling plot-level ICE (alpha diversity) as a function of the plot-level CV of environmental variables. Stem number has a known efect on species richness (the "density efect" sensu Denslow, 1995), so we corrected for this by including plot-level stem number as a covariate in the models (full model: ICE ~ variable CV + stem number). Mean plot-level stem number was 216.67 in the planted plots (range: 27 – 329), 441.0 (69 – 677) in the natural regeneration plots and 2139.67 (768 – 3252) in the reference plots. In all cases, adding stem number improved the model performance (indicated by AIC). Previous studies have suggested that mean resource levels also impact species richness (Balvanera & Aguirre, 2006; Lundholm, 2009) and can be confounding with resource CV, so we also

modelled ICE as a function of mean plot-level values of environmental values, both independently and in combination with the CV, again correcting for stem number (ICE ~ variable mean + stem number; ICE ~ variable mean + variable CV + stem number). We used partial regression plots to visualise the relationships between ICE and the CV and mean of environmental variables, correcting for stem number by plotting the residuals of each variable following independent regressions against stem number (Balvanera & Aguirre, 2006). We found the percentage of the variance in ICE explained by each explanatory variable by calculating a Type-II analysis of variance table for the model and calculating the sum of squares (SSQ) of the explanatory variable as a percentage of the total SSQ.

We then tested for relationships between small-scale environmental heterogeneity and between-quadrat species turnover (small-scale beta diversity). We performed partial Mantel tests to see whether distance decay of Bray-Curtis dissimilarity within plots (between quadrats) was correlated with environmental distance after correcting for spatial autocorrelation (Legendre & Fortin, 1989). The environmental distance matrix was calculated using both Euclidean and Manhattan distances, which produced qualitatively identical results, so results using Euclidean distance are reported. A separate partial Mantel test was run for each plot, so p-values were Bonferroni corrected to account for the inflated Type I error risk. We performed the partial Mantel tests using an environmental distance matrix constructed using all environmental variables together, as well as separate tests for canopy openness and soil variables to explore the importance of above- and below-ground heterogeneity separately.

We also performed PERMANOVA on the Bray-Curtis dissimilarity matrix for all quadrats to test whether quadrat-level environmental conditions directly predicted community composition in that quadrat. Permutations were restricted to within-plots, to test whether between-quadrat variability in environmental conditions at these small spatial scales explained community composition. Then, we tested whether quadrat-level environmental variables predicted quadrat-level species richness. All stems in a quadrat were recorded, so there is no need to estimate quadrat-level richness with ICE. For all quadrats that also

contained a sampling point (N = 194), we modelled species richness as a function of quadrat-level values for all environmental variables.

3.2.4.3 Does large-scale heterogeneity increase recruit diversity at the landscape level?

To test whether compositional dissimilarity (the species turnover component of large-scale beta diversity) between plots (N = 16) was correlated with environmental dissimilarity between plots, we performed another partial Mantel test. Community composition data within each plot was pooled before calculating the Bray-Curtis dissimilarity matrix. We tested whether this dissimilarity matrix was correlated with the distance matrix for mean environmental variables of each plot after correcting for spatial autocorrelation. We again performed the partial Mantel tests using an environmental distance matrix constructed using all environmental variables together, as well as separate tests for canopy openness and soil variables. We also repeated the PERMANOVA, but restricted permutations to within-intervention type (allowing between-plot permutations), to test whether the combination of between-quadrat and between-plot variability in environmental variables explained community composition.

Finally, we explored how much of the variation in community composition and environmental variables occurred within-plots, between-plots or between-intervention types. We used nested ANOVA to partition the variance in community composition and environmental variables into these hierarchical nested scales. For environmental variables, the proportion of variance explained by intervention type, plot and residual variance was found by dividing the sum of squares for each scale by the total sum of squares. For community composition, we performed two (partial) constrained ordinations on the data. To find the variance explained by intervention type we constrained by type. To find the variance explained by plot we constrained by plot and conditioned by type to remove its efect. The proportion of variance explained by each scale was calculated as the sum of eigenvalues for the ordination constrained by that scale, divided by the sum of all eigenvalues.

3.3 Results

3.3.1 How does restoration intervention (tree planting versus natural regeneration) impact the level of small-scale environmental heterogeneity?

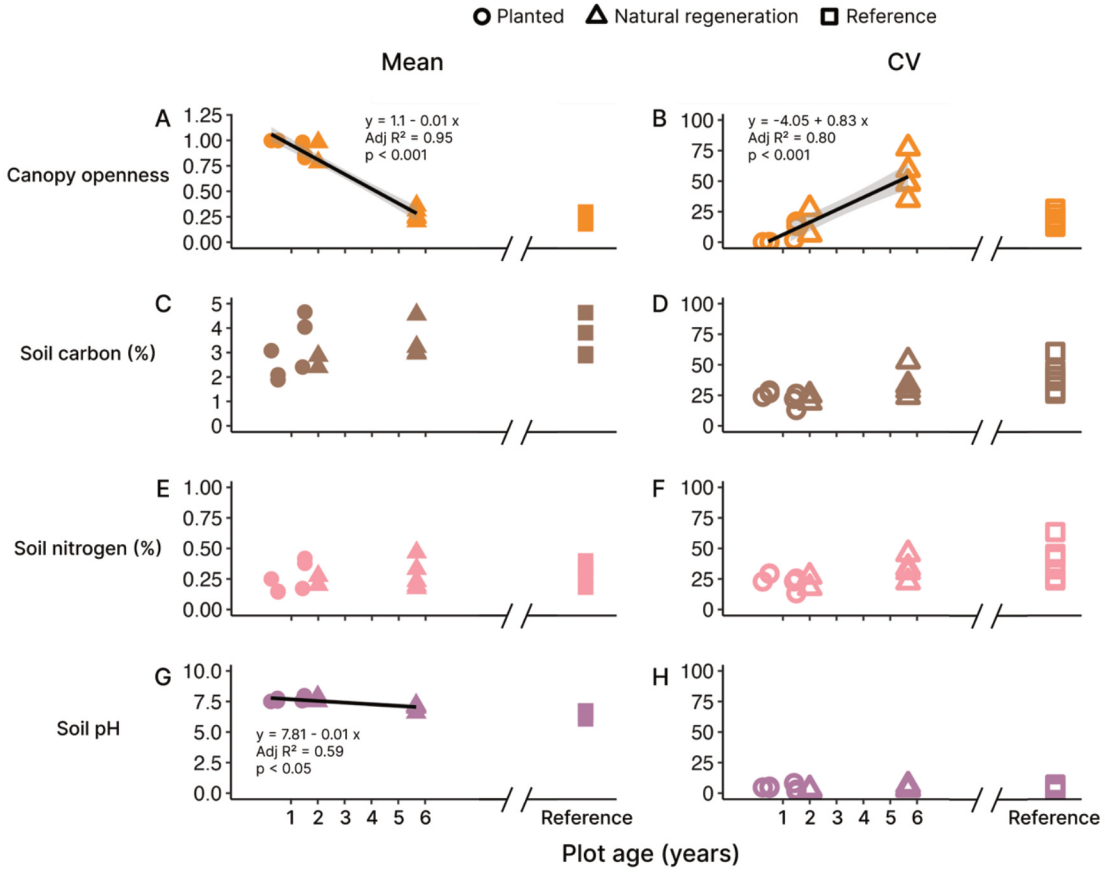


Figure 3.2 Mean and CV of environmental variables by intervention type and plot age. Planted N = 6, natural regeneration N = 7, reference N = 7. Closed symbols represent plot-level mean values, open symbols represent plot-level CV. Shaded area indicates the 95% confidence interval.

No environmental variable was predicted by intervention type after plot age was adjusted for (Table 3.2). Mean canopy openness declined substantially with plot age, dropping from over

0.99 (nearly completely open) to 0.20, representing an 80% reduction (Fig. 3.2A). Soils also became slightly more acidic with age, as mean pH dropped from 7.98 to 6.59 (Fig. 3.2G). The only measure of environmental heterogeneity that changed significantly between plots was the CV of canopy openness, which increased by three orders of magnitude from 0.06% to 77.02% over the first 6 years post-restoration (Fig. 3.2B).

	Explanatory variable			
	Intervention type		Plot age	
Response variable	F value	P value	F value	P value
Openness mean	1.85	0.20	103.65	<0.01
Openness CV	0.01	0.94	15.91	<0.01
Soil carbon mean	0.78	0.40	2.99	0.11
Soil carbon CV	0.07	0.80	1.97	0.19
Soil nitrogen mean	0.30	0.59	0.74	0.41
Soil nitrogen CV	0.07	0.80	1.94	0.19
Soil pH mean	0.43	0.53	9.06	0.01
Soil pH CV	0.88	0.37	0.46	0.51

Table 3.2 Type III ANOVA results. All linear models included the additive efects of both explanatory variables; F-values and p-values are reported for each model coeficient in the Type III ANOVA performed on these linear models. Significant results at a= 0.05 are highlighted in bold.

3.3.2 Does small-scale environmental heterogeneity increase tree seedling diversity?

3.3.2.1 Species richness (alpha diversity)

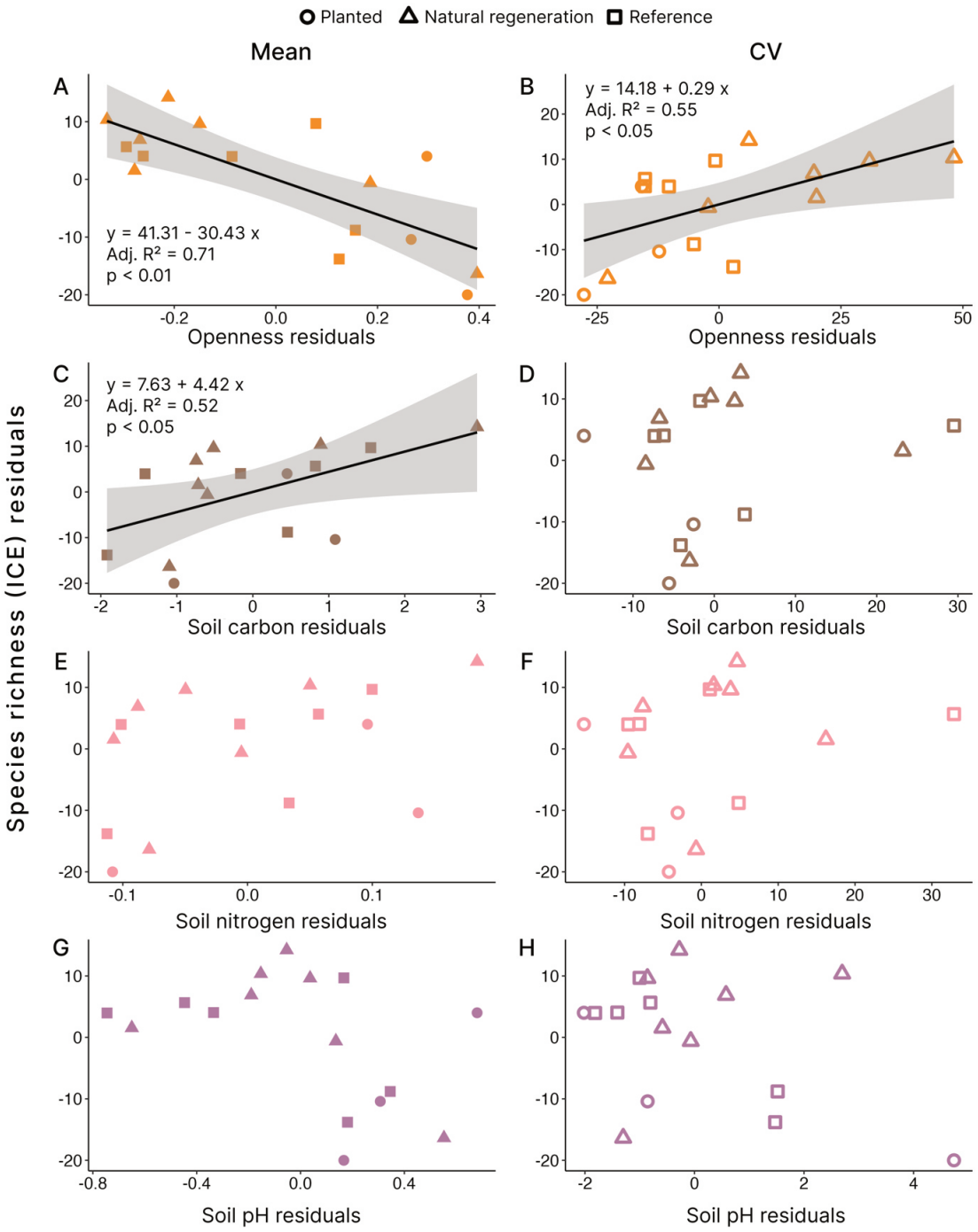


Figure 3.3 Partial regressions of species richness (ICE) against the mean (closed symbols) and CV (open symbols) of environmental variables (canopy openness, soil carbon, soil nitrogen, and soil pH) after correcting for stem number. Partial regression

plots show the residuals of each variable from independent regressions against stem number. Model coeficients, adjusted R^2 and p-value are reported for the explanatory variable after adjusting for stem number. Shaded area indicates the 95% confidence interval.

The CV of canopy openness was positively associated with species richness at the within plot scale (N = 16), after adjusting for stem number (Fig. 3.3B), indicating a positive relationship between heterogeneity and recruit diversity. By contrast, mean canopy openness had a consistently negative relationship with species richness, even after adjustingfor stem number(Fig.3.3A).Mean canopy openness was negativelycorrelated with the CV of canopy openness (Pearson's r = - 0.63); more open plots had lower variation in canopy cover. Furthermore, when both mean and CV of openness were included in the same model (adjusted for stem number), CV of canopy openness explained almost no variation in species richness, as most of the variance previously attributed to the CV was instead attributed to the mean of canopy openness (CV: 2%, mean: 33%, stem number: 13%). The relationship between species richness and CV was therefore no longer significant when mean openness was also included in the model (CV: $p = 0.57$; mean: $p < 0.05$; stem number: $p = 0.11$; model Adj. $R^2 = 0.70$).

Species richness was also positively associated with mean soil carbon content after adjusting for stem number (Fig.3.3C) but did not respond to the mean or CV of any other soil variables (Fig. 3.3D – H).

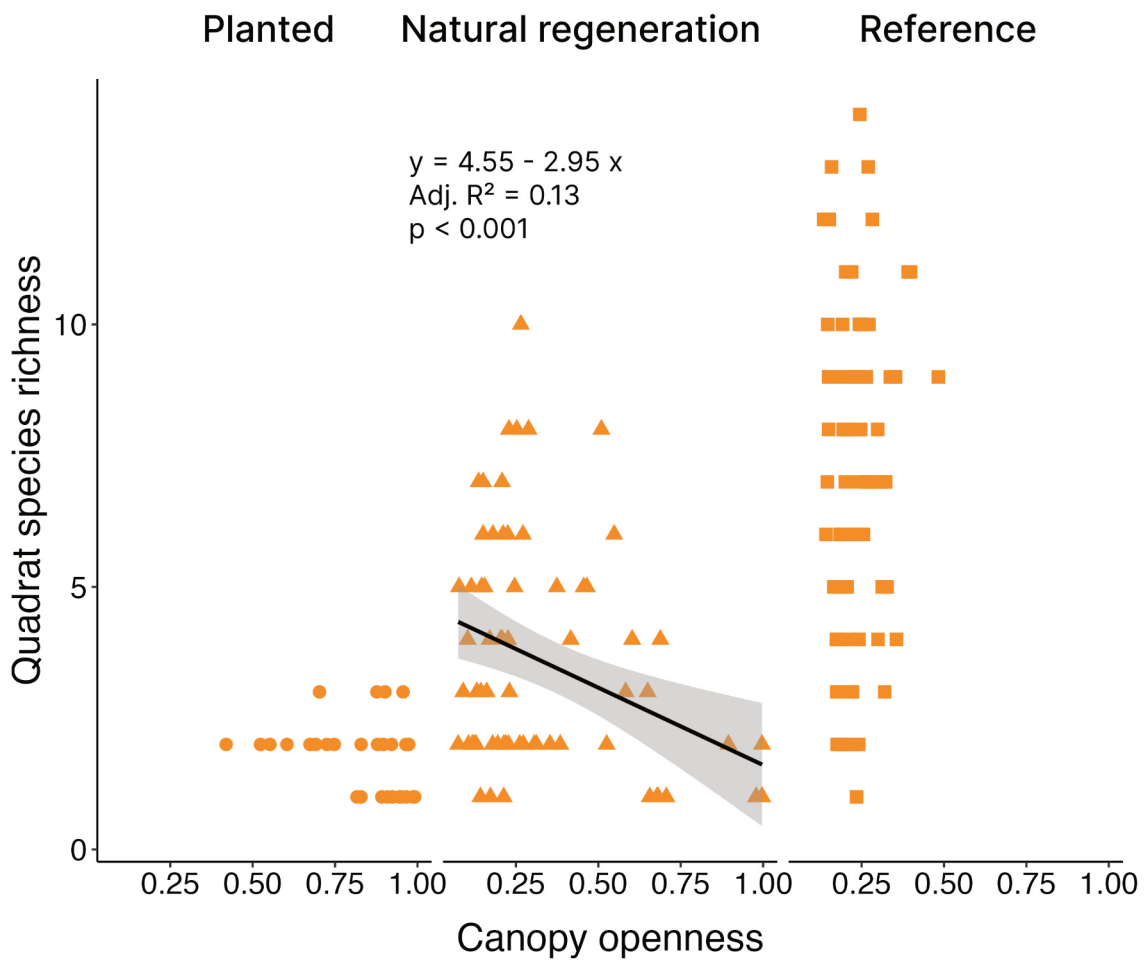


Figure 3.4 Quadrats with a less open canopy had higher species richness in natural regeneration plots. Only quadrats that also contained an environmental sampling point were included (N = 194). Shaded area indicates the 95% confidence interval.

To see if mean resource levels impacted plant alpha diversity at small scales as well as at the whole-plot scale, we investigated relationships between species richness and environmental variables at the quadrat level (N = 194). There was a negative relationship between quadrat-level canopy openness and quadrat species richness (i.e., more shaded quadrats had higher species richness) in the natural regenerationplots (coeficient estimate = -2.95, $p < 0.001$, Adj. $R^2 = 0.13$), but not in the planted plots or reference plots (Fig. 3.4).

Quadrat species richness was also positively related to quadrat soil C and N content in the reference plots only (carbon coeficient estimate = 0.52, $p < 0.01$, Adj. $R^2 = 0.12$; nitrogen coeficient estimate = 7.32, $p < 0.01$, Adj. $R^2 = 0.07$), and was negatively related to quadrat soil pH in the natural regenerationplots only (coeficient estimate = -1.94, $p < 0.001$, Adj. $R^2 = 0.15$).

3.2.2 Compositional turnover (beta diversity)

Partial Mantel tests within each plot showed no significant correlations between compositional dissimilarity (Bray-Curtisdissimilarity) and overall environmental distance at small scales (i.e., within each plot), except for one plot in the reference forest (plot 14; Table S3.2). Dissimilarity in environmental conditions between quadrats was therefore mostly not correlated with dissimilarity in community composition at the within-plot scale. These results were qualitatively the same when only testing for a correlation with distance of soil variables (Table S3.3), and no correlations were significant with distance of canopy openness (Table S3.4). Similarly, quadrat-level environmental conditions did not predict quadrat-level species composition when permutations were restricted to within-plots (PERMANOVA: $F_{4,182} = 11.94$, $p = 0.07$, $R^2 = 0.21$). All the environmental variables together explained 21% variation in community composition.

3.3.3 Does large-scale environmental heterogeneity increase tree seedling diversity at the landscape level?

At the landscape scale (i.e., using whole plots as the unit of replication), compositional dissimilarity (Bray-Curtis dissimilarity) was also not correlated with overall environmental distance after correcting for geographic distance (Pearson's $r = -0.04$, $p = 0.59$). However, the correlation was significant for distance of canopy openness only ($r = 0.61$, $p = 0.001$), but not significant for distance of soil variables ($r = -0.07$, $p = 0.71$). Diferences in mean light levels between plots were therefore correlated with diferences in recruit community composition, while diferences in mean soil conditions were not.

