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Recruitment and dispersal limitations in a chronosequence of secondary forests in tropical Australia

by

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A thesis

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Dedication

To my family and my dearest friends.

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Finally thanks to all my family and my amazing friends for always being there for me wherever I am.

Recruitment and dispersal limitations in a chronosequence of secondary forests in tropical Australia

Ana Cristina Palma Gartner, PhD candidate
James Cook University, 2016

Supervisors: Susan G.W. Laurance
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Statement of contributions

Chapters 2-5 are based on manuscripts that have been published or are in review or preparation for submission to peer-review journals. Different researchers have made contributions to this thesis.

Chapter 2 looks at the recruitment of species and their functional traits in understorey and adult communities along the chronosequence of secondary forests. This manuscript is in review in Journal of Plant Ecology (Palma A.C., Goosem M., Fensham R.J., Goosem S., Preece N.D. and Laurance S.G.W. Species recruitment and functional traits are influenced by forest age along a secondary forest chronosequence. Journal of Plant Ecology, in review). Ana C Palma conceived the main idea, carried out fieldwork, analyzed data and wrote the manuscript. Miriam Goosem carried out fieldwork and helped editing and writing the manuscript. Rob Fensham, Steve Goosem and Noel Preece, helped editing and writing the manuscript. Susan Laurance carried out fieldwork, and helped developed the idea and writing the manuscript.

Chapter 3 has been prepared for submission as: "Limitations in dispersal and recruitment along a secondary tropical forest chronosequence". Ana C Palma developed the idea and methodology, conducted fieldwork, performed statistical analyses and wrote the manuscript. Miriam Goosem and Susan Laurance, helped developing the idea and methodology, conducted fieldwork, analyzed photographs and satellite imagery and helped writing the manuscript.

Chapter 4 in this thesis is a literature review on experiments using direct seeding and/or planting of seedlings for ecosystems restoration. This was published in Applied Vegetation Science (Palma A.C and Laurance S.G.W. 2015. A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? Applied Vegetation Science 18: 561-568). Ana C Palma and Susan Laurance conceived the main idea. Ana C Palma reviewed the literature, analyzed the data and wrote the manuscript. Susan Laurance also assisted with writing.

Chapter 5 is being prepared for submission as: "Direct seeding and planting of seedlings in secondary forests. The roles of dispersal and recruitment limitations." Ana C Palma developed the idea, conducted fieldwork, analyzed the data and wrote the manuscript. Miriam Goosem helped with fieldwork and editing the manuscript. Susan Laurance helped with fieldwork, developing the idea and writing the manuscript.

Susan G.W Laurance guided all the work that made this thesis possible and read the entire thesis. Miriam Goosem also helped editing all the chapters. My PhD was supported by Colciencias (Colombian Department for the Administration of Science, Technology and Innovation). James Cook University also granted me a tuition fee waiver for my final semester. Funding for my research came from the ARC Linkage Grant LP110201093 awarded to Susan G.W. Laurance, Rod Fensham, William Laurance, Steve Goosem, and Noel Preece from the Australian Research Council, Queensland Herbarium Wet Tropics Management Authority and Biome5 Pty Ltd. Fieldwork was also supported by Wet Tropics Management Authority Student Research Grant Scheme.

General Abstract

Tropical forests harbor the greatest biodiversity on the planet and play important roles regulating climate and capturing atmospheric carbon. However, they are being transformed by agricultural practices and development projects at unprecedented rates causing a considerable loss of ecosystem services and threatening thousands if not millions of species.

Environmental restoration provides an important solution to mitigate the ecological damaged associated with forest loss. As human-altered lands in the tropics are abandoned due to multiple social and economic factors, the restoration of these fallow lands has gained more opportunity and relevance.

This thesis aims to explore factors that affect forest recovery in a forest chronosequence in tropical Australia. Using data gathered in the field, together with greenhouse and field experiments, I examined the effects of secondary forest age on plant communities in the soil seed bank, and the seedling and adult plant cohorts. I further assessed seed germination and seedling survival and growth in direct seeding and seedling experiments. The findings provide a deeper understanding of the factors influencing forest regeneration in the Australian tropics.