Quadrat-level environmental conditions did predict quadrat-level species composition when permutations were restricted to within-intervention type (i.e., permutations between

plots were permitted; PERMANOVA:$F_{4,182}$= 11.94, p = 0.001, R^2 = 0.21) and the marginal efects were significant for all environmental variables except for soil pH (openness: p = 0.001; carbon: p = 0.001; nitrogen: p = 0.002; pH p = 0.44).

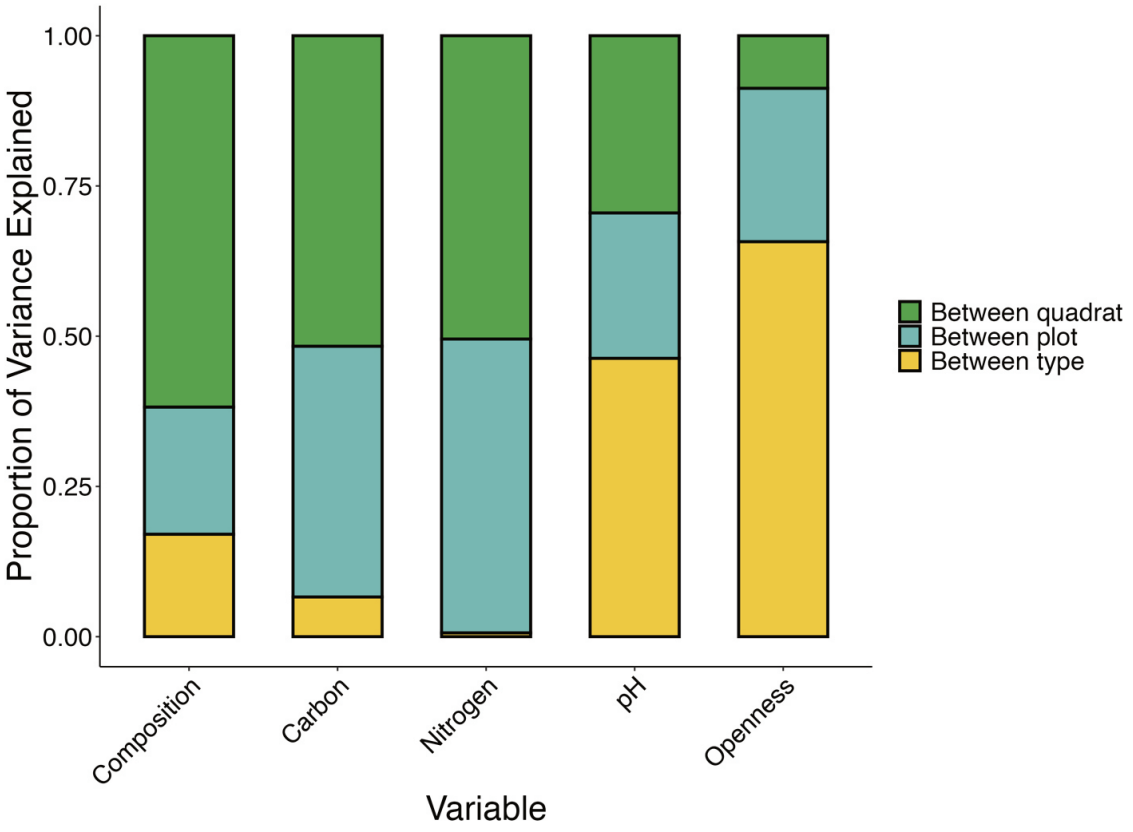


Figure 3.5 The proportion of variance in recruit community composition and environmental variables explained by the nested hierarchical factors of quadrat within plot within intervention type. Most of the variation in community composition was between quadrats, while environmental variables showed more variation at larger spatial scales.

The nested variance partitioning analyses (Fig. 3.5) showed that more of the variance in environmental variables occurred at larger scales than did variance in recruit composition. Soil carbon and nitrogen content varied most from quadrat to quadrat (within plots) but also showed a lot of variation from plot to plot (between plots). Soil pH and canopy openness

varied most between intervention type (natural regeneration versus planted versus reference forest). In contrast, most of the variance in recruit community composition occurred at small spatial scales (between quadrats, within plots).

3.4 Discussion

We have demonstrated that, in our study site, time since disturbance was a key driver of changes to the mean availability and spatial variability of key plant resources, and that this had consequences for the diversity and composition of tree recruits. Unexpectedly, we found no relationship between soil heterogeneity and tree recruit diversity, but we did find a positive relationship between the heterogeneity of canopy openness and recruit diversity. Whole-plot mean canopy closure explained recruit community composition at large spatial scales. Within plots, common species in the recruit community were found across all levels of canopy openness in small-scale patches, while rare species appeared to respond to small-scale variation in canopy openness. Therefore, the overwhelming importance of the light environment for recruit diversity was supported at multiple spatial scales. Below, we discuss how spatial scale, mean site conditions, and dispersal limitation all afect whether a HDR is observed, and how such information might be leveraged to restore tree recruit diversity in this vulnerable tropical dry forest ecosystem.

3.4.1 How does restoration intervention impact the level of small-scale environmental heterogeneity?

Small-scale heterogeneity in canopy openness (CV) increased by three orders of magnitude over the first 6 years of restoration, concurrent with an 80% decrease in mean canopy openness. In our study, restoration intervention was confounded with plot age, and there was no efect of intervention treatment on the mean or CV of canopy openness after adjusting for plot age. This suggests that it is the stage of secondary succession, rather than the method of forest establishment, that dictates patterns of light availability and variability. It is interesting that the CV of canopy openness appeared to increase linearly towards the mid-successional stage in this dry tropical forest, as this contrasts with the 4-phase model of succession in wet tropical forests where homogeneous canopy closure in mid-succession

reduces light heterogeneity (Denslow & Guzman G., 2000). Surprisingly, small-scale soil heterogeneity did not respond to intervention type or plot age. Our results indicate that natural regeneration did not increase soil heterogeneity within 6 years, consistent with Veldkamp et al. (2020) who found that the efects of anthropogenic degradation on soil are very slow to be reversed. Soil carbon and nitrogen content did show significant small-scale within-plot heterogeneity that was not related to plot age or intervention type, and also showed a lot of variation between plots, highlighting the multi-scale nature of soil heterogeneity in tropical forest ecosystems (Powers, 2006).

3.4.2 Does small-scale environmental heterogeneity increase tree recruit diversity?

3.4.2.1 Plot-level species richness

At the whole-plot scale, recruit species richness was positively correlated with the CV of canopy openness and negatively correlated with the mean of canopy openness. However, when both mean and CV of openness were included in the same model, only mean openness significantly predicted species richness, suggesting that mean light levels exert an overwhelming influence on recruit diversity. The importance of low mean light levels for high species richness of tropical forest tree recruits was also found by Holl et al. (2013).

In our study system, mean and CV of openness were negatively correlated, so the positive relationship between CV of openness and species richness may in part be an artefact of this relationship. A consequence of this confounding of CV and mean canopy openness is that mean resource levels can obscure HDRs, or otherwise suggest HDRs that are caused by variation in mean resource levels. This is a well-known challenge for experiments that manipulate heterogeneity of soil resources by adding fertiliser, as, without proper controls, the “heterogeneity” treatment can also increase the mean amount of fertiliser in the plot, often resulting in competitive exclusion by the species most able to exploit the high-nutrient environment (Baer et al., 2004). Studies of HDRs that include light heterogeneity should also take care to control for the confounding efect of mean light levels in their analyses.

Theory predicts that relationships between mean resource levels and species richness are driven by the density efect (Denslow, 1995), so it is surprising that we found positive efects

of mean canopy closure and soil carbon on species richness even after adjusting for stem number. One possible explanation is that, in this region, the species pool of closed-canopy specialists is larger than the pool of light-tolerant and light-demanding species, so the high temperatures and light levels associated with open-canopy conditions excluded most species. This interpretation was also considered by Holl et al. (2013), who argued that mean environmental conditions may be more important than variation in those conditions early in succession.

The observed relationships between canopy openness and recruit diversity were unexpected, as we predicted that canopy openness would be too temporally variable in this ecosystem to have a consistent efect on tree recruits. We are aware of only one study that found a positive relationship between light heterogeneity and plant diversity after controlling for mean light levels (Helbach et al., 2022), but this correlation was only found under certain conditions. In addition, we are not aware of any studies that have demonstrated a relationship between mean light availability and plant diversity while fully controlling for stem number (Hubbell et al., 1999). While the density efect is clearly strong and pervasive, our results highlight an additional mechanism that may drive relationships between resource availability and diversity: diferently sized species pools. Furthermore, as noted by Lundholm (2009), if a homogeneous environment is colonised by species from a rich species pool and a heterogeneous environment is colonised by species from both a rich and a poor species pool, the heterogeneous environment may have lower overall species richness if the patches suitable for the rich species pool cover less area overall and are more isolated from one another. This shows that ecological processes such as the HDR must be considered in the context of the phylogeographic assembly processes (speciation, extinction and migration) that generate the species pool that is available to local community assembly processes (Götzenberger et al., 2012; Murphy & Smith, 2021; Nishizawa et al., 2022).

3.4.2.2 Within-plot community dissimilarity

We also did not find any evidence that small-scale environmental heterogeneity is associated with compositional turnover within our plots, as measured by Bray-Curtis

dissimilarity between quadrats ('patches'). Between-quadrat compositional dissimilarity was not explained by environmental distance (except by soil variable distance in one plot) and quadrat composition was not explained by any environmental conditions in the patch. Community dissimilarity indices are strongly influenced by shared common species. This may therefore imply that the common species in the tree recruit community were found across all levels of environmental variables in small-scale patches. Rare species, however, did respond to small-scale environmental variation. Notably, in the natural regeneration plots, more shaded quadrats had higher species richness. These results suggest that patches of shade in the natural regeneration plots, which are those currently transitioning from an open to a closed canopy and span the full range of canopy cover from full sun to full shade, allowed rare closed-canopy specialists to co-occur with the common species community. This had the effect of increasing species richness while not impacting compositional dissimilarity indices. For example, in the natural regeneration plots, Bonellia flammea and Talisia floresii were only found in the quarter of quadrats that had the most closed canopy, and only in very small numbers (1 and 2 individuals respectively). Both species are more common in the reference forest plots and are typical of wet tropical forests, which tend to have dense closed canopies and dark understoreys. This finding is consistent with the theory advanced by Yang et al. (2015) and Heidrich et al. (2020) that HDRs emerge under harsh mean environmental conditions because they create more benign patches that can provide a refuge from the adverse conditions (Stein et al., 2014).

By considering two diferent measures of diversity that are diferentially sensitive to rare species, and by analysing the same data at multiple nested scales, we were able to uncover the mechanisms driving the positive HDR that we observed between small-scale heterogeneity in canopy openness and species richness. Closed canopies were found to increase recruit richness at both the plot and the quadrat scale. When these small, shaded patches were found in the high-light matrix of an early successional forest, it increased both light heterogeneity and species richness. Therefore, while the two are correlated, it would be misleading to say that light heterogeneity per se increases species richness, as this relationship depends on the surrounding context (i.e., species richness only increased

because the baseline richness in the high-light matrix was low). In other words, we found a positive relationship between small-scale environmental heterogeneity and the nestedness component of beta diversity, but not the species turnover component. This is consistent with Balvanera & Aguirre (2006), who found a positive HDR between heterogeneity in water availability and tree beta diversity that was partially caused by species turnover and partially caused by the exclusion of many species from the driest patches (i.e., nestedness).

3.4.3 Does large-scale environmental heterogeneity increase tree recruit diversity at the landscape level?

For landscape-scale heterogeneity, each large circular plot can be considered a 'patch'. Compositional dissimilarity of tree recruits between these patches was correlated with cross-plot variation in canopy openness but not soil variation. Furthermore, environmental variables (canopy openness, soil carbon and nitrogen content) predicted recruit community composition in quadrats when permutations were allowed between plots, but not when permutations were restricted to within plots. Therefore, environmental conditions (especially canopy closure) appeared to dictate community structure when considering large spatial scales, but not at small spatial scales. Species-environment relationships are often found to be scale-dependent, and this is usually attributed to small spatial scales encompassing less variation in environmental variables (Balvanera & Aguirre, 2006; Davies et al., 2005; Garzon-Lopez et al., 2014; Nishizawa et al., 2022). For example, Freestone & Inouye (2006) found that community dissimilarity was correlated with diferences in environmental variables only at the larger scales that encompassed a broader gradient in those variables. However, other studies have shown that scale is inherently important for the emergence of species-environment relationships. Gómez-Aparicio et al. (2005) found that soil and light variables predicted seedling performance at a larger spatial scale but not a smaller spatial scale, even though the magnitude of variation for soil variables was the same at both scales. Many soil variables can vary with the same magnitude across multiple diferent scales; Palmer & Dixon (1990) found that variance in soil pH on a scale of less than 5 m was almost as great as the variance within 20 ´ 50 m plots. Scale-dependency has also been hypothesised to arise due to an increased importance of stochasticity at smaller

scales (Bongalov et al., 2019; Garzon-Lopez et al., 2014; Lundholm, 2009). The scale-dependency observed in our results is possibly a combination of both mechanisms, as canopy openness and soil pH did indeed seem to vary most over larger spatial scales, while just over half of the variation in soil carbon and nitrogen content and nearly two-thirds of the variation in recruit community composition occurred at the within-plot scale.

Overall, our results suggest that between-plot environmental heterogeneity is an important driver of variation in tree recruit species composition at the landscape level. However, most of the variance in community composition was found within plots, also highlighting the importance of stochastic processes that operate at smaller scales for community composition.

3.4.4 Implications for restoration practice

Here we consider the relevance of our findings to two diferent conceptual approaches to restoration. Many projects aim to recreate a "climax" community with a species composition guided by a reference forest. To achieve this, practitioners may plant late-successional tree species or attempt to create the same environmental conditions that are found in the reference forest. On the other hand, some researchers have argued that ecological functionality and resilience should be the ultimate goals of restoration, instead of the recreation of a specific reference community (Bullock et al., 2022). Such an approach would likely emphasise increasing species richness, as functionality and resilience are often emergent properties of diversity (Bullock et al., 2022; Mori et al., 2017), and may place emphasis on creating heterogeneity in the abiotic environment to promote co-existence. Indeed, Hernández-Stefanoni et al. (2011) have advocated for low-intensity land use to increase environmental heterogeneity and therefore species diversity.

Our results suggest that attempting to increase recruit diversity by creating environmental heterogeneity at small scales (~1 -2 m^2) may only appear to be efective, in that it creates patches that can support the larger pool of late successional species in sites that are otherwise unsuitable. We found that uniformly shaded sites had both the highest species richness and the environmental conditions typical of a reference forest. In cases where

financial restrictions or site conditions limit the success of traditional large-scaleplantings, applied nucleation may allow available resources to be concentrated on ensuring the success of tree islands, which can act as refugia for low-light specialists (Derroire et al., 2016b; Holl et al., 2020). We note, however, that the planted plots also contained some shaded quadrats in a high-light matrix, but these did not have higher species richness. This could be because dispersal limitation prevented rare species from arriving at these patches (Holl et al., 2013), or possibly because the adult trees that provide shade are more likely to be deciduous species early in tropical dry forest succession (Lohbeck et al., 2015), which provide less of a refuge to shade-tolerant species (Derroire et al., 2016b; 2016c).

At the landscape scale, we found that increased environmental heterogeneity was associated with increased beta diversity due to compositional turnover. This suggests that Forest Landscape Restoration (FLR) approaches, which advocate for the coexistence of multiple diferent forest management approaches within a landscape (Sayeret al., 2013), should increase the landscape-level beta diversity of tree recruits.

3.5 Conclusion

Our results are consistent with Holl et al. (2013) in highlighting that mean canopy openness is a strong predictor of recruit diversity and community composition in tropical forest restoration, as would be expected if microclimatic conditions drive vegetation dynamics (Werden et al., 2018b). This explains why recruit species richness was correlated with mean canopy openness across plots, species turnover was correlated with canopy openness across plots, and, even within plots, more shaded quadrats had higher species richness.

Despite this, most of the variation in recruit community composition occurred at the within-plot level, at a scale smaller than the dominant spatial grain of environmental variation, and was not explained by the environmental variables we measured. Only rare species appeared to respond to small-scale heterogeneity in the light environment. This suggests a large role of stochastic processes in community assembly.

There is therefore potential for environmental variation to be leveraged by restoration practitioners to enhance tree recruit diversity, for example by creating shaded patches where rare shade-tolerant specialists, often absent in secondary forests, can coexist with the more generalist tree community, or by using diferent restoration interventions across the landscape to increase large-scale heterogeneity.

Chapter 4: Interacting abiotic and biotic gradients during tropical dry forest succession: natural enemy pressure increases seedling mortality most in the low-resource environment of late succession

4.1 Introduction

Secondary tropical forests are becoming increasingly widespread, covering up to 28% of the lowland Latin American tropics (Chazdon et al., 2016) as socio-economic changes lead to land abandonment (Chazdon & Guariguata, 2016; Poorter et al., 2021; Wright & Muller-Landau, 2006). Secondary forests recover through the process of secondary succession, which follows the rules of ecological community assembly (Chazdon & Guariguata, 2016; Norden et al., 2009b), so understanding how these rules operate in anthropogenic landscapes will improve our ability to predict the outcomes of forest recovery. According to one model of community assembly, the tree species that make up the new forest community following a disturbance are those that are able to pass through a series of hierarchical filters (Götzenberger et al., 2012). In this model, each filter removes some species from the species pool, either due to some feature of the species that prevents it from passing through a specific filter, or due to random chance (Lebrija-Trejos et al., 2010b; Norden et al., 2015). For example, if a species arrives at a site as a seed, but the site lacks the environmental conditions required for it to germinate, it has passed through the dispersal filter but been limited by the establishment filter. These filters may be created by both the abiotic and biotic environment (Lebrija-Trejos et al., 2010b), and much of contemporary community assembly research attempts to resolve the relative balance of abiotic and biotic filters across gradients of succession (Bhaskar et al., 2014; Martínez-Ramos et al., 2021), disturbance (Ding et al., 2012; Döbert et al., 2017) and spatial scale (Götzenberger et al., 2012). Most of this research has taken place in wet tropical forests, so community assembly processes in tropical dry forests (TDF), which represent 42% of tropical forests globally (Murphy & Lugo, 1986), remain

relatively understudied (Guariguata & Ostertag, 2001; Jakovac et al., 2021). Long-term experiments and chronosequence studies, mainly in the TDF of Costa Rica (Becknell & Powers, 2014; Buzzard et al., 2016; Werden et al., 2018b, 2020a) and Mexico (Bravo-Monzón et al., 2022; Dupuy et al., 2012; Lebrija-Trejos et al., 2010a; Martínez-Ramos et al., 2021; Saynes et al., 2005), have gone some way to redressing this imbalance (Derroire, 2016; Derroire et al., 2016a). This developing body of research has highlighted multiple abiotic filters that change with TDF succession, but studies have not found consistent correlations with plant functional trait turnover. Resolving this inconsistency requires mechanistic experiments that link these abiotic gradients to the demographic processes (growth and survival) that arise from community assembly filtering. In addition, attempts to disentangle the importance of abiotic versus biotic filtering using functional trait responses are limited by correlations and trade-ofs between traits related to each type of filter (Box 1.1; Kraft et al., 2015). Experimental manipulations of biotic conditions are therefore essential to determine the combined efects of both abiotic and biotic filters on demographic processes throughout succession.

There are three major abiotic resource availability gradients that correlate with TDF succession: water, light, and soil nutrients. Water availability increases with succession (Pineda-García et al., 2013; Werden et al., 2020a) as an increasingly closed canopy increases soil and air humidity in the understory, though this may only be the case during the dry season (Derroire, 2016; Werden et al., 2020a). Light levels decrease with succession (Lebrija-Trejos et al., 2010b), though the light availability gradient is less steep than in wet tropical forests (Lebrija-Trejos et al., 2011; Lohbeck et al., 2013). There is no generally agreed pattern of soil nutrient availability with succession. Soil nutrient levels early in succession are highly dependent on prior land use, which often depletes nutrients (Gei et al., 2018; Jakovac et al., 2021) but can increase nutrient levels (Aguilar-Peralta et al., 2020; Saynes et al., 2005). As a consequence, soil nitrogen (N) availability has been found to be limiting in both early successional (Ceccon et al., 2003) and old-growth forests (Bravo-Monzón et al., 2022). Water availability is thought to be the most important of these abiotic gradients for vegetation turnover with succession (Borchert, 1994; Lohbeck et al., 2015), though all three

gradients may contribute to species compositional turnover independently and/or in combination (Lebrija-Trejos et al., 2011).