I reviewed restoration methods in different ecosystems by evaluating experiments into the use and relative success of direct seeding and planting of seedlings**.** Overall, I found that direct seeding experiments use more species than seedling studies, yet have lower survivorship. Species availability is a major barrier to the selection of species, regardless of the technique used, and is an important bias in the experiments. Although costs are extremely important when planning a restoration project, only a few studies report on this aspect. Interestingly, none of the studies addressed the impacts of climate change on restoration efforts or provided information regarding how studies should consider future shifts in the environment.

Assessing the species composition and the functional traits of plant communities in secondary forests of different ages can give us insight into the recovery of these forests. I found that understorey communities in young secondary forest had lower species diversity and functional traits associated with early stages of forest succession (e.g. small-seeded species, herbs, grasses). Soil seed banks in these young forests were dominated by exotic species and existing grasses, herbs and small trees. As succession unfolds, soil seed banks, understorey and adult plant communities in these forests showed higher species diversity and a wider range of functional traits (e.g. more trees and late successional species). However, even old secondary forests had low numbers of large-seeded (< 20mm) species, a key distinguishing feature of tropical forests. This finding suggests that these secondary forests are limited by either a lack of dispersal or recruitment of these important tropical forest species.

To further explore the mechanisms of recruitment and dispersal limitations, I undertook direct seeding and planting of seedlings experiments. Using species of different seed sizes and successional status, I found that species identity was more important than forest age for growth and survival in seeds and seedlings. There was no relationship between seed size and/or successional status on growth or survival of the different species. Seeds had a much lower rate of survival compared to seedlings. As all species germinated irrespective of forest age (and the variation in site conditions), I concluded that dispersal limitation is possibly a greater barrier to the recovery of secondary forests at our sites than recruitment limitations experienced during this study.

Increasing awareness of the repercussions of forest lost and its implications on human well-being and ecosystems health make forest restoration a key area for current and future research, policy-making and environmental management. Results from this thesis show a delayed recovery in tropical secondary forests and the absence of key functional plant groups (e.g. large-seeded trees) even in 40 year-old forests. This finding makes restoration efforts necessary if we want to preserve local biodiversity and enhance the conservation value of these forests. Restoration efforts seeking to accelerate biodiversity recovery and the protection of the local flora should include species limited by seed dispersal. When possible, these initiatives should include multiple species and various seed sizes. Further, the inclusion of species with higher tolerance to drier conditions could improve restoration outcomes and prepare the region for future climatic scenarios.

As restoration gains importance, it also creates a unique opportunity to transform the way we see ecosystems and the services they provide. Restoration approaches should include realistic goals that match the local communities’ needs and expectations. It is important to take into account changes in climatic conditions and prioritize actions in a crowed world. Multidisciplinary efforts that match goals of conservation, policy and human behavior and well-being will also help improve the future of ecosystems restoration.

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

1.1 BACKGROUND

Tropical forests are the most diverse and productive ecosystems on Earth (Myers et al. 2000, Stegen et al. 2011) and regrettably they are rapidly being transformed into pasture and crop lands. This landscape transformation is creating a mosaic of human-dominated land uses where forest fragments are embedded in an agricultural and grazing matrix (Houghton 1994, Kammesheidt 2002, Baccini et al. 2012). Although there may be signs of decreasing deforestation rates in some countries, forest loss continues at an alarming rate in others. Around 13 million hectares of forest was converted to other uses or lost through natural causes each year over the last decade (FAO 2010). Forest degradation in the tropics is also extensive totaling between 30-40% of the total forested area (Blaser et al. 2011).

One of the main drivers of deforestation is the conversion of land for agricultural uses (Ellis et al. 2010). Tropical forest lands transformed for agriculture may be used for several years. However, due to the low fertility of most tropical soils, economic and/or socio-political changes (Thomlinson et al. 1996, Kammesheidt 2002, Rey-Benayas 2005), deforested areas may be abandoned after only a few years, allowing forests to regrow. This type of forest regrowth on abandoned lands is known as secondary forest (Kammesheidt 2002), and often differs from primary forest in species composition, physical structure and the quality of the habitat provided for different species (Letcher and Chazdon 2009).