Species turnover along abiotic successional gradients is mediated by plant functional traits, which dictate species' survival and competitive ability in a given water, light, or nutrient environment. The resource economics spectrum places species along a continuum from resource-conservative, with higher survival in low-resource environments (e.g., low-light, low-nutrients), to resource-acquisitive, with faster growth in high-resource conditions (Reich, 2014). It is unclear, however, whether the resource economics spectrum adequately captures trade-ofs in plant traits relevant to drought strategy, as represented by leaf phenological habit. In TDF, drought-deciduous trees are generally thought to have an acquisitive suite of traits. They grow rapidly during high-resource wet periods and then avoid drought stress during dry periods by shedding their leaves. In contrast, evergreen species have high wood density and greater resistance to cavitation, so are able to retain their leaves during drought, but at the cost of more resources invested in drought-resilience and slower growth (Méndez-Alonzo et al., 2012). Poorter & Markesteijn (2008) explained 69% of interspecific variation in seedling drought survival with phenological habit. However, Lohbeck et al. (2015) found that, while TDF succession was associated with a shift from drought-avoiding deciduous species to drought-tolerant evergreen species, this shift was independent of the resource economics spectrum that governs plant strategies for intercepting light and soil nutrients. Furthermore, Werden et al. (2018b) and Werden et al. (2020a) found that resource use traits (e.g., high LDMC, thought to indicate drought tolerance) were mostly not correlated with successional gradients. The weak link between a species' position on the resource economics spectrum, its drought tolerance/avoidance strategy, and its successional status in TDF may be further exacerbated by the combination of both conservative and acquisitive traits within the same species (Werden et al., 2018a). This is particularly notable for N-fixing species in the Fabaceae family; Gei et al. (2018) showed that biological nitrogen fixation (BNF) confers an additional advantage in early successional TDF due to their ability to fix N during extreme drought, even though many TDF legumes are also deciduous with low wood density (Palomo-Kumul et al., 2021). Thus, more

work is needed to determine how traits related to drought tolerance/avoidance and resource acquisition are linked along successional gradients in TDF.

Biotic assembly filters also change with secondary succession, including pressure from natural enemies (e.g., insect herbivores, fungal or bacterial pathogens). The frequency and impact of attack by natural enemies can vary due to their population dynamics, intrinsic plant traits (i.e., resistance), and environmental conditions (Aguilar-Peralta et al., 2020). Plant resistance can be achieved by escape (e.g., growing out of reach, dormancy), direct defences (e.g., secondary metabolites, trichomes), indirect defences (e.g., ant symbionts), and tolerance (Boege & Marquis, 2005). Natural enemy populations tend to be larger in early successional or disturbed forests (Jakovac et al., 2021; Pablo-Rodríguez et al., 2023; Poorter et al., 2004) but the negative impact of natural enemies on plant performance tends to be more severe and/or more species-specific in late successional forests (Bagchi et al., 2010; Krishnadas et al., 2018; Kulikowski et al., 2022). This may be because the species that are associated with late successional environments invest more in defence traits, thus requiring increased specialisation by natural enemies (Kulikowski et al., 2022; Mariano et al., 2018; Poorter et al., 2004), or it may be driven by interactions between natural enemies and abiotic conditions. For example, efective specialisation of natural enemies on hosts can be driven by the efect of the abiotic environment on the fitness of both pathogens and host plants (Benítez et al., 2013; Hersh et al., 2012). The impact of succession on the turnover of functional traits associated with natural enemy resistance is therefore complex.

Further complexity lies in the way that the resource use traits and the natural enemy resistance traits of plants may interact. Some have suggested that there is a positive correlation between drought-tolerance and natural enemy resistance, whereby resource-conservative species with high wood density also tend to have direct defences against insect herbivores and pathogens, and are better able to compartmentalise natural enemy damage (Poorter et al., 2014). However, a negative correlation between shade-tolerance and natural enemy defence has also been proposed, as phytochemicals are involved in both tolerance of high radiation levels and chemical defence (Bravo-Monzónet al., 2022). Therefore, if the forest microclimate becomes both more humid and more shaded with succession, it is

unclear what indirect consequences this may have on the natural enemy resistance of the plants associated with late successional environments. Perhaps more importantly than resistance to attack, the ability to recover lost biomass (i.e., resilience) also determines a species' ability to pass through this biotic filter (DeWalt et al., 2004). Allocation of resources to defence requires a trade-off with growth (Poorter & Kitajima, 2007), so plants generally follow a slow-growth, high-defence strategy or a fast-growth, low-resistance strategy (Krishnadas et al., 2020). This trade-off has been shown to modify observed associations between species and the abiotic environment (Fine et al., 2004). This means that natural enemy pressure can reduce a species' realised niche relative to the range of abiotic conditions in which it could potentially survive in the absence of natural enemies (fundamental niche), so that apparent abiotic filtering may in fact be caused by the combined effects of both abiotic and biotic processes (Kraft et al., 2015). Overall, resource-use traits may affect both the resistance and resilience of plants to natural enemy attack.

Understanding the relationships among plant traits related to drought tolerance/avoidance, resource acquisition, and natural enemy resistance has important practical applications in the context of restoration ecology. Community assembly research is increasingly integrated into restoration projects (Wainwright et al., 2018), allowing large-scale tests of successional theory (Werden et al., 2020a), as well as contributing to national and international restoration targets (e.g., the Bonn Challenge, https://www.bonnchallenge.org/). Such work has revealed that the main causes of seed and seedling mortality in active restoration programs of TDF are both abiotic (i.e., desiccation) and biotic (i.e., herbivory; Cárdenas et al., 2022). The species that are planted in (or recruited to) a restored site must therefore have a suite of functional traits that will enable them to tolerate both their biotic and abiotic environment (Werden et al., 2018a). Depending upon the successional context of the site being restored, restoration projects may need to overcome strong abiotic filters associated with early successional habitats (as when tree seedlings are planted in former cropland or pasture). Alternatively, site managers may need to focus on protecting restored vegetation from natural enemies (e.g., if underplanting is used). However, species selection based on one set of traits (e.g., drought tolerance) could have unintended implications for the

community response to other stressors, such as disease – and these trait correlations continuously change over the course of succession. Furthermore, forest restoration projects must also restore the processes of non-random mortality and interspecific competitive dynamics that promote species coexistence to ensure that restored forests are able to self-propagate diversity into the future. It is therefore important to address unresolved questions about the relative importance of diferent community filters along successional gradients in TDF, and the role of functional traits in coordinating plant responses to both abiotic and biotic stressors.

We established a large-scale experiment to explore the efect of these abiotic and biotic successional gradients, as well as potential interactions between them, on tree seedling growth and survival in a TDF ecosystem in southern Mexico. Ten species with varying functional trait profiles were planted in early, middle, and late-successional habitat, with and without natural enemy exclusion, and monitored to determine growth and survival over fifteen months. The study was designed to address three hypotheses:

Hypothesis 1: Species performance (growth and survival) rankings change with water availability along a successional gradient

1a: Drought-tolerant evergreen species have higher survival later in succession.

1b: Drought-avoidant deciduous species have faster growth early in succession.

Hypothesis 2: The impact of natural enemy exclusion varies with the successional environment

2a: The frequency of natural enemy attack (extent of leaf damage) is higher on all species in early successional environments, because natural enemy populations are larger.

2b: The negative impact of natural enemy attack on seedling performance (growth and survival) is higher in late successional environments, because plant-natural enemy interactions are more specialised, and plant resources are more limited.

Hypothesis 3: Abiotic (water availability) and biotic (natural enemy) filters interact to drive species turnover along successional gradients

3a: Natural enemy exclusion is more beneficial to drought-avoidant deciduous species because drought-tolerance traits are also natural enemy resistance traits.

4.2 Materials and methods

4.2.1 Study system

The experiment took place from December 2022 to March 2024 at a site adjacent to the Calakmul Biosphere Reserve in Campeche, Mexico (18°40'46.2"N, 90°08'24.4"W), described in detail in section 1.5 (Main introduction).

The experiment was situated within a landscape with a mosaic of land use intensity, duration and time since abandonment. Land use ranges from historical slash-and-burn agriculture by the Mayan civilisation, present from approximately 2,000 BCE to 900 CE, to contemporary clearances for cattle ranching and agriculture (Bohn et al., 2014; Ceccon et al., 2004; Veldkamp et al., 2020). We established nine 10 ´4 m plots in this landscape, with three replicate plots situated within forests at three stages of secondary succession (early, mid and late). Potential forests were initially identified based on visual assessment of a map of Normalised Diference Vegetation Index (NDVI) from May 2021 (late dry season) across the site (Hartter et al., 2008), followed by field visits and examination of satellite images to verify successional stage. The early successional forest had been used for rice cultivation and, later, cattle pasture for over 30 years, up until abandonment 3 years before the experiment began (O. E. Verduzco-Salazar, pers. obs.). Based on Google Earth historical satellite photography, the mid successional forest was cleared and briefly used for cattle grazing 6 years before the experiment began. Occasional larger trees were left standing, and the area was not used further and has been naturally regenerating since that time. The late successional forest has continuously remained closed-canopy forest for at least the past 30 years, based on historical Google Earth satellite imagery, and only a few trees have been removed (pers. obs.). Three plots were randomly located within each of these successional

environments. The averaged distance between plots within a successional environment was 161 m, and the averaged distance between plots in diferent successional environments was 1806 m. The early and mid successional plots were both ~ 1 km from the late successional plots, and ~ 2 km from one another, and both surrounded by a similar landscape configuration and forest cover.

4.2.2 Experiment design and installation

The experiment used a split-split-plot design with three treatments (forest successional environment, natural enemy exclusion, and species identity) to explore how tree seedling growth and survival changed with the abiotic and biotic gradients associated with TDF secondary succession (Fig. 4.1). The successional environment treatment had three levels (Early, Mid, and Late) and was applied at the whole-plot scale. The natural enemy exclusion treatment had two levels (Control and Exclusion, via insecticide and fungicide spraying) and was applied at the sub-plot scale. The species treatment had 10 levels and was applied at the sub-sub-plot (quadrat) scale.

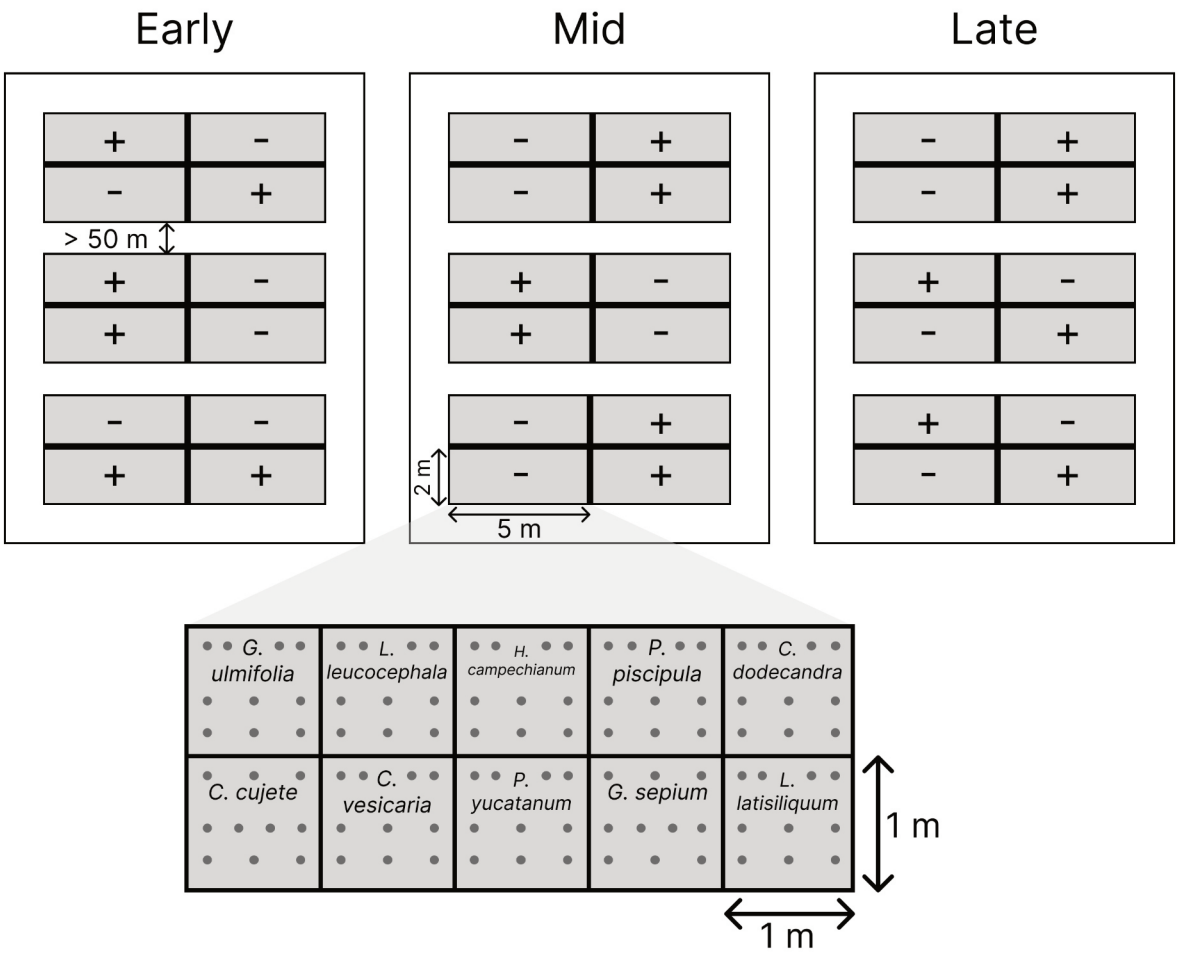


Figure 4.1 Design of the split-split-plot experiment. (+) indicates natural enemies present (control), (-) indicates natural enemies excluded. Dots within each quadrat represent individual tree seedlings. Three whole plots were randomly located within each of three successional environment treatments (Early, Mid, or Late) and were > 50 m apart. Bold lines indicate 1 m walkways dividing subplots.

Each whole plot was divided into four subplots (5 ´ 2 m each). Two subplots per plot were randomly allocated to the natural enemy exclusion treatment (- plots in Fig. 4.1), while the other two plots were used as controls (+ plots in Fig. 4.1). Each subplot was further divided into ten sub-sub-plots (1 ´ 1 m quadrats). Each quadrat was randomly allocated to one of

ten tree species selected for the experiment (see section 4.2.3 for more detail on species selection), and ten individuals of that species were planted in the quadrat, with a minimum spacing of 20 cm. Existing vegetation was left in place as much as possible to create an environment representative of each successional stage, though some vegetation removal and cutting of larger shrubs was necessary to facilitate planting.

The total number of trees at the start of the experiment was 3,600 in 360 quadrats. Tree seedlings were planted over a 1.5 month period during the growing season from 28/09/2022 to 19/11/2022. Of the trees initially planted, 19% died due to transplant shock within the first ~ 1 month. These were replanted in the two weeks between 22/11/2022 and 05/12/2022. Each individual tree was tagged with a unique number to facilitate measurement of survival and growth. Mean initial seedling height was 34.83 cm, and the standard deviation was 27.10 cm.

4.2.3 Species selection

Ten native tree species were chosen (Table 4.1) to encompass a gradient from drought-avoidance (characterised by deciduous phenology) to drought-tolerance (characterised by evergreen phenology). This was found of be the main axis of functional trait variation with TDF succession by Lohbeck et al. (2015). While species have been assigned to binary categories, these represent the extremes of a spectrum of leaf retention times, which often show intraspecific variation due to climatic diferences within a species' range (Méndez-Alonzo et al., 2012); for example, P. yucatanum has been variously categorised as both evergreen (Huechacona-Ruiz et al., 2020) and deciduous (Ochoa-Gaona et al., 2018). We have therefore based our categorisations on observations within our study system or the most geographically proximate literature source. We further note that these categorisations are often based on adult trees and may not represent the drought strategy of seedlings, which are generally less able to cope with drought due to small root systems and lack of storage tissues (Poorter & Markesteijn, 2008).

Species	Family	Nursery	Phenology	Successional status
Cordia dodecandra	Boraginaceae	Private	Deciduous	Generalist
Crescentia cujete	Bignoniaceae	Commercial	Evergreen	Late
Gliricidia sepium	Fabaceae	Commercial	Deciduous	Early
Guazuma ulmifolia	Malvaceae	Commercial	(Brevi) Deciduous	Early
Haematoxylum campechianum	Fabaceae	Commercial	Evergreen	Mid - Late
Leucaena leucocephala	Fabaceae	Private	(Brevi) Deciduous	Early
Lysiloma latisiliquum	Fabaceae	Commercial	Deciduous	Generalist
Piscidia piscipula	Fabaceae	Private	Deciduous	Generalist
Platymiscium yucatanum	Fabaceae	Private	Evergreen	Late
Tara vesicaria	Fabaceae	Private	Evergreen	Early

Table 4.1 Species used in the experiment. Phenology data from Huechacona-Ruiz et al. (2020), Ochoa-Gaona et al. (2018); Pennington & Sarakhán (2005), Powers & Tifin (2010) and Verduzco-Salazar, O. E., pers. obs. Successional status data from Cárdenas et al. (2022), Estrada-Medina et al. (2013), Pineda-García et al. (2013), Sorensen (2006), Villanueva (2016), and Verduzco-Salazar, O. E., pers. obs.

4.2.4 Natural enemy exclusion

The subplots allocated to the natural enemy exclusion treatment were sprayed with an insecticide and a fungicide. This has been used as an efective natural enemy exclusion treatment by Bagchi et al. (2010), DeWalt et al. (2004), Krishnadas et al. (2018, 2020), and the global research network BugNet (https://www.bug-net.org). We chose pesticides based on the criteria of low toxicity to non-target organisms, systemic action, and long-lasting efects (Krishnadas et al., 2018). The pesticides and spraying schedule were developed in consultation with a local agrochemical expert and BugNet researchers. The fungicide

(BAYERPREVICURâENERGY)contains propamocarb 530 g L^{-1} and fosetyl 310 g L^{-1} and was applied at a rate of 1 L per hectare. It is a systemic fungicide efective against oomycetes. The insecticide (BAYERMuralla Maxâ) contains imidacloprid 19.6% and beta-cyfluthrin 8.4% and was applied at a rate of 3 L per hectare. Imidacloprid is a systemic insecticide and beta-cyfluthrin is a non-systemic contact insecticide. Thetreatment was applied everyother month during the wet season and everyfour months during the dry season. Application was by knapsack sprayer following BugNet (2021). Each application took place over two days, with the fungicide applied on the first day and the insecticide applied on the second day. The pesticides were mixed with a non-ionic surfactant (COSMOCELâInex-A) and water to achieve the target dosage. Thecontrol subplots were sprayed with an equal volume of water containing the same volume of surfactant. 1 m walkways were left between each subplot (indicated by bold lines in Fig. 4.1) to facilitate access and to minimise drift of pesticides into the control subplots.

4.2.5 Data collection

Thefirst full tree census took place in December 2022 and was repeated every four months until the end of the experiment in March 2024. In each census, we determined survival and measured the height (at the apical meristem) of all planted trees. Seedlings were assumed to be dead if they lacked leaves and had a completely dry stem.

In December 2023 (after 12 months of the experiment) we estimated natural enemy damage on a stratified random sample of the planted trees followingBruna et al. (2024). We randomly selected three individual seedlings per quadrat (or all individuals if three or fewer had survived) for estimates of leaf damage. We recorded the percentage of the 60 uppermost fully expanded leaves that had insect damage, fungal damage, or both, and pooled these into one metric (percentage of leaves damaged). We also estimated the percentage of leaf surface area that had been damaged by natural enemies. Both observers were trained to estimate leaf area by ZAXHerbivory Trainer (Xirocostas et al., 2022) until a ten-leaf running accuracy of 98% was achieved. Six individuals per plot were randomly selected and

assessed by both observers independently to allow estimates of observer accuracy. We found high inter-observer validity (Fig. S4.2).