The differences in species composition observed in secondary forests are likely to be the result of interactions among multiple factors. Agricultural fields are subject to soil erosion (Long et al. 2006) and when abandoned usually are the target of invasion by exotic species (Florentine and Westbrooke 2004). Since all types of cultivation can leave a legacy (different soil characteristics, hydrology, biomass and plant communities, among others) that alters successional patterns and outcomes, understanding the changes on recovering plant communities is crucial for conservation and restoration (Cramer et al. 2008). Long-term research has provided a general understanding of the impacts of rainforest disturbance, however we know very little about how we can facilitate the regeneration and increase diversity in tropical secondary forests.

Restoring tropical forests is important to preserving biodiversity and reestablishing ecosystem functions (Chazdon 2008). However, the recovery of forests may be restricted by multiple factors. For example, recruitment limitation is one of these factors defined as the failure of a species to be present in all sites favorable for its growth and survival (Hubbell et al. 1999) is considered one of the main barriers for forest recovery. A second and related process influencing forest recovery, termed dispersal limitation, is the failure of rainforest seeds to arrive at a site, thereby constrains the germinating seed pool. Unlike other terrestrial ecosystems, many plant species in tropical forests are strongly dependent on vertebrates to disperse their seeds (Howe and Smallwood 1982). In these regenerating landscapes, the seed dispersal process becomes disrupted perhaps driven by the lack of or inability of dispersers to reach site and as a result dispersal limitation can also be barrier for their recovery. Recruitment limitations shaping forest succession and recovery of abandoned lands include: seedling competition (with exotics that establish once the land is abandoned), poor soil conditions (e.g. low nutrients and/or moisture) and seed predation (Uhl 1987, Aide and Cavelier 1994, Clark et al. 1999, Holl 1999). Although these factors delaying regeneration are well known, there is still an eminent need to expand our knowledge regarding how we can facilitate the rehabilitation process and increase biodiversity and carbon storage in areas of tropical regrowth, which have become an increasingly important feature of the tropical landscape (Chazdon 2014).

Worldwide, tropical secondary forests account for the largest recent increase of live biomass (Pan et al. 2013). This rapid accumulation of carbon stocks will likely have a significant contribution towards mitigating climate change and helping reach the goals of the COP2015 meeting (FCCC 2015). Experimental research should help to provide the necessary information to allow development of management strategies that aid the process of forest succession (Bentos et al. 2013). An overall understanding of the diverse factors that limit and influence secondary forests recovery in different environments is therefore important to enable restoration that increases biodiversity in these systems.

Figure 1.1 Overview of the general landscape in the Atherton Tableland. A mixture of active pastures and secondary forests of different ages.

1.2 THESIS SCOPE AND STRUCTURE

This doctoral thesis investigates recruitment limitations along a chronosequence of secondary forests in Tropical Australia. Using data gathered in the field, together with greenhouse and field experiments, I examined the seedling and adult plant communities, the soil seed bank, and factors affecting seed germination and seedling success (growth and survival). The findings provide a deeper understanding of different factors influencing forest regeneration in the Australian tropics.