4.2.6 Statistical analysis

All statistical analysis was done using R version 4.2.3 (R Core Team, 2023).

4.2.6.1 Response variables

We used the percentage of leaves damaged as our metric of leaf damage. The unit of replication was the individual (N = 282; data missing from 78 quadrats with no surviving individuals at 12 months), and values were Box-Cox transformed (l= 2.63) to improve normality of model residuals. The unit of replication for survival and growth was the quadrat (N= 360). We calculated quadrat-level survival as the proportion of the 10 individuals in each quadrat that remained alive at the end of the 16-month experiment. Survival proportion was logit transformed to improve the normality of model residuals, where:

$$\text{logit (survival)} = \log (\text{survival}/1-(\text{survival})).$$

We calculated the relative growth rate (RGR) of plant height in mm per day for each individual over the 16 month (480 day) experiment period using the classic RGR equation (Hofmann & Poorter, 2002):

$$\ln (\text{height}_{\text{final}}) - \ln (\text{height}_{\text{initial}}) / (\text{day}_{\text{final}} - \text{day}_{\text{initial}}).$$

Negative growth rates were either due to measurement error or because the plant was dying from the tip downwards, so RGR was set to 0 to indicate that the plant had stopped growing. We then averaged RGR over each quadrat. If all plants in a quadrat died, RGR was also set to 0 to indicate that all plants stopped growing. RGR values were square root transformed to improve the normality of model residuals.

We tested for relationships between both measures of leaf damage and RGR using linear regression. It was not possible to examine the relationship between leaf damage and survival because leaf damage could only be measured on individuals that had survived to 12 months.

4.2.6.2 Split-split-plot models

All response variables were modelled using linear mixed-efects models (lme4 package; Bates et al., 2025). The models of leaf damage and RGR included successional environment, natural enemy treatment, and species identity as fixed efects, and whole plot and nested whole plot: subplot identity as random efects. All two-way and three-way interactions between fixed efects were also included:

> Leaf damage or RGR ~ successional environment ´ natural enemy exclusion ´ species + (1|plot code) + (1|plot code: subplot code).

The model of survival included the same fixed efects and an additional fixed efect of average initial seedling height in the quadrat:

> Survival ~ successional environment ´ natural enemy exclusion ´ species + initial height + (1|plot code) + (1|plot code: subplot code).

Diagnostic plots were visually assessed to ensure the assumptions of homogeneity of variance and normality of residuals and random efects were met, and conditional and marginal R^2 was calculated following Nakagawa & Schielzeth (2013).

Five species were sourced from a commercial tree nursery and five were sourced from a private restoration nursery (Table 4.1). We tested for an efect of nursery source by including it as a fixed efect in our models (with species as a random efect) and in all cases it was not significant and the model marginal R^2 decreased, so there was no evidence that the nursery that seedlings were sourced from impacted the results.

4.2.6.3 Planned contrasts and post hoc analyses

We performed planned contrasts to address three of our hypotheses. Hypotheses 1 predicted that species' drought strategy (deciduous versus evergreen) would predict changes in survival and growth rankings across successional environments, and Hypothesis 3a predicted that drought strategy would explain changes between levels of the natural enemy treatment. We therefore contrasted survival and growth of deciduous versus evergreen species at each level of the successional environment and natural enemy exclusion treatments. Hypothesis 2b predicted that natural enemy exclusion would increase

growth and survival more in the late successional forest than the early successional forest due to a stronger biotic filter at that late stage, so we contrasted survival and growth in control versus exclusion treatments at each level of the successional environment treatment. Planned contrasts were performed using estimated least-square means (emmeans package; Lenth et al., 2024). Contrasts between drought strategy groups were performed by weighting species in the evergreengroup by negative 0.25 (so that the weights of the four species in this group summed to negative 1) and species in the deciduous group by 0.16 or 0.17 (so that the weights of the six species in this group summed to positive 1). Changes in logit survival were converted to the odds ratio for interpretation by calculating $;^{!"\#\$\%\&'\$)'\$*+\&\$)}$. This indicates the change in the odds of survival under the contrasting treatments.

We also performed post hoc analyses of the interactions between successional environment or natural enemy treatment and species identity in the full split-split-plot models. For each treatment, we used pairwise comparisons (Tukeycorrected) of estimated least-square means to perform pairwise comparisons between each pair of treatment levels for each species. For example, for the successional environment treatment, this post hoc analysis compared Early – Mid, Early – Late, and Mid – Late estimated means for each species, and p-values were adjusted using the Tukeymethod for comparing a family of three estimates. We considered a post hoc comparison to be statistically significant if the adjusted p-value was < 0.05.

4.3 Results

4.3.1 Species' growth and survival rankings change with successional environment, and this is partially predicted by drought strategy (Hypothesis 1)

4.3.1.1 Hypothesis 1a: Drought-tolerant evergreen species have higher survival later in succession

Seedling survival in each quadrat (N = 360) ranged from full mortality (all 10 individuals in a quadrat died) to full survival (all 10 individuals survived) in every successional environment

and both natural enemy treatments. Overall, an averageof 42.8% of individuals in a quadrat survived to the end of the experiment, although this decreased by more than half across the full successional gradient, dropping from 60.6% early in succession to 44.0% in mid succession and further to 23.6% in late succession (Table 4.2).

Fixed ef ects	NumDF	DenDF	F value	P value
Successional environment	2	5.96	11.57	< 0.001
Natural enemy exclusion	1	24.00	1.85	0.19
Species	9	270.96	15.19	< 0.001
Initial height	1	291.23	14.64	< 0.001
Successional environment ´ natural enemy exclusion	2	24.06	4.45	0.02
Successional environment ´ species	18	269.34	13.62	< 0.001
Natural enemy exclusion ´ species	9	269.11	0.41	0.93
Successional environment ´ natural enemy exclusion ´ species	18	269.07	0.68	0.83

Table 4.2 Type III ANOVA Table for linear mixed-ef ects model of seedling survival. Fixed efects that were significant at a = 0.05 are highlighted in bold.

68% of the variation in survival was explained by the mixed efects model, and most of this was attributed to the fixed efects (R^2_c = 0.68, R^2_m = 0.61). Survival was predicted by initial height, as well as by two independent two-way interactions: successional environment ´ natural enemy exclusion (see section 4.3.2), and successional environment ´ species (Table 4.2). The interaction between successional environment and species identity demonstrated that species survival rankings changed along the successional gradient (Fig. 4.2A), supporting Hypothesis 1. Survival of most species decreased along the successional gradient, though there were exceptions to this. Survival of C. cujete remained constant across the successional gradient, such that it had the highest survival in the late successional plot. P. yucatanum had a peak in survival in mid-succession, but survival rates were equal early and late in succession.

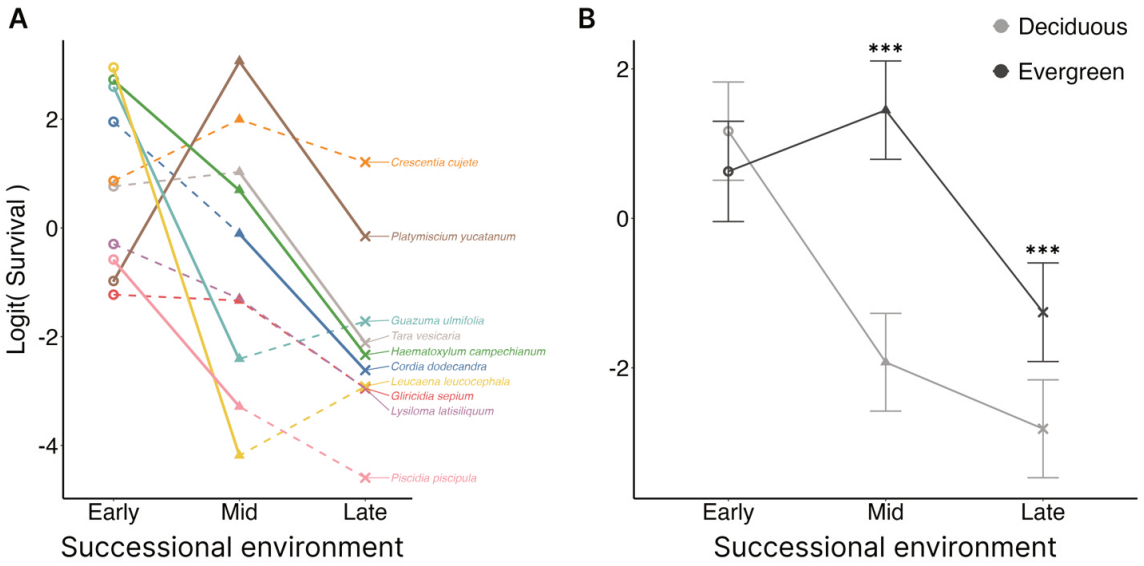


Figure 4.2 (A) Survival across the successional gradient was species-specific, such that species survival rankings changed with succession. (B) Survival decreased with succession for the deciduous species group more than the evergreen species group. In (A) solid lines indicate significantly diferent survival of a species between successional environments at a= 0.05. In (B) p-values are shown for planned contrasts between drought strategy groupings in each successional environment with ± SE bars, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

The decrease in survival with succession difered in magnitude between drought strategy groups (Fig. 4.2B), consistent with Hypothesis 1a. In early successional environments there was no diference in survival between deciduous and evergreen species (t ratio = 1.55, p = 0.12), but evergreen species had higher survival in mid (t ratio = -10.40, $p < 0.001$) and late (t ratio = -4.65, $p < 0.001$) successional environments. This is because the survival of deciduous species decreased more with succession than the survival of evergreen species (Fig. 4.2B). The diference between deciduous and evergreen species appears to be driven by the high survival of C. cujete and P. yucatanum (both evergreen species) in the later

successional environments. The remaining evergreen species (T. vesicaria and H. campechianum) did not fit this pattern (Fig.4.2A).

4.3.1.2 Hypothesis 1b: Drought-avoidant deciduous species have faster growth early in succession

Relative Growth Rate (RGR) at the quadrat level (N = 360) ranged from 0 – 5.4 ´ 10^{-3} mm d^{-1}, with a mean of 8.0 ´ 10^{-4} mm d^{-1}. Average RGR was six to eleven times higher early in successional environments (mean: 1.9 ´ 10^{-3}; range: 0 – 5.4 ´ 10^{-3}) than in mid (2.8 ´ 10^{-4}; 0 – 1.3 ´ 10^{-3}), and late succession (1.7 ´ 10^{-4}; 0 – 1.5 ´ 10^{-3}), respectively (Table 4.3).

Fixed effects	NumDF	DenDF	F value	P value
Successional environment	2	6	61.13	< 0.001
Natural enemy exclusion	1	24	5.22	0.03
Species	9	270	12.33	< 0.001
Successional environment ´ natural enemy exclusion	2	24	0.88	0.43
Successional environment ´ species	18	270	6.46	< 0.001
Natural enemy exclusion ´ species	9	270	1.51	0.14
Successional environment ´ natural enemy exclusion ´ species	18	270	0.93	0.54

Table 4.3 Type III ANOVA Table for linear mixed-effects model of seedling RGR. Fixed effects that were significant at a = 0.05 are highlighted in bold.

The mixed-effects model explained 76% of the variation in RGR, and of which 72% was explained by the fixed effects (R^2_c = 0.76, R^2_m = 0.72). RGR was predicted by a main effect of natural enemy treatment (see section 4.3.2) and a two-way interaction between successional environment ´ species identity (Fig. 4.3A), supporting the hypothesis that species RGR rankings change with succession (Hypothesis 1).

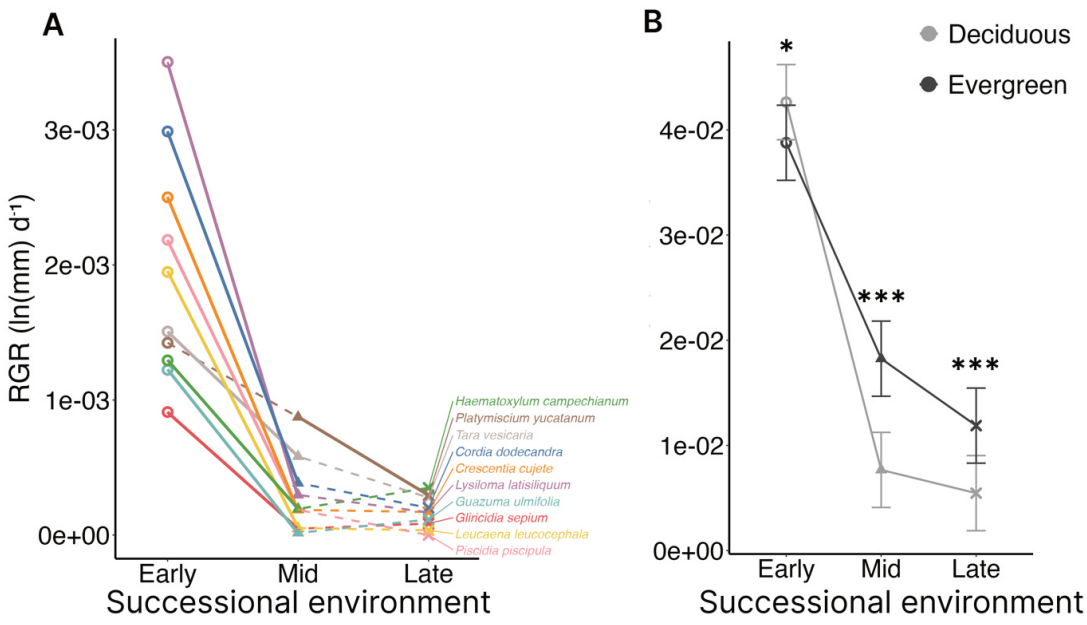


Figure 4.3 RGRof all species (A) and both drought strategy groups (B) was highest in the early successional forest. (B) The RGRof deciduous species decreased more over the successional gradient than the RGRof evergreen species, so that deciduous species had higher RGRearly in succession, but evergreen species had higher RGRin mid and late succession. In (A) solid lines indicate significantly diferent RGRof a species between successional environments at a= 0.05. In (B) p-values are shown for planned contrasts between drought strategy groupings in each successional environment with ± SEbars, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Variation in RGRwith succession was partially explained by drought strategy. Consistent with Hypothesis 1b, deciduous species had slightly higher RGRthan evergreenspecies early in succession (t ratio = 2.06, $p = 0.04$), whereas evergreen species had higher RGRin mid (t ratio = -5.74, $p < 0.001$) and late (t ratio = -3.51, $p = < 0.001$) succession (Fig. 4.3B).

4.3.2 Natural enemy exclusion impacts vary with succession, although attack rate does not (Hypothesis 2)

4.3.2.1 Hypothesis 2a: The frequency of natural enemy attack is higher on all species in early successional environments

We quantified leaf damage both to ensure that our natural enemy exclusion treatment had its intended efect, and to assess whether the level of damage depended upon the successional environment, as predicted by Hypothesis 2a. Observed leaf damage from natural enemies was variable, but generally high. It ranged from 0 – 100% leaves damaged, with an average of 82.85% leaves damaged; the mixed-efects model explained just 43% of the variation in observed leaf damage, with 33% attributed the fixed efects (R^2_c= 0.43, R^2_m = 0.33). Unexpectedly, mean leaf damage was consistent across the levels of the natural enemy exclusion treatment; 83.93% in the control and 81.85% when natural enemies were excluded (Table 4.4). Mean leaf damage changed in the direction expected under Hypothesis 2a, decreasing from 86.46% early in succession, to 81.60% in mid successional forest and 78.91% in late successional forest, but the main efect of successional environment was not significant (Table 4.4).

Fixed ef ects	NumDF	DenDF	F value	P value
Successional environment	2	33.15	0.87	0.43
Natural enemy exclusion	1	33.99	0.03	0.87
Species	9	199.01	7.32	< 0.001
Successional environment ´ natural enemy exclusion	2	33.15	1.00	0.38
Successional environment ´ species	18	198.50	2.23	< 0.01
Natural enemy exclusion ´ species	9	199.01	2.05	0.04
Successional environment ´ natural enemy exclusion ´ species	18	198.50	0.97	0.50

Table 4.4 Type III ANOVA Table for linear mixed-ef ects model of leaf damage. Fixed efects that were significant at a= 0.05 are highlighted in bold.

The absence of treatment and successional environment main efects is likely due to strong species-specific interactions within these treatments. The percentage of leaves damaged

was predicted by independent two-way interactions between successional environment ´ species (Table 4.4, Fig. 4.4A) and between natural enemy exclusion ´species (Table 4.4, Fig. 4.4C). There was no significant change in the percentage of leaves damaged across the successional gradient for most species (Fig. 4.4A). The overall interaction was driven by just two significant successional environment ´species interactions: C. cujete had on average 19% lower leaf damage in early successional forest than late in succession (t ratio = -2.50, p = 0.03), and G. ulmifolia had on average 19% higher damage in early successional forest than late in succession (t ratio = 3.05, p < 0.01). There was also no diference in the percentage of leaves damaged when natural enemies were excluded compared to the control for most species (Fig. 4.4B). The two exceptions were H. campechianum, which had on average 14% lower leaf damage when natural enemies were excluded (t ratio = 2.71, p < 0.01), and C. cujete, which saw a surprising increase in leaf damage of 14% when natural enemies were excluded (t ratio = -2.43, p = 0.02).

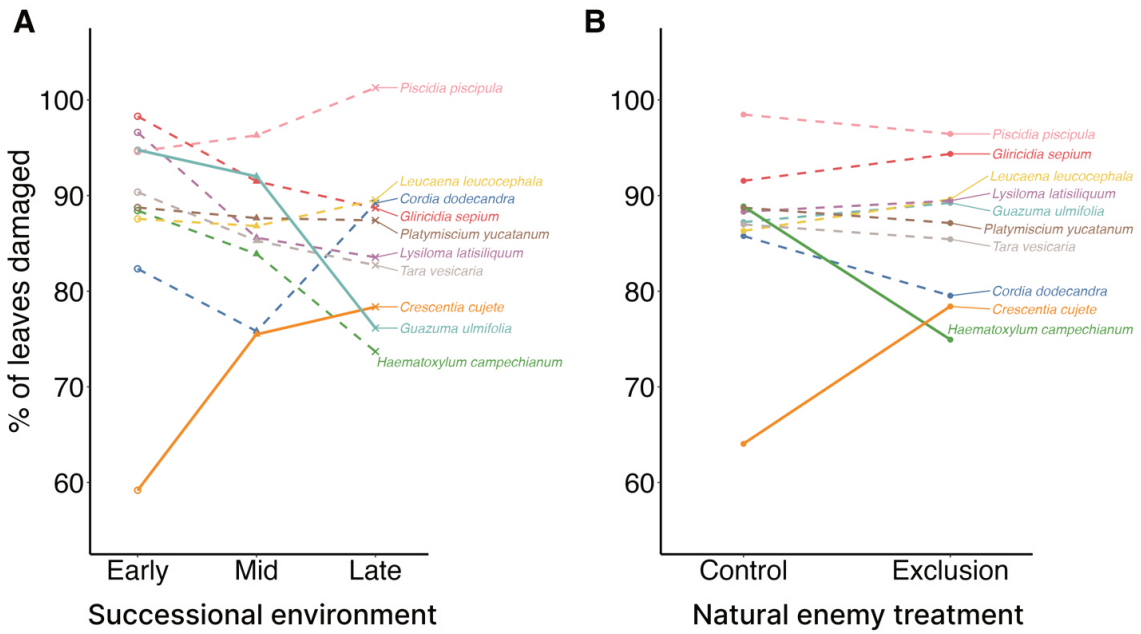


Figure 4.4 (A) Leaf damage by natural enemies was universally high across successional environments and (B) did not change with natural enemy exclusion. Percentage of leaves damaged was measured of the 60 uppermost fully expanded leaves of up to three individuals

per quadrat (N= 282). Solid lines indicate significantly diferent survival of a species between (A) successional environments and (B) levels of the natural enemy exclusion treatment at a = 0.05.