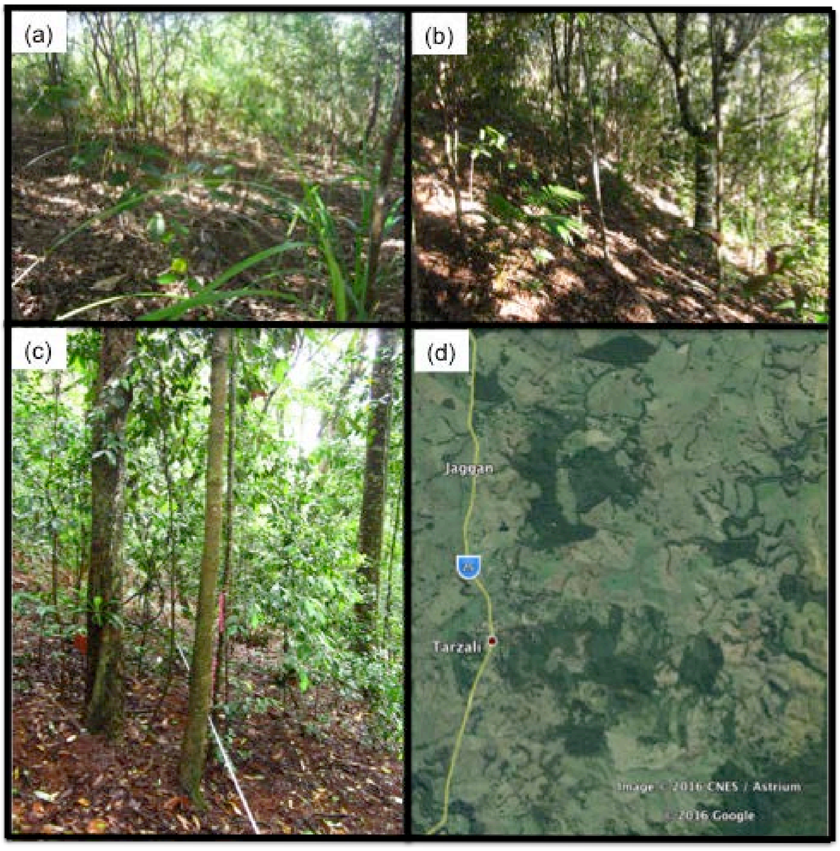

Figure 2.1 Secondary forests in the Atherton Tableland. (a) young secondary forests (4-12 years), (b) intermediate-aged secondary forests (16-23 years), (c) old secondary forest (27-41 years); (d) aerial view of the study region, a mosaic of mature forest fragments, secondary forest fragments of different ages and pasture lands.

This thesis consists of six chapters: the introduction, four chapters based on empirical data (that have been prepared for submission to ecological journals), and a general concluding chapter that integrates my findings with the current literature. As each chapter was prepared as a stand-alone manuscript for publication, this thesis contains some repetition mainly in the introduction and methods sections of some chapters.

A summary of the content and major findings of the chapters is presented below.

1.3 Summary of chapter 2

Species recruitment and functional traits are influenced by forest age along a secondary forest chronosequence

Secondary forests play an increasingly important role in conserving biodiversity and ecosystem functions and services. However, little is known about how different plant traits reassemble structurally and functionally in the understory of recovering secondary forests. In this chapter (in review at Journal of Plant Ecology), I investigated how forest age influences the diversity and functional traits of the understorey plant communities along a chronosequence of secondary forests ranging from 4 to 41 years since canopy formation.

I described the plant community composition in each site by identifying all trees, shrubs and lianas (≥2.5 cm diameter at breast height [dbh]) in a 3 × 50 m plot embedded in a 10 × 50 m permanent transect where all trees ≥ 10 cm dbh were identified. The understorey plant community was surveyed using ten 1m2 quadrats spaced at 5 m intervals along the permanent transect where all plant species ≤1 m in height were counted and identified. Species were characterized according to the following functional traits: life form, regeneration strategy, forest strata occupied when mature, seed dispersal mode, seed length and native/non-native status.

I found that plants recruited into young (4 - 12 years) and intermediate-aged forests (16 - 23 years) had significantly lower species and trait diversity than old secondary (27 - 41 years) and mature forest sites. The understorey communities in young and intermediate-aged forests were dominated by early successional species. Old secondary and mature forest sites contained more tree and vine species in the understorey community, with > 80% of the recruiting species classified as intermediate to late successional. These results provide evidence of a successional transition in understorey species and trait composition along the chronosequence. However, given the low numbers of late successional and large-seeded species, active restoration may be necessary for areas of high conservation priority.

1.4 Summary of chapter 3

Limitations in dispersal and recruitment along a secondary tropical forest chronosequence.

In this chapter (prepared for submission to Oecologia), I explored dispersal and recruitment limitations that may delay forest recovery. I estimated species composition and used plant traits to characterize emerging seedlings from soil samples, and compared them to the understorey and adult plant communities along the chronosequence.