4.3.2.2 Hypothesis 2b: The impact of natural enemy attack on seedling growth and survival is higher in late successional environments

Survival increased with natural enemy exclusion in mid and late successional environments, but not in the early successional forest environment (Fig. 4.5A), resulting in an interaction between successional environment ´natural enemy exclusion (Table 4.2) consistent with Hypothesis 2b. When natural enemies were excluded, the odds of survival were ~1.94 times greater than the control in late succession ($t\ ratio_{24} = 2.12$, $p = 0.04$) and ~1.80 times greater in mid succession ($t\ ratio_{24} = 1.88$, $p = 0.07$), but the odds of survival with natural enemy exclusion were just ~0.6 times that of the control in early succession ($t\ ratio_{24} = -1.65$, $p = 0.11$). RGR also increased by 5.25×10^{-3} with natural enemy exclusion in the late successional environment ($t\ ratio_{24} = 2.36$, $p = 0.03$), but did not change with natural enemy exclusion in the early ($t\ ratio_{24} = 0.54$, $p = 0.59$) or mid ($t\ ratio_{24} = 1.06$, $p = 0.30$) successional environments (Fig. 4.5B), though the interaction between successional environment ´ natural enemy exclusion was not significant in the full split-split-plot model of RGR(Table 4.3).

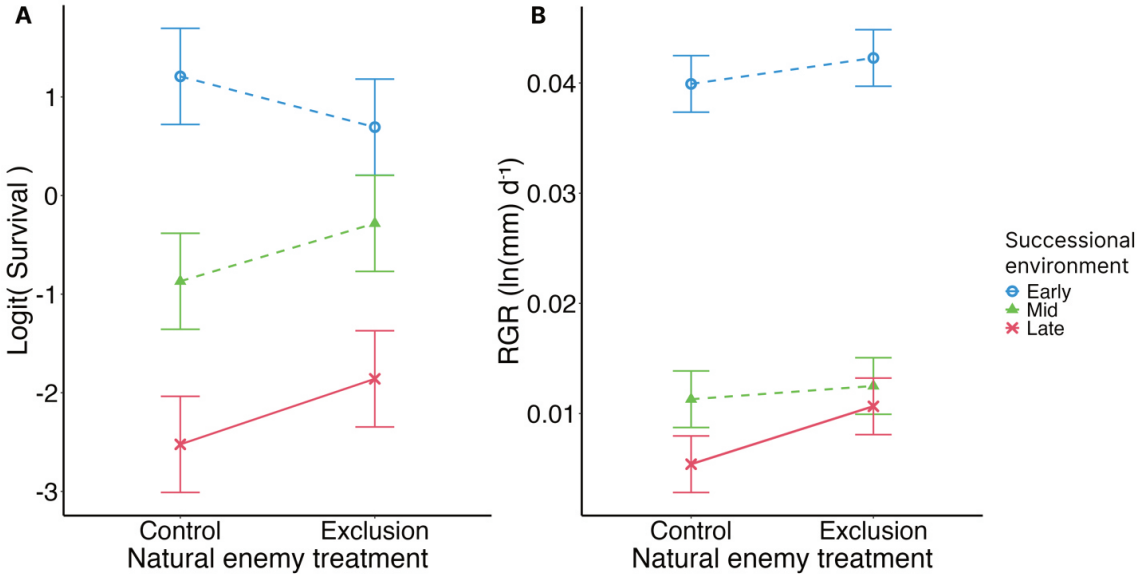


Figure 4.5 (A) Survival and (B) growth rates increased significantly with natural enemy exclusion in the late successional environment, but not in the early or mid successional environments. Planned contrasts were performed between levels of natural enemy treatment within each successional environment, solid lines indicate significant contrasts at a= 0.05, error bars show ± SE.

There was no relationship between the percentage of leaves damaged on an individual seedling and its RGR ($p = 0.26$, Adj. $R^2 = 0.001$). We also measured the average area of each leaf that was damaged, and this metric did have a weak negative correlation with RGR (Fig. S4.3; $p < 0.01$, Adj. $R^2 = 0.03$).

4.3.3 Hypothesis 3a: Natural enemy exclusion is more beneficial to drought-avoidant deciduous species because drought-tolerance traits are also natural enemy resistance traits

As predicted by Hypothesis 3a, deciduous species showed more leaf damage than evergreen species across all successional environments (Fig. 4.6A) and levels of the natural enemy exclusion treatment (Fig. 4.6B). Furthermore, a planned contrast of deciduous and evergreen species groups at each level of the natural enemy exclusion treatment revealed that natural enemy exclusion increased the survival and RGR of deciduous species slightly

more than evergreen species. The impact on survival rates was very small; the survival odds for deciduous species were ~ 21% that of evergreen species in the control (t ratio$_{275}$ = -5.46, $p < 0.001$) and ~ 24% that of evergreen species when natural enemies were excluded (t ratio$_{275}$ = -5.09, $p < 0.001$; Fig. 4.6C). The impact on RGR was clearer; evergreen species had a higher RGR than deciduous species by 5.1×10^{-3} on average in the control (t ratio$_{270}$ = -3.37, $p < 0.001$), but by only 3.8×10^{-3} on average in the exclusion treatment (t ratio$_{270}$ = -2.50, p = 0.01; Fig 4.6D).

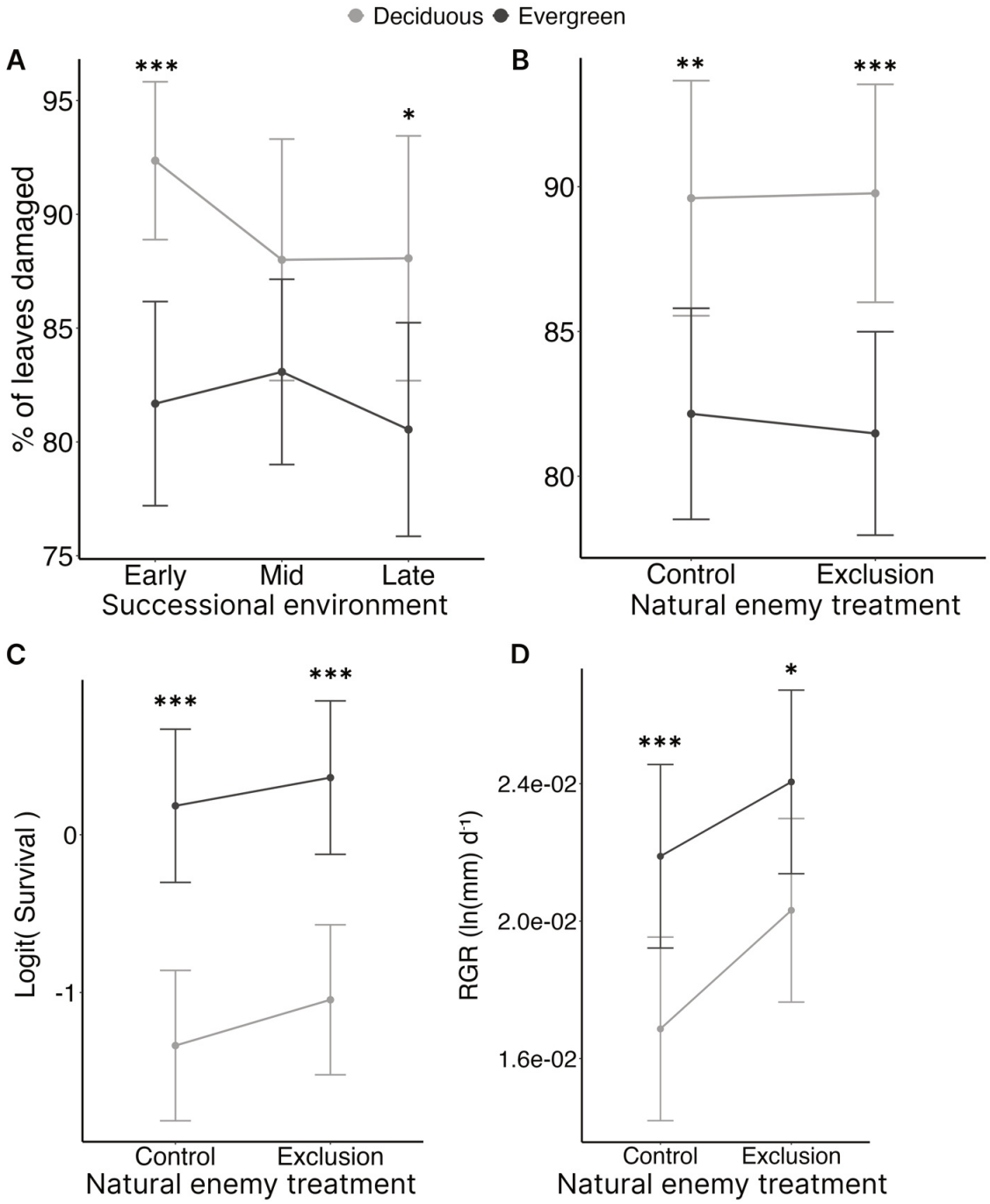


Figure 4.6 Leaf damage was highest on deciduous species across (A) successional stages and (B) levels of natural enemy treatment. (C) Survival and (D) growth rates of evergreen species were always higher than deciduous species but natural enemy

exclusion reduced the magnitude of the dif erence. P-values are shown for planned contrasts between drought strategy groupings in (A) each successional environment and (B, C & D) each level of the natural enemy exclusion treatment with ± SE bars, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4.4 Discussion

Overall, our results show that abiotic and biotic successional gradients interact to determine seedling survival and growth. The successional gradient encompasses multiple abiotic gradients, in terms of water, light, and nutrient availability, as well as biotic gradients, in terms of natural enemy pressure and competition from adult trees. We were able to untangle these various drivers of seedling performance by examining the responses of diferent functional trait groupings and the efects of natural enemy exclusion.

Changes to the relative growth and survival rankings of the ten species planted in the experiment across the successional gradient indicated habitat filtering (Hypothesis 1), as diferent species attained the highest performance in diferent abiotic environments. Drought-strategy groups partially explained these species-environment associations; drought-avoidant deciduous species showed higher mortality (Hypothesis 1a) and lower growth rates (Hypothesis 1b) than drought-tolerant evergreen species later in succession. Frequency of natural enemy damage did not change with succession (Hypothesis 2a), but natural enemy pressure had a greater impact late in succession (Hypothesis 2b); exclusion of natural enemies increased average survival and RGR in late succession only. This suggests that seedlings are not able to regrow biomass following natural enemy damage in the low-light environment of late succession, so the impact of natural enemy damage on survival is more severe. Natural enemy exclusion also increased the growth rates of deciduous species more than evergreen species, possibly because evergreen species have intrinsic natural enemy defence traits (Hypothesis 3a). Together, these results suggest that the fundamental successional niches of these ten species, as defined by drought-strategy traits, was further

reinforced by natural enemy pressure, thereby defining the realised successional niches (Kraft et al., 2015).

4.4.1 Abiotic successional gradients impacted seedling survival and growth

Relative growth rates were highest early in succession for all species. This is consistent with Werden et al. (2020a), who found that seedlings had dramatically higher growth rates in an early successional environment. Early successional TDF tends to have higher light availability (Lebrija-Trejos et al., 2010b) and possibly higher nutrient availability (Aguilar-Peralta et al., 2020; Bravo-Monzón et al., 2022; Saynes et al., 2005). Werden et al. (2020a) were able to attribute the diferent growth rates to microclimatic conditions and/or surrounding vegetation, ruling out edaphic diferences because the early successional vegetation was created experimentally. Furthermore, despite clear gradients of nutrient availability between environments, Holl (1999) and Holl et al. (2011) did not find that soil nutrients limited seedling growth, and Werden et al. (2018b) found that successional status was not related to soil nutrient niche. Finally, direct measures of soil samples across our successional gradient demonstrated that soil carbon and nitrogen content was highest in the late successional forest, while soil pH was highest in the early successional forest (section 1.5). We therefore consider it more likely that light limitation, rather than nutrient limitation, explains the low growth rates of seedlings later in succession.

4.4.2 Drought-strategy groups explained species performance with succession

Drought-strategy categories (deciduous versus evergreen phenology) were good predictors of the changes in growth and survival across the successional gradient, consistent with Poorter & Markesteijn (2008). Growth and survival rates decreased more with succession for deciduous species than evergreen species, thereby creating a large fitness gap between these categories later in succession. The diference between deciduous and evergreen species may be related to both the light and water availability gradients; low light levels later in succession reduce the ability of deciduous species to regrow leaves every season, and alleviation of water limitation reduces the need for drought-avoidance through leaf drop (Lohbeck et al., 2013; Pineda-García et al., 2013). Furthermore, Werden et al. (2020a) found

that early successional TDF growing on Vertisols had lower soil moisture than mid successional TDF in the dry season, but higher soil moisture in the rainy season, which might promote drought-avoidant strategies that are more resource-acquisitive and able to take advantage of the high-resource rainy season. This is consistent with multiple studies of TDF succession that have found a shift from deciduous to evergreen species with succession (Gee et al., 2025; Lohbeck et al., 2015). This suggests that the performance of seedlings planted during TDF restoration will be enhanced by matching of drought-strategy categories to successional environments, i.e., planting drought-deciduous species in early successional environments and drought-tolerant evergreen species in later successional environments.

4.4.3 The biotic filter was stronger in the late successional forest than in the mid and early successional forests

Notably, natural enemy exclusion improved survival and growth rates in late succession, but not in early succession. This supports our hypothesis that the biotic filter is stronger later in succession (Martínez-Ramos et al., 2021). It was surprising that, like Lohbeck et al. (2014), we found no diference in absolute levels of leaf damage along the successional gradient. We note that growth rates were highest early in succession and natural enemy exclusion only increased survival and growth late in succession. These results are consistent with a model in which species had fewer resources to regrow lost biomass in the low light of the late successional environment (Aguilar-Peralta et al., 2020), so mortality from natural enemy damage was higher even though absolute levels of damage didn't change (Poorter et al., 2004). The increased impact of natural enemy pressure in low resource environments has been found by several other studies in a range of wet and dry tropical forest ecosystems (Bravo-Monzón et al., 2022; Derroire et al., 2016c; DeWalt et al., 2004; Fine et al., 2004) and should therefore be considered a widespread driver of species-habitat associations, which are often attributed to abiotic conditions alone.

4.4.4 Drought-strategy categories partially explained di_erences in the impact of natural enemy exclusion

The drought-strategy categories were less useful for explaining changes to growth and survival with natural enemy exclusion. It has been suggested that drought-tolerant evergreen species are also more resistant to natural enemy pressure (Bravo-Monzón et al., 2022; Poorter, 2009; Poorter et al., 2014). Our results partially supported this theory. Leaf damage was always higher on deciduous species, and natural enemy exclusion appeared to benefit deciduous species slightly more than evergreen species (though the diferences were very small).

Early successional growth and survival was high for legumes. Gei et al. (2018) have identified multiple traits of the Fabaceae that promote their dominance in early successional TDF systems (Maza-Villalobos et al., 2020). We included 7 species from the Fabaceae and 3 species from other families in this experiment and so were unable to perform a robust analysis of the efect of BNF ability on performance. However, early successional RGR was also high for the non-leguminous species C. dodecandra and C. cujete, and early successional survival was high for C. dodecandra and G. ulmifolia. While legume traits can be beneficial in the low-water, low-nutrient, high-light environment of early succession, there are alternative strategies that allow non-legume species to perform well in these conditions. Disturbed TDF ecosystems are often dominated by legumes, which can competitively exclude other species, so these results suggest that planting of non-legumes species with alternative drought-tolerance strategies may help to counteract this dominance and increase tree diversity.

4.5 Conclusions

We have demonstrated that abiotic and biotic filters interact to determine seedling growth and survival across a gradient of TDF succession, with consequences for community assembly and restoration outcomes. Planting suitable drought-tolerant species in early successional high-resource environments is likely to lead to rapid growth and may help to establish a closed canopy, under which the combined efects of natural enemy pressure and resource limitation can promote species turnover towards the development of tree seedling communities that are more typical of mature forests. Specifically, recruitment of evergreen

species under the closed canopy could be monitored to indicate whether these later successional community assembly processes have recovered in restored forests.

Our results suggest that the amelioration of drought stress is a key abiotic driver of species turnover with TDF succession, inferred from the increasing performance of evergreen species relative to deciduous species later in succession. However, there are also resources that decrease with succession (light and possibly soil nutrients), which may prevent seedlings from recovering from natural enemy damage later in succession, such that the impact of natural enemy pressure on seedling survival is more severe. Therefore, species turnover with TDF succession results from an interaction of abiotic resource availability with biotic natural enemy pressure; natural enemies reinforce species-habitat associations and make existing successional abiotic gradients more divergent.

Chapter 5: Main Discussion

5.1 Overview

The research presented in this thesis contributes to the ecological understanding of the recovery of tropical dry forests (TDF), a vulnerable but understudied ecosystem type. The focus is on testing fundamental ecological theories that are applicable to the practice of forest restoration.

Forest restoration can be thought of as making deliberate interventions in the process of secondary forest succession, guiding or assisting the natural community assembly mechanisms. Theseinterventions fall along a continuum from minimal human involvement (i.e., unassisted recovery) to major landscape modification (i.e., intensively assisted recovery sensu Chazdon et al., 2024). Identifying the appropriate intervention level and type requires an understanding of the community assembly processes being modified, and how these are related to the site history and the phylogeographicand landscape context.

This thesis addresses TDF succession along three interrelated community assembly continua: deterministic versus stochastic assembly (Chapter 2; Chapter 3), abiotic versus biotic filtering (Chapter 2; Chapter 4), and dispersal versus establishment limitation (Chapter 2; Chapter 3). Below I highlight my findings about the roles of successional stage, land use intensity, spatial scale and tree ontogeny in determining how local communities assemble from the regional pool. I next link these findings to their practical application in restoration. My results suggestthat the target community should be defined by its functional composition, rather than its taxonomic composition, that restoration interventions will be most efective when targeted at the recruitment stage in tree ontogeny, and that restoration projects must consider the larger phylogeographic and landscape contexts that they are working in.

5.2 The balance of community assembly processes changes with:

a) Succession

Community assembly processes determine the trajectory of secondary succession, but the balance of these processes also changes depending on the successional stage. Early successional assembly processes create the early successional tree community at a site, which in turn creates the conditions for mid successional assembly processes to act, and so on. In other words, the balance of community assembly processes is both a cause and a consequence of the progression of succession, and this positive feedback loop is inherent to the powerful ability of succession to transform a site with highly disturbed and diminished vegetation into a mature secondary forest that can provide multiple ecosystem goods and services (Poorter et al., 2021).

I found strong gradients of resource availability and variability with succession. Light availability decreased substantially from early to mid succession (Chapter 2; Chapter 3), but became more spatially variable (Chapter 3). Conversely, water availability tended to increase with succession, though strong interseasonal variability in early successional environments (Werden et al., 2020a) may have promoted the drought-avoidant, resource-acquisitive strategy of deciduous species (Chapter 4). Indeed, both juvenile and adult tree communities shifted from deciduous nitrogen-fixing species with compound leaves to simple-leaved evergreen and brevi-deciduous species with large seeds and a high maximum height (Chapter 2; Chapter 4).

The magnitude of the change in functional community composition was greatest in the earlier stages of succession (Chapter 2). While this could be interpreted as a greater influence of abiotic filtering in early succession, as suggested by Bhaskar et al. (2014), Lohbeck et al. (2014), and Maza-Villalobos et al. (2020), my results provide mixed evidence for this. I did indeed find that the biotic filter had a greater impact on tree seedling performance later in succession (Chapter 4), though it does not necessarily follow that the abiotic filter is stronger early in succession. Furthermore, there was no evidence that functional traits related to resource use explained patterns of dispersal or establishment

limitation at any successional stage (Chapter 2). Levels of dispersal and establishment limitation were high throughout succession, and variation between species was instead explained by conspecific density across all successional environments (Chapter 2). Furthermore, natural enemy pressure limited seedling growth and survival in the late successional environment only, possibly due to a lack of resources to enable plants to recover lost biomass (Chapter 4). Tree recruitment is a combination of dispersal, establishment and survival, and I have shown that the biotic environment (in terms of conspecific density and natural enemy pressure) is important for all three of these demographic processes. Overall, my results show that both the abiotic and biotic environments change with succession due to the development of closed canopy vegetation, and that these gradients interact to afect the community assembly processes involved in tree recruitment, such that it is dificult to infer these processes from patterns of functional traits alone (Kraft et al., 2015; Kraft & Ackerly, 2010; Li et al., 2015). The experimental approach taken in Chapter 4 was necessary to demonstrate the interaction between abiotic and biotic filtering, so observational research (e.g., Chapters 2 and 3) is limited by the potential for misinterpretation of patterns that arise from multiple interacting mechanisms.

b) Land use intensity

The successional gradient across my study site was confounded with a gradient of prior land use intensity. This is a common phenomenon in human-modified landscapes, as the least productive or accessible sites are likely to both be used less intensively and be abandoned first (Chazdon & Guariguata, 2016; Jakovac et al., 2021). Additionally, restoration interventions had been applied non-randomly across the landscape, as less disturbed sites were prioritised for natural regeneration, while more disturbed sites were planted with a native species mix. Therefore, both historical and contemporary human land use may have influenced community assembly processes.