I collected 1280 soil seed bank samples (5 cm diameter, 5 cm deep), and compared the community composition across demographic stages using 160 (1 x 1 m) seedling quadrats and 16 large permanent plots (50 m x 10m) where adult vegetation was surveyed. I estimated soil seed bank densities and calculated similarities with the standing vegetation (understorey and adults). I found that young (4 - 12 years) and intermediate-aged (16 - 20 years) forests had significantly lower species diversity and higher seed densities compared to mature forest sites. Seed banks in these young forests were dominated by early successional species, while seed banks in old (23 - 34 years) secondary forests and mature forest sites comprised more trees and late successional species with large seeds (> 19 mm length). Overall, seed banks in these secondary forests, particularly <20 years of age, support only a minor subset of the local plant community. There was a greater overall similarity between plant communities in the soil seed bank and the understorey, compared to soil seed bank and adult plants. These results suggest that secondary forests in the region assemble slowly with dispersal limitation constraining their recovery. Patterns of recruitment limitation are stronger between demographic stages than between forests of different ages.

1.5 Summary of chapter 4

A review of the use of direct-seeding and seedling plantings in restoration, what do we know and where should we go?

In this chapter (published in Applied Vegetation Science 18 (2015) 561–568), I examined the efficacy and costs of the two most widely-used techniques for ecosystem restoration: direct seeding and planting of seedlings. I reviewed 120 scientific peer-reviewed publications reporting on experiments using seeds or seedlings. For each study I examined different issues, including species diversity, survival, species selection, costs and how future climate change may influence restoration efforts.

I found that although direct seeding experiments generally use more species than seedling studies, survivorship in direct seeding studies is far lower. Species availability causes the major barrier to the selection of species, regardless of the technique used. Although costs are extremely important when planning a restoration project, only a few studies report on this aspect. Additionally, none of the studies addressed the impacts of climate change on restoration efforts or provided information regarding how studies should consider future shifts in the environment.

1.6 Summary of chapter 5

Seed and seedling experiments in secondary forests; the roles of dispersal and recruitment limitations.

Dispersal and recruitment limitations are crucial processes shaping forest composition. In secondary forests, these mechanisms may operate differently than in mature forests, because early-aged and isolated secondary forest suffer stronger limitations due to a lack of suitable dispersers and harsh environmental conditions (e.g. elevated competition with exotics and grasses, altered microclimates).

In this chapter, I assessed dispersal and recruitment limitations in secondary forests using experiments using seeds and seedlings in the chronosequence of secondary forests. I used 3 large-seeded (>20 mm in length) late successional species, 2 small-seeded (<15 mm in length) early successional species and 1 small-seeded late successional species. The seeds experiment (5 spp) included three treatments: 1) exposed seeds, 2) fenced seeds and 3) buried seeds.

After 14-17 months, all species germinated in all secondary forests, however, in young secondary forest sites (4 - 12 years) seed survival was lower. Buried seeds survived best in all forest age categories (27.25%) while exposed seeds had the lowest survival rates (6%). Planted seedlings had greater survival (63.08%) and higher growth rates in old secondary forest sites (27.39% more than in intermediate-age and 9.58% more than in young forest sites). I found that species identity is important for growth and survival in both experiments, but I detected no effect of successional status or seed size. As all species germinated irrespective of the variation in site conditions, I concluded that dispersal limitation might be a greater barrier to the recovery of secondary forests in the region than recruitment limitations experienced during this study.

1.7 Chapter 6 Synthesis

My research has demonstrated that the recovery of secondary forests in tropical Australia is protracted. Herbs, grasses and exotics dominated the soil seed bank and understorey plant communities of young forests (4 - 12 years). Native rainforest trees and shrubs become more abundant as succession unfolds, but late successional and big-seeded species are scarce even in old secondary forest (27 - 41 years). Dispersal limitation is a strong barrier to the recovery of these forests, however, the use of direct seeding and planting of seedlings results in the successful recruitment of late successional, big-seeded species. High removal rates for unburied seeds suggests that burying seeds would yield better results, when direct planting of seedlings is not possible.

Restoration efforts using direct-seeding and planting of seedlings should include different species and various seed sizes. Additionally, including species with higher tolerance to drier conditions could improve restoration outcomes and prepare the region for future climatic scenarios. Long-term monitoring of experiments would provide more insight into the recovery of these forests.

Chapter 2: Species recruitment and functional traits are influenced by forest age along a secondary forest chronosequence *

2.1 ABSTRACT

Currently, secondary and degraded tropical forests cover a larger area than mature forest. These modified forests play an increasingly important role in conserving biodiversity and ecosystem functions and services. However, little is known about how different functional traits reassemble structurally and functionally in the understory of these recovering secondary forests. I investigated how forest age influences diversity and functional traits of the understory plant community along a chronosequence of secondary forests in tropical Australia. I determined plant community composition in 18 secondary and six mature forest sites. In each site, all trees, shrubs and lianas (≥2.5 cm diameter at breast height [dbh]) were identified in a 3 × 50 m plot embedded in a 10 × 50 m permanent transect where all trees ≥ 10 cm dbh were identified. I surveyed the understorey plant community using ten 1m^2 quadrats spaced at 5 m intervals along the permanent transect. All plant species ≤1 m in height were counted and identified. I characterized species according to the following functional traits: growth form, regeneration strategy, forest strata occupied when mature, seed dispersal mode, seed length and native/non-native status. Species diversity and trait similarity of the understorey plant communities were evaluated using Fisher's alpha and non-metric multidimensional scaling (NMDS) ordination. I compared the species composition between the understorey to the adult plant

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* This chapter is based on the following manuscript: Palma A.C Palma A.C., Goosem, M., Fensham, R.J., Goosem, S., Preece, N.D. and Laurance S.G.W 2016. Species recruitment and plant traits are influenced by forest age along a secondary forest chronosequence. Journal of Plant Ecology, (In review).

communities and calculated Jaccard's similarity coefficient. Trait diversity was measured using Rao's quadratic entropy (FD_Q). I found that plant recruitment in young (4 - 12 years) and intermediate-aged forests (16 - 23 years) had significantly lower species and trait diversity than old secondary (27 - 41 years) and mature forest sites. The understorey communities in young and intermediate-aged forests were dominated by early successional species such as grasses and exotics. Old secondary and mature forest sites comprised more tree and vine species, with > 80% of the recruiting species classified as intermediate to late successional. Plant functional traits that increased along this secondary forest chronosequence were the position occupied in the forest strata when mature and seed length. These results provide evidence of a successional transition in species and trait composition along the chronosequence. However, the slow recovery of old secondary forests regarding the recruitment of late successional and large-seeded species is worrying. Active restoration to introduce these key rainforest species may be necessary.

2.2 INTRODUCTION

Tropical forests contribute to more than half of all the carbon stored in the world's forests (Pan et al. 2011), harbor more than half of the Earth's terrestrial species (Dirzo and Raven 2003), and are a key component of hydrological processes (Avissar and Werth 2005). However, less than 5% of tropical forests are legally protected from human exploitation (Chapman et al. 2000), and approximately 70% of the tropical rainforest biome has been modified leaving a matrix of remnants, agricultural fields, and secondary forests of different ages (Dent et al. 2013; van Breugel et al. 2013).

Due to this worldwide shift from mature forests to regenerating forests and abandoned farmlands, secondary forests represent a fundamental part of the remaining tropical landscapes (Faria et al. 2009). Their significance for carbon sequestration and connectivity among forest fragments is increasingly being recognized (Chazdon 2014). Given the high levels of anthropogenic degradation and fragmentation, the conservation of tropical forest biodiversity depends on managing and understanding how secondary forests reassemble (Dent et al. 2013). To fully comprehend the pathways of forest regeneration it is not only important to understand key ecological processes, but also to define the potential of recovery following disturbance (Whitmore 1998).