I identified some changes to community assembly processes that are likely attributable to diferences in land use intensity. For example, a positive relationship between light heterogeneity and tree recruit diversity was caused by shaded patches within a high-light

matrix that provided refugia for species from the richer shade-tolerant species pool (Chapter 3). However, this did not occur in all cases, possibly because extreme dispersal limitation, caused by the loss of nearby closed-canopy forest to act as a propagule source (Holl, 1999), prevented species from reaching all sites with a suitable light environment. This suggests that positive heterogeneity-diversity relationships (HDRs) are more likely to emerge in sites with intermediate levels of disturbance, where the abiotic environment is more heterogeneous, but suficient seed sources remain to overcome dispersal limitation.

However, my research overall suggests that successional gradients overcame any diferences in land use intensity across this landscape to determine the functional composition of the tree community. While the taxonomic composition of juvenile and adult tree communities was generally stochastic (Chapter 2; Chapter 3) and may partially reflect ecological contingencies created by land use legacies, there was clear functional similarity between each adult community and the juvenile community that preceded it in a successional chronosequence despite diferent land use histories (Chapter 2). This indicates that deterministic functional secondary succession overcame land use legacies.

c) Spatial scale

Spatial scale repeatedly emerged as a key factor that determined the balance of community assembly processes observed across the study landscape. Deterministic assembly was detected at larger spatial scales (where study extent was 0.5 – 6 km) but not at small spatial scales (where study extent less than 140 m; Chapter 2; Chapter 3). Large-scale deterministic assembly of the recruit community was likely caused by filtering by the abiotic environment, which resulted in a predictable community composition in terms of functional traits and a positive relationship between landscape scale environmental heterogeneity and beta diversity of recruits through compositional turnover (Chapter 2; Chapter 3).

The abiotic environment exhibited variation at multiple scales, and there was a remarkable amount of variation in soil carbon and nitrogen content even at spatial scales below 30 m. There was also a lot of species turnover at these small spatial scales. Despite this, recruit community composition and species turnover was mostly not explained by the abiotic

environment at small spatial scales (Chapter 3). Instead, conspecific negative density dependence was found to predict species' level of dispersal and establishment limitation at smaller spatial scales (Chapter 2). Overall, community assembly processes tended to be more deterministic and abiotic filtering dominant at larger spatial scales, but more stochastic and with an increasing importance of biotic filters at smaller spatial scales.

d) Ontogenetic stage

While community assembly processes can act at multiple ontogenetic stages of the tree community (Marques & Burslem, 2015), the focus of this thesis was on tree recruitment. While there is no generally accepted definition of when a tree can be considered to be "recruited" (Oliveira et al., 2019), the focus on the earliest ontogenetic stages (specifically dispersal, establishment, and seedling growth and survival) is justified as this is when most non-random mortality occurs (Green et al., 2014). Indeed, I showed that the deterministic processes that created a predictable functional community composition occurred between the reproductive adult stage and the juvenile stage, defined here as trees between 10 – 200 cm tall (Chapter 2).

Dispersal and establishment limitation were found to be strong and pervasive throughout succession (Chapter 2) and mediated the emergence of patterns such as HDRs that are predicted by ecological theory (Chapter 3). In Chapter 4, I used a planting experiment to overcome dispersal limitations and explore post-germination assembly processes. Growth and survival of the planted seedlings responded to the independent and combined efects of both abiotic and biotic filters. Specifically, the performance of deciduous species decreased with succession more than evergreen species. This occurred even though all species have a poor ability to cope with drought when small (Poorter & Markesteijn, 2008). When dispersal limitation was not controlled for, functional traits did not predict establishment limitation (Chapter 2), and small-scale species-habitat associations did not appear (Chapter 3). This highlights the importance of strong dispersal limitation in community assembly, which may preclude the action of other assembly mechanisms later in tree ontogeny.

5.3 Implications for TDF restoration

There are increasing calls for the practice of forest restoration to be improved through the application of ecological theory (Wainwright et al., 2018). This is of particular concern in tropical dry forest (TDF) ecosystems; nearly 90% of TDF globally has been disturbed by agriculture or ranching, and 70% of the pre-Hispanic TDF in Mexico has been deforested (Mesa-Sierra et al., 2022). The negative consequences of such forest loss for ecosystem services like soil fertility and the regulation of climatic and hydrological systems have led to national and international ecosystem restoration commitments, which cover 8 million hectares in Mexico alone (Mesa-Sierra et al., 2022). My research successfully utilised the infrastructure of a large-scale forest restoration project to test community assembly hypotheses within a restoration framework. The following recommendations for restoration best practice have emerged from my work:

1. Define the target community by its functional composition, rather than its taxonomic composition

Restoration projects often select one (or several) reference site(s) that help to define the target species composition for the project (Nelson et al., 2024; Rodrigues et al., 2011). This approach has the advantage of ensuring that the restored vegetation is appropriate to the climatic and edaphic conditions of the site and can help to ensure that targets are suficiently ambitious, for example in terms of species richness. However, there are drawbacks to this approach. Firstly, the goals of restoration projects, which should be developed in meaningful consultation with all relevant stakeholders (Nelson et al., 2024), may require the landscape to provide additional or alternative ecosystem goods and services to those provided by the reference ecosystem (Lamb, 2005, 2018; Martin et al., 2021). Secondly, climate and environmental change may mean that conditions are no longer suitable for species that historically existed at a site (Howe, 2014). Thirdly, identification of a suitable reference site is dificult, as 91% forests have experienced the impacts of some form of anthropogenic disturbance (Grantham et al., 2020) over the many centuries of human-forest interactions, so establishing a baseline “undisturbed” condition is often

impossible in practice. For example, the impacts of extensive deforestation and forest management by the Mayan civilisation until 1,100 years ago (Bohn et al., 2014; Vester et al., 2007) still afect the vegetation and soil of the forests of southern Mexico and northern Guatemala (Chazdon et al., 2007; Veldkamp et al., 2020). Finally, natural succession can be highly stochastic, and the chosen reference forest represents just one possible outcome of that natural process (Norden et al., 2015; Rodrigues et al., 2011).

Instead of defining the target of a restoration project based on the taxonomic composition of a reference forest, I concur with Brancalion & Holl (2016) that the functional composition of late-successional forests may represent a more appropriate target. This would address each potential drawback of the reference forest approach. Firstly, functional traits that provide the desired ecosystem goods and services can be actively promoted (Meli et al., 2014). Secondly, functional redundancy means that multiple species fulfil the same functional role in a forest (Cadotte et al., 2011), so a species that is expected to be suited to future climatic and environmental conditions may be a functional substitute for a climatically obsolete species. Thirdly, a focus on the functional composition of a forest reduces the need to identify appropriate baseline sites or historical periods. Finally, my own work in Chapter 2 demonstrated that TDF succession was functionally deterministic, despite stochasticity in the taxonomic trajectories of diferent sites. The functional composition of the tree community is more important for ecosystem functioning (Cadotte et al., 2011), and as such should be the focus of applied restoration work.

2. Identify and remove barriers to natural regeneration at the recruitment stage

Natural regeneration (i.e., unassisted recovery) has multiple benefits as an approach to forest restoration (Chazdon & Guariguata, 2016). Consistent with this argument, I found that natural regeneration restored the functional composition of the secondary forest studied in this thesis (Chapter 2) and appeared to increase environmental heterogeneity over time (Chapter 3). However, natural regeneration may be limited, leading to a state of arrested succession (Chazdon et al., 2007; Chazdon & Guariguata, 2016). To overcome arrested

succession, the barriers preventing natural regeneration must be identified and removed. Chapter 2 identified that processes acting during tree recruitment mostly determined the functional composition of the adult tree community, so management interventions are likely to be most efective if targeted at this stage in tree ontogeny.

For example, Chapter 3 suggested that strong dispersal limitation prevented shade-tolerant specialists from growing in environmentally suitable patches in early successional or highly disturbed areas. In TDF, shade-tolerant late-successional tree species tend to have large zoochorous seeds (Lohbeck et al., 2013, 2015). Therefore, planting trees with fleshy fruits to attract animal dispersers may help to reduce this dispersal limitation (Derroire et al., 2016b; Parrotta, 1995; Reid et al., 2015; Sanseverо et al., 2011).

My results also suggest that establishment of some species was limited by light availability (Chapter 3; Chapter 4). The open canopy of early succession promoted the growth and survival of the ten species planted in the experiment (Chapter 4), but high radiation levels and temperatures can also be damaging to shade-tolerant species (Chapter 3; Bazzaz, 1979; Benítez-Malvido et al., 2005; Bonilla-Moheno & Holl, 2010; Holl et al., 2011). Therefore, while open canopy conditions may be best for the growth and survival of planted trees in this ecosystem (Werden et al., 2020a), recovery of all functional groups may be promoted by the re-establishment of a closed canopy (Bourgeois et al., 2016; Viani et al., 2017).

3. Consider the phylogeographic context

Götzenberger et al. (2012) use the term “phylogeographic assembly” to refer to the processes that define the regional species pool, which is the species pool that ecological assembly rules (the focus of this thesis) act upon. Phylogeographic assembly processes are speciation, extinction and migration. Restoration projects rarely consider such processes (Hamilton et al., 2020), but in Chapter 3 I demonstrated the relevance of the phylogeographic context to patterns of tree recruitment at a landscape scale. An apparently positive HDR between heterogeneity in canopy openness and recruit species richness was caused by the colonisation of abiotic patches by species from diferently sized species pools. A common aim of restoration projects is to increase the alpha diversity of tree recruits, and these results

suggest that one way to achieve this is to create the appropriate abiotic conditions for the largest regional species pool.

There are also ways in which restoration can increase the size of the regional species pool by ensuring there is suficient genetic diversity to provide the material for speciation (Kardos et al., 2021). In other words, the maintenance or restoration of diversity-promoting processes should be encouraged. This research identified two diversity-promoting processes: conspecific negative density dependence (CNDD; Chapter 2) and species-specific natural enemy pressure (Chapter 4). CNDD has been shown to enhance diversity at multiple ontogenetic stages, including during dispersal (Chapter 2; Hille Ris Lambers et al., 2002), across the seed to seedling transition (Harms et al., 2000), and during the juvenile stages (Chapter 2; Green et al., 2014; LaManna et al., 2017; Webb & Peart, 1999). I found that CNDD acted during dispersal and establishment in all successional environments, though it has been suggested that CNDD is eroded in disturbed or early successional habitats (Pillay et al., 2018). In contrast, the results of Chapter 4 did show that natural enemy pressure only impacted seedling growth and survival in a late successional environment, suggesting that the diversity-promoting efects of species-specific natural enemy pressure may not act earlier in succession or in disturbed environments (in accord with Krishnadas et al., 2018 and Kulikowski et al., 2022).

It is also important for restoration planners and practitioners to ensure that they do not afect speciation, extinction and migration in ways that may decrease the size of the regional species pool. There is a risk that restoration work leads to biotic homogenisation (Holl et al., 2022). For example, a limited number of species are commonly planted in restoration projects because they are easier to propagate and have a record of successful establishment (Holl et al., 2022). The ten species planted in the experiment in Chapter 4 illustrate this point well; they were chosen based on availability in local plant nurseries, suggesting they are commonly planted. However, many of these species are likely to regenerate naturally anyway, and so planting will further exacerbate their existing dominance in disturbed landscapes. A clear example of this is Guazuma ulmifolia, which is commonly found in abandoned pastures and thrives in anthropogenic landscapes (Griscom & Ashton,

2011; Holl et al., 2022; Jakovac et al., 2022), but is also the 18th most commonly planted species by tree planting organisations in the tropics and subtropics (Martin et al., 2021) and the most commonly planted species in reported TDF restoration projects in Mexico (Mesa-Sierra et al., 2022). The widespread propagation and promotion of such species risks reducing genetic, functional and phylogenetic diversity (Holl et al., 2022) and therefore the potential for adaptation to changing climatic conditions, or even speciation.

4. Think at a landscape scale

Restoration projects often focus on increasing alpha diversity, but less attention is paid to beta or gamma diversity, with potential negative consequences for landscape multifunctionality and resilience (Holl et al., 2022). Forest Landscape Restoration (FLR) approaches aim to counter this by promoting landscape-level planning that incorporates multiple land uses and forest management approaches (Sayer et al., 2013). My results in Chapter 3 suggested that a combination of diferent restoration interventions across the landscape was associated with high compositional turnover of recruits (i.e., beta diversity). FLR approaches may therefore be efective in promoting landscape scale beta diversity of tree recruits and may have the additional benefits of increasing landscape-level resilience through redundancy efects and moving towards the systemic experimental restoration advocated by Howe & Martínez-Garza (2014).

5.4 Future work

Here I suggest future research that could be conducted to fill knowledge gaps that were not resolved in this thesis, or to address new questions raised by the work presented here.

Overcoming the limitations of large-scale observational plant surveys

There were three aspects of the design of my research that limited my ability to draw robust conclusions or make statements about the wider applicability of my results: the replication-scale trade-of, the confounding of successional stage with disturbance history, and the confounding of restoration plot age with restoration intervention type. Here I address each of these limitations and suggest how they could be overcome in future work.

In Chapter 1, I conducted spatially explicit nested surveys of the seed, juvenile and adult tree communities across three 1-hectare plots, each of which represented a different successional stage. Due to the time required to intensively survey such a large area (I surveyed a total of 19,465 juvenile and 879 adult trees), I was not able to increase the number of replicate plots within each successional stage. Such a trade-off between plot size and plot replication has been made in several studies (Capers et al., 2005; Huang et al., 2022; Norden et al., 2009b; Powers, 2006) but has clear disadvantages for the replicability and applicability of the results. It is therefore vital that future studies leverage opportunities to increase plot-level replication, while also using large, intensively surveyed plots, without which I would not have been able to demonstrate the scale-dependency of abiotic and biotic community assembly processes. It has been suggested that large-scale forest restoration projects could represent one such opportunity (Howe & Martínez-Garza, 2014); many projects globally are already planting trees across large areas, and some are monitoring the outcomes (Schubert et al., 2024). These planting designs and monitoring plans could be adapted to allow restoration-focused projects to also act as large-scale experimental tests of ecological theory, as demonstrated by Werden et al. (2020a) and Chapter 4 of this thesis.

Increased replication would also help to address the issues with confounded variables in this research. Firstly, the successional gradient explored in Chapters 2 and 4 was confounded with land use history, as is common in human-modified landscapes (Jakovac et al., 2021). This meant I was not able to attribute observed changes in the abiotic and biotic environment to either secondary succession or disturbance intensity. For example, the level of canopy openness, which was repeatedly identified as a key factor in tree recruitment, is a result of the balance of tree removal by humans and canopy recovery through secondary succession. Future research into secondary succession in TDF should either control for differences in historical land use intensity or include well replicated plots where land use intensity and successional stage vary orthogonally, so that their relative effects can be evaluated statistically. This could be used to test the hypothesis that different land use histories send secondary forests along different successional trajectories, for which the evidence is currently mixed (Derroire et al., 2016a; Estrada-Villegas et al., 2020; Guariguata

& Ostertag, 2001; Jakovac et al., 2021, 2022; Lebrija-Trejos et al., 2010a; Norden et al., 2009b, 2015; Rozendaal et al., 2019).

Similarly, the confounding of plot age with restoration intervention type in Chapter 3 meant that I was unable to identify the independent efects of diferent restoration interventions. This further highlights the value of long-term experimental restoration projects (e.g., Holl et al., 2020). However, there is tension between the need for randomisation in the application of restoration interventions as experimental treatments and the need to tailor the intervention to the site. In my study site, plot age and intervention type were confounded because natural regeneration (i.e., unassisted recovery) was more appropriate in less intensively used sites that had more remnant vegetation, while tree planting (i.e., moderately assisted recovery sensu Chazdon et al., 2024) was more appropriate in more intensively used sites, as per restoration best practice guidelines (Chazdon, 2013). This is a clear limitation to the use of restoration projects to experimentally test ecological theories, and in each case the trade-of should be made clear to all relevant stakeholders and decisions made based on the circumstances and aims of each project. In addition, some ecological research may require vegetation removal (e.g., Werden et al., 2020a) to disentangle the efects of diferent community assembly processes (Götzenberger et al., 2012; experimental removal of conspecific seeds or juveniles may have helped to uncover the mechanistic causes of the relationships between conspecific abundance and recruitment limitation in Chapter 2), which may be antithetical to the goal of increasing woody plant biomass through forest restoration. Communication and collaboration between projects (e.g., The Atlantic Forest Restoration Pact; Viani et al., 2017) may further allow for coordination to ensure that both restoration and research aims are met, and are each pursued in the most appropriate sites.

Selection and measurement of relevant functional traits

In Chapter 2, I was unable to explain variation in recruitment limitation by functional traits. This was unexpected because the study site encompassed strong abiotic gradients and clear changes to the functional composition of juvenile and adult communities. I attributed

this result to the spatial scale of the analysis, but it must also be considered that the selection of relevant functional traits is challenging (de Bello et al., 2021). It has been suggested that easy to measure "soft" traits are less relevant for growth and survival of seedlings in TDF than ecophysiological "hard" traits, and that hard and soft traits are generally uncorrelated (Werden et al., 2020a). Similarly, drought strategy categories of species were based on their phenological categories in Chapter 3. However, these binary categories did explain variation in natural enemy damage, growth and survival, even though deciduous and evergreen phenological habit can also be considered to be two extremes of a continuum of leaf retention time (Lohbeck et al., 2015; Méndez-Alonzo et al., 2012). There may therefore be a trade-of between the ease of measurement of a functional trait and its relevance to community assembly processes, and the appropriate amount of efort put into measuring functional traits will depend on the aims of future research.

5.5 Summary

In conclusion, I have shown that the ecological community assembly rules that act during tree recruitment changed throughout secondary succession of a TDF. Abiotic filtering dominated earlier in succession (Chapter 2; Chapter 4), leading to predictable changes in the functional community composition of recruits, while biotic filters provided important diversity-promoting mechanisms in late successional forests (Chapter 2; Chapter 4). My results further demonstrated that deterministic abiotic filtering only emerged between patches 0.5 – 6.0 km apart (Chapter 2; Chapter 3), suggesting that landscapes should be managed to promote environmental heterogeneity at larger spatial scales. By testing community reassembly theories in a relatively understudied tropical dry forest ecosystem, I have produced results that can be applied to the restoration of this ecosystem and suggested how such large-scale restoration work could be leveraged to further test hypotheses generated by classical ecological theory.

6. References

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7. Supplementary Material

7.1 Main introduction

Table S1.2 Definitions of seedling, sapling and adult stages in tree ontogeny. All papers on Web of Science returned from the search string "tropical forest seedling sapling" were checked for a quantitative definition of a seedling, sapling, or adult tree.