An important question in secondary succession is whether regenerating forests are likely to attain the same community structure, composition and function as a mature forest, or whether species composition and function are likely to change, resulting in the creation of novel or hybrid ecosystems (Chazdon et al. 2007; Hobbs et al. 2009). The literature is not consistent on the capacity of secondary forests to recover the attributes of mature forest. Some studies have highlighted the ability of these ecosystems to recover plant diversity within a few decades (Finegan 1996; Denslow and Guzman 2000; Chazdon 2003; Katovai et al. 2012). Others, however, report significantly lower levels of diversity after more than five decades (Chua et al. 2013; Goosem et al. 2016). Even if secondary forests recover diversity, species composition is often very different from mature forests (Aide et al. 1995; Peña-Claros 2003; van Breugel et al. 2006; Piotto et al. 2009; Chazdon et al. 2010; Mullah et al. 2012; Dent et al. 2013). Some factors that can influence secondary forest recovery (species diversity and composition) include a high abundance of generalist species, effective seed dispersal, and presence of nearby mature forest remnants (Norden et al. 2009). Nonetheless, secondary forests succession pathways seem to be highly variable even under the same of local and regional influences (Norden et al. 2015; Poorter et al. 2016).

Changes in the species composition of recovering forests may alter ecosystem function and processes (Tilman et al. 1997; Tilman 2001; Naeem et al. 2012). Examining functional traits of species in secondary forests can clarify how land-use impacts recruitment, ecosystem function, and the assembly processes that may alter natural regeneration (Kahmen and Poschlod 2004; Asanok et al. 2013; Mayfield et al. 2013). Additionally, the analysis of traits and not only species, allows for comparisons between different systems to elucidate general trends (Diaz and Cabido 2001), dynamic changes through time (Uriarte et al. 2010) and to interpret the implications of species reduction across fragmented landscapes (Haddad et al. 2015). For instance, comparing floras of different tropical forests may not be feasible or appropriate if they have undergone different biogeographic histories (Ricklefs and Schluter 1994), but we can compare functional traits and their recovery over time in any regenerating forest.

To assess the recovery of regenerating forest across a chronosequence of secondary forests in tropical Australia, I explored differences in species composition and functional traits of the understorey plant community Using mature forest sites as a reference, and the species and trait composition of the understorey and adult plant communities, I assessed how plant functional traits reassemble in the understory throughout the chronosequence. Additionally, I explored which species and functional traits were absent from regenerating forests and its implications for forest recovery. If secondary forests were recovering with time, one would expect to find the accumulation of plant species and functional traits to resemble mature forests as succession unfolds. Therefore, young secondary forest would have low diversity of plant species and functional traits associated with early stages of succession in altered landscapes (e.g. more grasses, herbs, small-seeded and non-native species). In contrasts, old secondary forest would have more species diversity, and their functional traits should coincide with mature forest (e.g. more trees, big-seeded and native rainforest species). If I do not find these patterns, secondary forests in this landscape may require active intervention to overcome dispersal and recruitment limitations to increase diversity and protect the local flora.

2.3 MATERIALS AND METHODS

2.2.1 STUDY AREA AND SITE SELECTION

The study was carried out on the southern Atherton Tableland (17°23.3’S 145°35.8’E - 17°27.0’S 145°38.2’E), a highly fragmented landscape in north-eastern Australia. The climate is tropical, with mean annual rainfall ranging from 1700 to 2600 mm, a distinct dry season from July to October (BOM 2014). Mean monthly temperatures range from a mean minimum of 10ºC in the drier months to a mean maximum of 29ºC during the wet season.

Rainforest fragmentation began with European settlements and rainforest logging in the 1890s. By the 1920s, much of the plateau of the region was converted to pasture for the dairy industry (Frawley 1987; Gilmore 2005). Some pastures were abandoned in the 1940s and then in the 1980s when economic conditions changed (Gilmore 2005). Following pasture abandonment, forest regenerated and currently secondary forests of different ages dominate parts of the landscape.