Reference	Seedlingdefinition	Saplingdefinition	Adult definition
(Norden & Stevenson, 2015)	< 170 cm height and < 1 cm DBH	1 - 5 cm DBH	> 10 cm DBH
(Vargas-Rodriguez et al., 2005)	< 130 cm height	≥ 130 cm height and < 2.5 cm DBH	≥ 2.5 cm DBH
(Dupuy & Chazdon, 2006)	20 - 100 cm height	≥ 100 cm height and < 5 cm DBH	
(Russell-Smith, 1996)		≤ 200 cm or > 200 cm height but < 5 cm DBH	
(Slot & Winter, 2018)		30 - 250 cm height	
(Chaturvedi et al., 2014)		100 - 680 cm height and 3.6 - 9.6 cm stem diameter	
(Ramage et al., 2017)		1 - 5 cm DBH	
(Walker, 2000)	< 10 cm height	10 - 100 cm height	
(Velázquez et al., 2016)		1 - 4 cm DBH	
(McLaren et al., 2005)	0 - 2 mm RCD	< 130 cm height and 2 - 20 mm RCD	≥ 2 cm DBH
(Dent et al., 2013)	20 - 100 cm height	≥ 100 cm height and < 5 cm DBH	≥ 5 cm DBH
(Gilbert et al., 2006)	≤ 50 cm height	1 - 3.9 cm DBH	
(Guariguata, 1998)			
(Paine et al., 2009)	10 - 50 cm height	> 1 m height and ≤ 10 cm DBH	
(Olvera-Vargas et al., 2014)	< 130 cm height	≥ 130 cm height and < 5 cm DBH	≥ 5 cm DBH and ≥ 130 cm height
(Toledo-Aceves et al., 2009)	50 - 100 cm height	> 100 cm height and ≤ 10 cm DBH	
(T. O. Vieira et al., 2015)	< 50 cm height and < 2 cm diameter at ground level	160 - 200 cm height and < 8 cm diameter at ground level	

(Nishimura & Suzuki, 2001)	< 98 cm height		> 15 cm DBH
(Krishnadas et al., 2018)		1 - 5 cm DBH	> 5 cm DBH
(Queenborough et al., 2009)	> 1 cm height and < 1 cm DBH		
(Oliveira et al., 2021)	< 1 cm DBH	1 - 5 cm DBH	≥ 5 cm DBH
(Chang-Yang et al., 2021)	< 1 cm DBH		
(Saavedra et al., 2017)	< 10 cm height	15 - 100 cm height	
(Zhu et al., 2015)	≤ 20 cm height and < 1 cm DBH	1 - 4.9 cm DBH	≥ 10 cm DBH
(Teegalapalli et al., 2010)	< 25 cm height	25 - 100 cm height	
(Botzat et al., 2015)	≤ 1 cm diameter at base or ≤ 75 cm height	≤ 5 cm diameter at base or ≥ 75 cm height	≥ 5 cm DBH

7.2 Chapter 2

Table S2.1 Functional traits of woody plant species surveyed. Traits used in this study: Growth form; Maximum height (m); Leaf phenological habit; Seed mass (g); Petiole length (mm); Leaf type; SLA (mg mm^{-2}); Capable of biological nitrogen fixation (Y/N). Field measurements were taken for the 10 species in bold, sources of trait data for all other species are given in the reference list below.

Species	Family	Growth form	Max height	Leaf Phenology	Seed mass	Petiole length	Leaf type	SLA	N fix
Amyris elemifera	Rutaceae	Tree[1]	15[1]	Evergreen[8,9]	0.06[10]	40[11]	Compound[9]	7.62[12]	N[13]
Annona reticulata	Annonaceae	Tree[1]	10[1]	Deciduous[14]	0.19[10]	20[5]	Simple[14]	13.42[14]	N[13]
Aphelandra scabra	Acanthaceae	Shrub[1]	3.5[1]	Evergreen[15]		5[5]	Simple[15]		N[13]
Ateleia gummifera	Fabaceae	Tree[1]	15[1]	Deciduous[1]	0.02[10]	2[5]	Compound[16]		Y[7]
Bauhinia divaricata	Fabaceae	Tree/ shrub[1]	7[1]	Deciduous[2,3]	0.06[10]	37[17]	Simple[9]	17.4[18]	Y[7]
Bonellia flammea	Primulaceae	Tree/ shrub[1]	5[1]	Evergreen[3]		2	Simple[6]	11.7[18]	N[13]
Bursera simaruba	Burseraceae	Tree[1]	30[1]	Deciduous[3,19]	0.11[4]	110.53[20]	Compound[14]	18.5[18]	N[7]
Byrsonima bucidifolia	Malpighiaceae	Tree[1]	15[1]	Brevi-deciduous[2]			Simple[6]	17.1[18]	N[13]
Calophyllum brasiliense	Calophyllaceae	Tree[1]	20[1]	Brevi-deciduous[19]	2.5[4]	15[5]	Simple[26]	11.23[26]	N[7]
Cameraria latifolia	Apocynaceae	Tree/ shrub[1]	15[1]	Deciduous[2]		5[27]	Simple[15]		N[13]
Casearia emarginata	Salicaceae	Tree/ shrub[1]	6[1]	Evergreen[3]	0.20	3	Simple[6]	18.15 (genus)	N[13]

Cenostigma gaumeri	Fabaceae	Tree[1]	20[1]	Deciduous[1,3]			Compound[6]	12.47[21]	Y[22]
Chamaedorea seifrizii	Arecaceae	Palm[1]	5[1]	Evergreen[2]		200[28]	Compound[15]	15.11 (genus)	N[13]
Chloroleucon mangense	Fabaceae	Tree[1]	15[1]	Deciduous[3]	0.04[29]	18[5]	Compound[15]	25.57[30]	Y[7]
Chrysobalanus icaco	Chrysobalanac-eae	Tree/ shrub[1]	10[1]	Evergreen[3]	1.7[31]	4[32]	Simple[15]		N[13]
Coccoloba acapulcensis	Polygonaceae	Tree[1]	20[1]	Deciduous[2]			Simple[9]	19.8[18]	N[13]
Coccoloba barbadensis	Polygonaceae	Tree[1]	12[1]	Deciduous[2]	0.03[10]	20[5]	Simple[15]	9.69[33]	N[7]
Coccoloba cozumelensis	Polygonaceae	Tree/ shrub[1]	15[1]	Deciduous[2]			Simple[6]	13.7[18]	N[13]
Coccoloba spp	Polygonaceae	Tree/ shrub[1]		Deciduous[2]	0.05[6]		Simple[6]		N[13]
Cochlospermum vitifolium	Bixaceae	Tree[1]	15[1]	Deciduous[1]	0.03[10]		Simple[1]	16.65[34]	N
Cordia alliodora	Boraginaceae	Tree[1]	25[1]	Deciduous[19]	0.009[4]	14.40[35]	Simple[26]	12.28[30]	N[7]
Cordia dodecandra	Boraginaceae	Tree[1]	25[1]	Deciduous[19]	2.44[10]	21.93[6]	Simple[15]	8.68[6]	N[13]
Coulteria mollis	Fabaceae	Tree[1]	25[1]	Deciduous[23]	0.12[10]		Compound[6]	13.4[18]	Y[22]
Crescentia cujete	Bignoniaceae	Tree[1]	10[1]	Brevi-deciduous[19]	0.03[10]	3.72[6]	Simple[15]	6.65[6]	N[7]
Croton arboreus	Euphorbiaceae	Tree/ shrub[1]	15[1]	Deciduous[2]	0.03[6]		Simple[6]	16.1[18]	N[13]
Dalbergia glabra	Fabaceae	Liana[5]	5[17]	Evergreen[3]	0.04[10]	25[17]	Compound[5]	30.49 (genus)	Y
Damburneya salicifolia	Lauraceae	Tree/ shrub	25	Evergreen[3]			Simple	11.7[18]	N[13]
Diospyros anisandra	Ebenaceae	Tree/ shrub[1]	10[1]	Evergreen[3]	0.15[10]	2[27]	Simple[15]	11.14 (genus)	N[13]
Diospyros bumelioides	Ebenaceae	Tree/ shrub[1]	10[1]	Evergreen[36]	0.51 (genus)	1[27]	Simple[6]	11.14 (genus)	N[13]
Diospyros salicifolia	Ebenaceae	Tree/ shrub[27]	6[37]	Brevi-deciduous[37]	0.51 (genus)	4.71[20]	Simple[20]	11.3[18]	N[13]
Diphysa carthagenensis	Fabaceae	Tree[1]	10[1]	Evergreen[3]	0.02[10]		Compound[6]	12.39[21]	Y[7]
Ehretia tinifolia	Boraginaceae	Tree[1]	25[1]	Brevi-deciduous[2]			Simple[15]	5.70 (genus)	N[13]
Entada polystachya	Fabaceae	Liana[32]	15[32]	Brevi-deciduous[38]	0.30[10]	70[17]	Compound[15]	15.12[12]	Y[7]
Erythrostemon yucatanensis	Fabaceae	Tree/ shrub[25]	10[25]	Deciduous[3]	0.21[10]		Compound[6]	7.73[21]	Y[22]
Erythroxylum bequaertii	Erythroxylaceae	Tree[25]	10[25]	Deciduous[25]			Simple[6]		N[13]
Erythroxylum rotundifolium	Erythroxylaceae	Tree/ shrub[1]	8[1]	Deciduous[2]	0.02[10]		Simple[15]	6.85[12]	N[13]
Eugenia axillaris	Myrtaceae	Tree/ shrub[25]	9[16]	Evergreen[3]	0.08[10]		Simple[15]	9.52[12]	N[13]
Eugenia capuli	Myrtaceae	Tree[1]	12[1]	Brevi-deciduous[1]			Simple[6]	12.72[30]	N[13]
Ficus cotinifolia	Moraceae	Tree[5]	20[5]	Evergreen[19]	0.0002[10]	90[5]	Simple[15]		N[13]
Gliricidia sepium	Fabaceae	Tree[1]	15[1]	Deciduous[14,19]	0.08[39]	29.64[6]	Compound[20]	12.05[6]	Y[7]
Guazuma ulmifolia	Malvaceae	Tree[1]	20[1]	Deciduous[14,19]	0.004[29]	15.05[6]	Simple[20]	13.47[6]	N[7]
Guettarda gaumeri	Rubiaceae	Tree/ shrub[1]	10[1]	Deciduous[2]	0.03[6]	7[27]	Simple[6]		N[13]
Gymnopodium floribundum	Polygonaceae	Tree/ shrub[1]	12[1]	Deciduous[2,3]	0.003[6]		Simple[15]	17.1[18]	N[7]
Haematoxylum campechianum	Fabaceae	Tree[1]	18[1]	Evergreen[19]	0.02[10]	8.09[6]	Compound[15]	13.55[18]	N[7,24]

Hamelia patens	Rubiaceae	Tree/ shrub[1]	4[1]	Deciduous[2]	0.00005[10]	80[5]	Simple[26]	51.74[26]	N[7]
Havardia albicans	Fabaceae	Tree[1]	10[1]	Deciduous[2,3]	0.07[10]	28[11]	Compound[15]	13.87[21]	Y[7]
Hiraea fagifolia	Malpighiaceae	Liana[40]	3.5			12[5]	Simple[15]		N[13]
Hyperbaena winzerlingii	Menispermaceae	Tree[1]	12[1]	Evergreen[2]		10[5]	Simple[6]		N[13]
Jatropha gaumeri	Euphorbiaceae	Tree/ shrub[1]	10[1]	Deciduous[2]		125	Simple[15]	18.58[21]	N[7]
Leucaena leucocephala	Fabaceae	Tree/ shrub[1]	12[1]	Evergreen[6]	0.05[39]	25.47[6]	Compound[15]	12.62[6]	Y[7]
Lonchocarpus rugosus	Fabaceae	Tree[1]	15[1]	Brevi-deciduous[14]	0.08[10]	38.01[20]	Compound[20]	19.7[18]	Y[24]
Lysiloma latisiliquum	Fabaceae	Tree[1]	25[1]	Deciduous[19]	0.03	25.43[6]	Compound[15]	16.06[6]	Y[7]
Machaerium salvadorense	Fabaceae	Shrub/ tree/ liana[5]	10[5]				Compound[26]	22.42[26]	Y[24]
Machaonia lindeniana	Rubiaceae	Tree/ shrub[1]	10[1]	Evergreen[3]		5[27]	Simple[6]		N[13]
Malpighia lundellii	Malpighiaceae	Tree/ shrub[25]	10[25]	Evergreen			Simple[6]		N[13]
Malvaviscus arboreus	Malvaceae	Shrub[1]	5[1]	Deciduous[2]	0.05[10]	46.37[20]	Simple[20]	28.34[20]	N[13]
Manilkara zapota	Sapotaceae	Tree[1]	25[1]	Evergreen[19]	0.13[10]	23[5]	Simple[15]	10.1[18]	N[7]
Mariosousa dolichostachya	Fabaceae	Tree[41]	15	Deciduous[19]	0.04[10]		Compound		Y[7]
Metopium brownei	Anacardiaceae	Tree[1]	25[1]	Deciduous[19]			Compound[15]	15.2[18]	N[13]
Mimosa bahamensis	Fabaceae	Tree/ shrub[1]	10[1]	Deciduous[2]	0.02[10]	20[11]	Compound[15]	10.6[18]	Y[7]
Mosannona depressa	Annonaceae	Tree[1]	15[1]	Deciduous[2]	0.36[4]		Simple[15]	10.4[18]	N[13]
Neea psychotroides	Nyctaginaceae	Tree/ shrub[1]	15[1]	Evergreen[3]	0.24[4]	2.09[42]	Simple[1]	18.0[43]	N[13]
Parathesis cubana	Primulaceae	Tree/ shrub[1]	12[1]	Evergreen[2]	0.08[6]	22[5]	Simple[15]		N[13]
Parmentiera millspaughiana	Bignoniaceae	Tree[1]	5[1]	Deciduous[3]		40	Simple[6]		N[13]
Paullinia bracteosa	Sapindaceae	Liana[32]		Evergreen[2]	0.06[6]	220[32]	Compound[15]	19.40[44]	N[13]
Piscidia piscipula	Fabaceae	Tree[1]	20[1]	Deciduous[45]	0.02[10]		Compound[15]	14.9[18]	Y[7]
Pithecellobium lanceolatum	Fabaceae	Tree/ shrub[1]	5[1]	Evergreen[2]		30[5]	Compound[15]	15.4[12]	Y[7]
Platymiscium yucatanum	Fabaceae	Tree[1]	25[1]	Evergreen[2]	0.05[10]	39.32[6]	Compound[15]	12.52[6]	Y[24]
Plumeria rubra	Apocynaceae	Tree[27]	20[27]	Deciduous[19]	0.04[10]	60[27]	Simple[15]	38.85[46]	N[7]
Pouteria amygdalina	Sapotaceae	Tree[1]	25[1]	Evergreen[2]	2.04 (genus)	19[27]	Simple[15]	22.50 (genus)	N[13]
Psidium oligospermum	Myrtaceae	Tree[27]	30[27]	Brevi-deciduous[19]	4.13 (genus)	3[32]	Simple[15]	11.39[30]	N[13]
Randia aculeata	Rubiaceae	Tree/ shrub[1]	7[1]	Deciduous[2]	0.10[47] (genus)	1[32]	Simple[15]	12.2[18]	N[7]
Randia longiloba	Rubiaceae	Tree/ shrub	12[1]	Evergreen[3]	0.10[47] (genus)		Simple[1]	14[18]	N[13]
Rinorea guatemalensis	Violaceae	Tree[6]	12	Evergreen[48]	0.05[4]	5.38[49]	Simple[15]	15.87[49]	N[13]
Roseodendron donnell-smithii	Bignoniaceae	Tree[50]	35[50]	Deciduous[19]	0.006[10]	260	Simple[15]	15.98[30]	N[13]
Sebastiania glandulosa	Euphorbiaceae	Tree[6]	10[1]	Evergreen[3]			Simple[14]		N[13]
Semialarium mexicanum	Celastraceae	Tree[1]	20[1]	Deciduous[2]	0.08[10]	3.19[20]	Simple[20]	13.50[20]	N[13]

Senegalia gaumeri	Fabaceae	Tree/ shrub[1]	20[1]	Deciduous[2]	0.04[39]		Compound[6]	14.61[21]	Y[7]
Senna racemosa	Fabaceae	Tree/ shrub[1]	10[1]	Deciduous[2]	0.03[6]	45[17]	Compound[15]	12.56[21]	N[7]
Sideroxylon salicifolium	Sapotaceae	Tree[1]	25[1]	Evergreen[3]	0.07[10]	12[27]	Simple[1]		N[13]
Simira salvadorensis	Rubiaceae	Tree[1]	25[1]	Evergreen[19]	0.03[10]	42[27]	Simple[15]		N[13]
Solanum erianthum	Solanaceae	Tree/ shrub[25]	8[25]	Deciduous[2]	0.0008[51]	100[5]	Simple[15]	14.90 (genus)	N[13]
Spondias spp	Anacardiaceae	Tree/ shrub[1]		Deciduous[3]	1.09 (genus)		Compound[1]		N[13]
Tabernaemontana alba	Apocynaceae	Tree/ shrub[5]	10[5]	Deciduous[2]	0.06[4]	25[27]	Simple[15]		N[13]
Talisia floresii	Sapindaceae	Tree[1]	25[1]	Evergreen[2]		65	Compound[15]		N[13]
Tara vesicaria	Fabaceae	Tree/ shrub[5]	9[5]	Evergreen[3]	0.17[6]	37.32[6]	Compound[6]	10.81[6]	N[24]
Terminalia buceras	Combretaceae	Tree[1]	30[1]	Evergreen[2]	0.01[10]	12[5]	Simple[15]	15.71[12]	N[13]
Trema micranthum	Cannabaceae	Tree[1]	10[1]	Evergreen[2]	0.002[29]	18[32]	Simple[6]	20.56[44]	N[7]
Trichilia glabra	Meliaceae	Tree[1]	15[1]	Deciduous[2]			Compound[14]	16.02[14]	N[13]
Vachellia cornigera	Fabaceae	Tree/ shrub[1]	7[1]	Deciduous[2,3]	0.08[4]	10[5]	Compound[6]	15.71	Y[7]
Wimmeria bartlettii	Celastraceae	Tree[27]	25[27]	Evergreen[26]		8[5]	Simple[26]	11.86[42]	N[13]
Xylosma flexuosa	Salicaceae	Tree/ shrub[1]	5[1]	Evergreen[2]	0.4[52]	1.52[20]	Simple[20]	11.54[20]	N[13]
Zygia conzattii	Fabaceae	Tree[6]	15[5]	Evergreen (genus)[3]	0.33[6]	3[5]	Compound[6]		Y[24]

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Box S2.1 Tests of the assumption of equal variance among groups for PERMANOVA

The early successional juvenile community had higher variance than the mid and late successional juvenile communities (for taxonomic composition, a mean diference with 95% CI of 0.16 (0.08 – 0.24) and 0.20 (0.13 – 0.28) respectively; for functional composition, a mean diference of 0.09 (0.03 – 0.14) and 0.07 (0.02 – 0.13) respectively). The mid successional adult community also had higher variance than the late successional adult community for taxonomic composition (mean diference of 0.28 (0.18 – 0.38) but not for functional composition (mean diference of 0.04 (-0.04 –0.11)).

Box S2.2 Recruitment limitation calculations

For calculations of establishment limitation, the number of stations with seeds present was multiplied by four to scale it to the same area as the area over which juveniles were measured (as the juvenile quadrats are four times the area of the seed traps; Werden et al., 2020b). This assumes that seeds would have been evenly distributed across the area of the quadrats at the same density as they were found in the traps. The establishment limitation calculation gives for each species the proportion of stations that received seeds that did not then have a juvenile. It is biologically impossible for a station to have juveniles but no seeds; any instances of this were an artefact generated by the temporal disconnect of the surveys of diferent life stages or the presence of seeds that were not caught in the seed traps, and were removed from the dataset. Establishment limitation was only calculated for species that had ³10 seeds in the plot to ensure the calculations had a suficiently high denominator to be robust. All species were included in the calculations of dispersal limitation, as rare seeds can be interpreted as highly dispersal limitated. Expected dispersal limitation is also equal to source limitation, as it is the number of traps that would be reached if the total number of seeds of a species in the plot were equally distributed between traps (Muller-Landau et al., 2002).

Table S2.2 Observed and expected dispersal limitation

Dispersal limitation						
	Early		Mid		Late	
Species	Observed	Expected	Observed	Expected	Observed	Expected
Arrabidaea spp			0.88	0.70 (0.51 - 0.88)	**0.96**	0.62 (0.41 - 0.82)
Bonellia flammea						
Bursera simaruba						
Casearia emarginata						
Cenostigma gaumeri						
Coccoloba acapulcensis					**0.84**	0.47 (0.26 - 0.67)
Coccoloba spp			**0.84**	0.26 (0.08 - 0.43)	**0.80**	0.01 (-0.03 - 0.05)
Cochlospermum vitifolium						
Cordia dodecandra					0.96	0.85 (0.71 - 1.00)
Croton arboreus	**0.20**	0.00 (0.00 - 0.00)	**0.08**	0.00 (0.00 - 0.00)	**0.16**	0.00 (-0.02 - 0.02)
Dalbergia glabra			**0.92**	0.70 (0.52 - 0.88)	0.92	0.93 (0.83 - 1.03)
Erythrostemon yucatanensis						
Erythroxylum bequaertii						
Gliricidia sepium			0.88	0.88 (0.75 - 1.01)		
Guettarda gaumeri			**0.80**	0.03 (-0.04 - 0.11)	**0.68**	0.21 (0.05 - 0.37)
Gymnopodium floribundum	0.96	0.96 (0.88 - 1.04)	0.00	0.00 (0.00 - 0.00)	**0.56**	0.02 (-0.04 - 0.08)
Haematoxylum campechianum			0.92	0.85 (0.71 - 0.99)	0.84	0.67 (0.48 - 0.87)
Havardia albicans	**0.96**	0.79 (0.62 - 0.95)	**0.48**	0.23 (0.07 - 0.38)		
Hiraea fagifolia					0.76	0.62 (0.43 - 0.82)
Hyperbaena winzerlingii						
ID 73						
ID 74						
ID 77						
Jatropha gaumeri						
Leucaena leucocephala			0.96	0.96 (0.88 - 1.04)		
Lonchocarpus rugosus					0.92	0.92 (0.81 - 1.03)
Lysiloma latisiliquum						
Manilkara zapota					0.92	0.92 (0.81 - 1.03)
Metopium brownei						
Mimosa bahamensis	**0.60**	0.01 (-0.03 - 0.06)	**0.52**	0.00 (0.00 - 0.00)		
Parathesis cubana					0.96	0.92 (0.81 - 1.03)
Paullinia bracteosa					**0.76**	0.11 (-0.02 - 0.23)
Piscidia piscipula	0.96	0.82 (0.66 - 0.98)				
Platymiscium yucatanum					0.96	0.96 (0.89 - 1.04)
Plumeria rubra						
Pouteria amygdalina						
Psidium oligospermum					**0.48**	0.00 (-0.01 - 0.02)
Sebastiania glandulosa						
Senna racemosa	**0.80**	0.38 (0.18 - 0.58)				
Talisia floresii						
Tara vesicaria	**0.80**	0.60 (0.41 - 0.80)				
Terminalia buceras					**0.08**	0.00 (0.00 - 0.00)
Vachellia cornigera	**0.96**	0.64 (0.45 - 0.83)			0.88	0.73 (0.56 - 0.90)
Zygia conzattii						

Table S2.3 Observed and expected establishment limitation

Establishment limitation						
	Early		Mid		Late	
Species	Observed	Expected	Observed	Expected	Observed	Expected
Arrabidaea spp					1.00	1.00 (1.00 - 1.00)
Coccoloba acapulcensis					1.00	1.00 (1.00 - 1.00)
Coccoloba spp			**0.94**	0.55 (0.31 - 0.78)	**0.95**	0.20 (0.04 - 0.36)
Croton arboreus	1.00	1.00 (1.00 - 1.00)	**0.92**	0.69 (0.51 - 0.87)	**0.95**	0.57 (0.36 - 0.78)
Guettarda gaumeri			**0.85**	0.64 (0.45 - 0.84)	1.00	0.96 (0.87 - 1.05)
Gymnopodium floribundum			**0.95**	0.40 (0.21 - 0.59)	1.00	1.00 (1.00 - 1.00)
Haematoxylum campechianum					1.00	0.96 (0.81 - 1.11)
Havardia albicans			1.00	1.00 (1.00 - 1.00)		
Hiraea fagifolia					1.00	0.72 (0.42 - 1.02)
Mimosa bahamensis	0.92	0.76 (0.59 - 0.93)	**0.92**	0.73 (0.56 - 0.90)		
Paullinia bracteosa					**0.79**	0.14 (-0.01 - 0.28)
Psidium oligospermum					**0.77**	0.00 (0.00 - 0.00)
Senna racemosa	1.00	1.00 (1.00 - 1.00)				
Tara vesicaria	1.00	0.81 (0.56 - 1.07)				
Terminalia buceras					0.97	0.86 (0.72 - 0.99)
Vachellia cornigera	1.00	0.89 (0.66 - 1.11)				

Table S2.4 Table of results for models of ∂ recruitment limitation.

		∂ dispersal limitation		∂ establishment limitation	
Explanatory variable	DF	c^2	p-value	c^2	p-value
Successional stage	2	0.58	0.75	1.25	0.53
Successional stage * Maximum height	2	21.71	<0.001†	-	-
Maximum height	1	-	-	0.47	0.49
Successional stage * Seed mass	2	-	-	8.19	0.02
Seed mass	1	0.23	0.63	-	-

Leaf phenological habit	3	-	-	3.78	0.29
Leaf type	1	-	-	1.19	0.28
SLA	1	-	-	0.51	0.47
Nitrogen fixation	1	-	-	0.72	0.40

† Fixed efects of model explained only 4% of variation (Marginal $R^2 = 0.04$, conditional $R^2 = 0.22$).

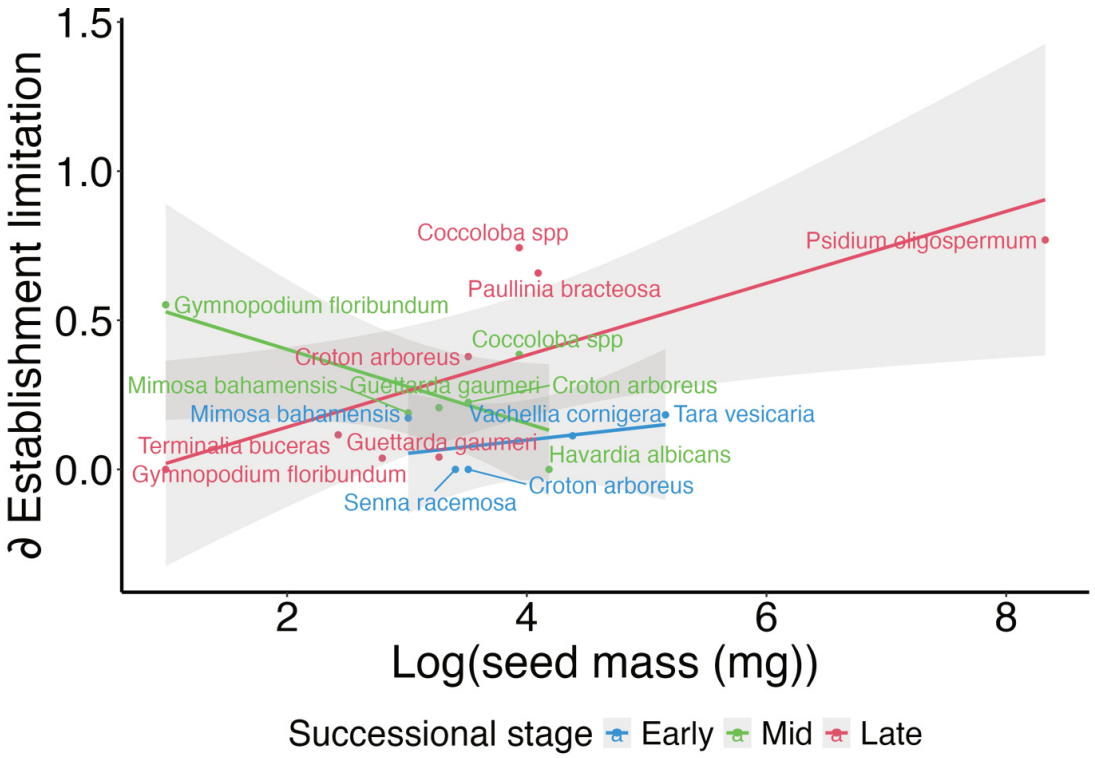


Figure S2.1 $\partial_{establishment}$ limitation increased with seed mass in the late-successional plot, but not in the early or mid successional plots. Grey area indicates 95% confidence interval.

7.3 Chapter 3

Table S3.1 Intervention type and age of plots. Reference plots have been continuously closed canopy for at least 30 years, and actual age is not known.

Plot number	Forest type	Age (years)
1	Planted	1
2	Nat. Regen.	6
3	Reference	30
4	Planted	0
5	Nat. Regen.	6
6	Nat. Regen.	6
7	Reference	30
8	Reference	30
9	Reference	30
10	Planted	1
11	Planted	1
12	Reference	30
13	Reference	30
14	Reference	30
15	Nat. Regen.	6
16	Nat. Regen.	6
17	Nat. Regen.	2
18	Nat. Regen.	2
19	Planted	2
20	Planted	2

Table S3.2 Within-plot partial Mantel tests of the correlation between compositional dissimilarity and environmental distance (all environmental variables), correcting for spatial autocorrelation.

Plot number	Pearson correlation	p-value	Corrected p-value	Forest type
1	NA	NA	NA	Planted
2	-0.24	0.80	1.000	Nat. Regen.
5	0.01	0.45	1.000	Nat. Regen.
6	-0.12	0.75	1.000	Nat. Regen.
7	-0.03	0.48	1.000	Reference
8	0.27	0.05	0.735	Reference
9	-0.09	0.66	1.000	Reference
12	0.32	0.10	1.000	Reference
13	-0.06	0.68	1.000	Reference
14	**0.46**	0.00	**0.015**	Reference
15	-0.02	0.51	1.000	Nat. Regen.
16	-0.09	0.76	1.000	Nat. Regen.
17	-0.24	0.73	1.000	Nat. Regen.
18	0.46	0.04	0.675	Nat. Regen.
19	0.06	0.40	1.000	Planted
20	0.03	0.43	1.000	Planted

Table S3.3 Within-plot partial Mantel tests of the correlation between compositional dissimilarity and environmental distance (soil variables only), correcting for spatial autocorrelation.

Plot number	Pearson correlation	p-value	Corrected p-value	Forest type
1	NA	NA	NA	Planted
2	-0.21	0.765	1.000	Nat. Regen.
5	0.01	0.440	1.000	Nat. Regen.
6	-0.12	0.771	1.000	Nat. Regen.
7	-0.03	0.491	1.000	Reference
8	0.31	0.031	0.465	Reference
9	-0.21	0.876	1.000	Reference
12	0.26	0.091	1.000	Reference
13	-0.05	0.684	1.000	Reference
14	**0.44**	0.001	**0.015**	Reference
15	-0.02	0.503	1.000	Nat. Regen.
16	-0.02	0.561	1.000	Nat. Regen.
17	-0.16	0.654	1.000	Nat. Regen.
18	0.43	0.047	0.705	Nat. Regen.
19	-0.02	0.538	1.000	Planted
20	-0.01	0.468	1.000	Planted

Table S3.4 Within-plot partial Mantel tests of the correlation between compositional dissimilarity and environmental distance (canopy openness only), correcting for spatial autocorrelation.

Plot number	Pearson correlation	p-value	Corrected p-value	Forest type
1	NA	NA	NA	Planted
2	-0.14	0.676	1.000	Nat. Regen.
5	0.40	0.025	0.375	Nat. Regen.
6	-0.13	0.823	1.000	Nat. Regen.
7	0.30	0.100	1.000	Reference
8	-0.18	0.944	1.000	Reference
9	-0.09	0.690	1.000	Reference
12	-0.26	0.974	1.000	Reference
13	-0.02	0.575	1.000	Reference
14	-0.23	0.972	1.000	Reference
15	-0.31	0.974	1.000	Nat. Regen.
16	0.00	0.496	1.000	Nat. Regen.
17	0.15	0.318	1.000	Nat. Regen.
18	0.20	0.206	1.000	Nat. Regen.
19	-0.06	0.556	1.000	Planted
20	-0.05	0.501	1.000	Planted

7.4 Chapter 4

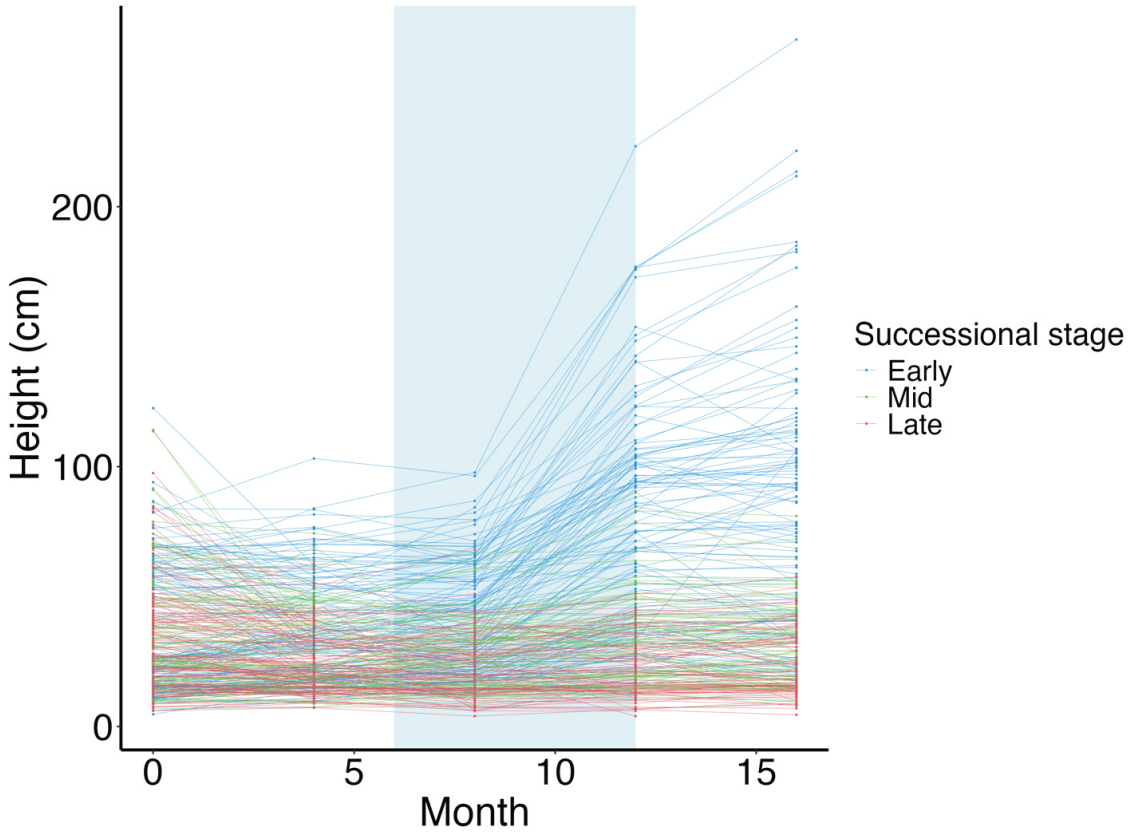


Figure S4.1 Most growth happened in the early successional treatment during the wet season (months 8–12). Season had a significant efect on growth. The fixed defect of season alone explained 10% of the variation in RGR (R^2_c = 0.28, R^2_m = 0.10). The fixed efects of season ´successional environment explained 40% of the variation in RGR (R^2_c = NA, R^2_m = 0.40). There was a significant interaction between season and successional environment – the fastest growth was in the early successional environment during the wet season.

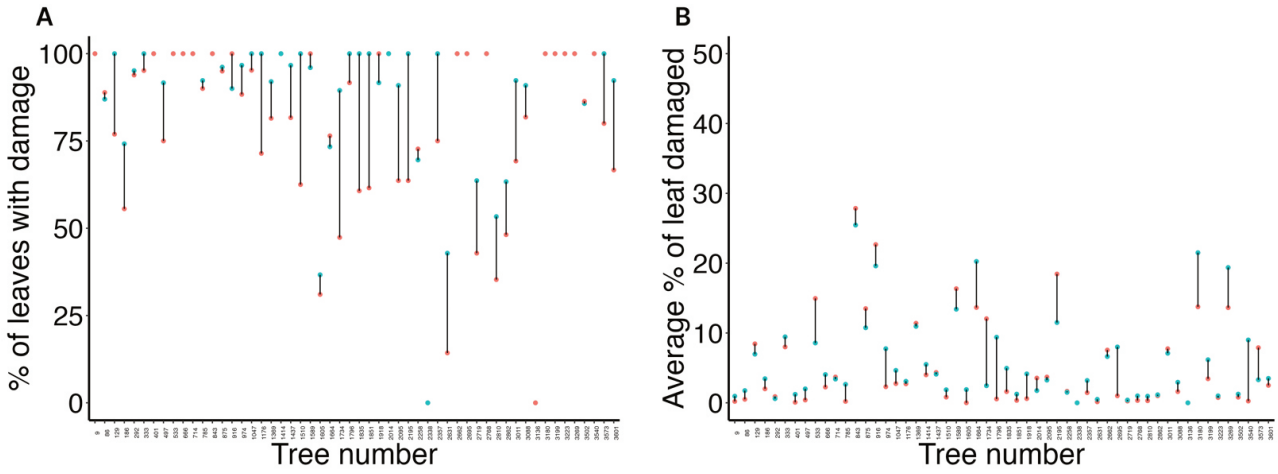


Figure S4.2 Observer accuracy for (A) the percentage of leaves with natural enemy damage on each individual, and (B) average area of leaf surface with natural enemy damage. Red points = Observer 1, blue points = Observer 2. Variation between groups was significantly bigger than variation within groups (A: $F = 7.95$, $p < 0.001$; B: $F = 11.47$, $p < 0.001$).

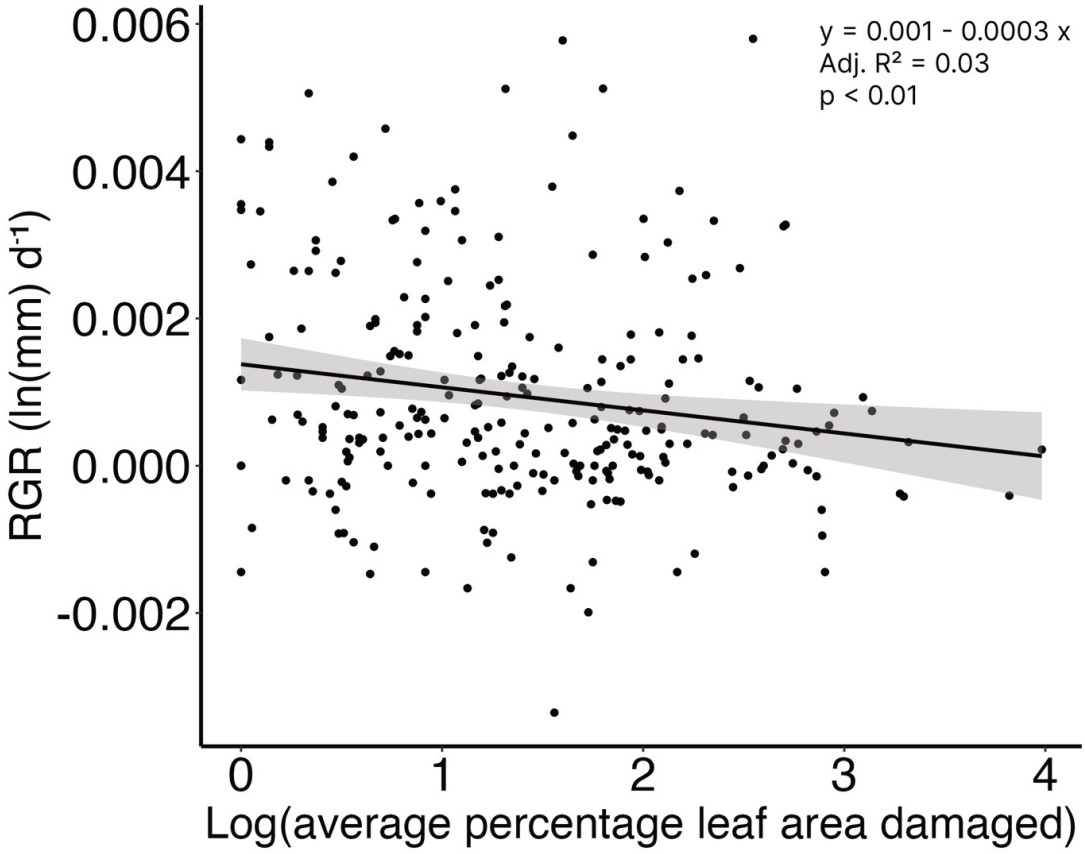


Figure S4.3 The average area of leaf that was damaged by natural enemies was negatively correlated with RGR.