2.2.2 Site ages and categories

Interpreting a time-series of aerial photographs and satellite imagery, different sites were selected comprising the range of ages of secondary forests available. This study encompasses 18 secondary forest and six mature forest sites (Figure 2.1). All sites are at least 1,000 meters away from a continuous forest block. The age of each site was determined by using a time series of Queensland State Government aerial photographs (From 1943 to 2011, 16 years of photographs used), satellite images from Google Earth (© 2014 Google Image, ©2014 DigitalGlobe), and imagery from Queensland Globe (©State of Queensland 2013, ©CNES 2012, Spot Image S.A. France, ©2013 Pitney Bowes). Each image was examined for any vegetation other than pasture, using stereo-pairs of images where available. Otherwise, aerial photographs were scanned at high resolution and successive pairs of digital images were compared side-by-side on-screen. Age since abandonment was determined to be the mid-point between consecutive images where another vegetation community had replaced pastures. Age since canopy formation was determined as the mid-point between successive stereo images pairs where visual estimate of canopy cover in the more recent image was at least 70% and canopy height greater than five metres. I classified secondary forests into three age categories using the number of years since canopy formation as a proxy of forest age. Age categories were: Young: forests of 4 to 12 years, Intermediate: forests of 16 to 23 years, and Old: forests of 27 to 41 years. I selected six sites in each age category and an additional six mature forest sites as reference.

Chronosequence studies have been criticised because calculating age since abandonment and determining previous land uses are a major challenge (Chazdon 2014), and because the explanatory power of age and land use history varies largely depending on the attributes analysed (Chazdon et al. 2007; Lebrija-Trejos et al. 2008; Dupuy et al 2012; Chazdon 2014). I have attempted to address these challenges through replication of independent sites that are within the same climatic region and share similar past land use. Additionally, I used age since closed-canopy formation as a proxy of forest age to limit variation between the initial conditions of different sites.

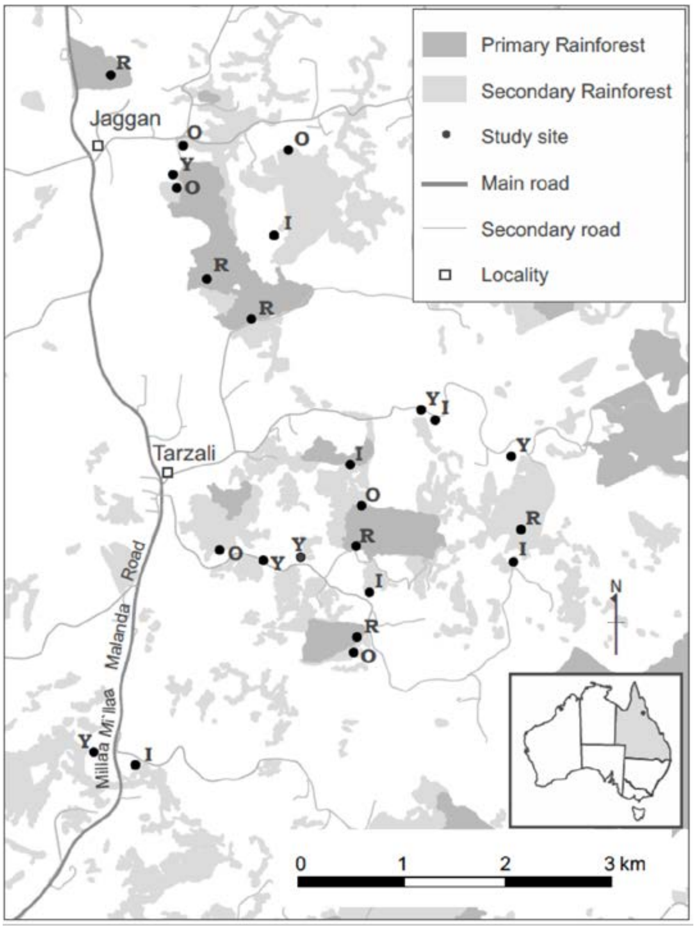

Figure 2.1 Map of the study area, southern Atherton Tableland, North Queensland, Australia. Different letters represent the different secondary and the mature forest sites. Y: Young secondary forests (4 – 12 years), I: Intermediate-aged (16 – 23 years), O: Old (27 – 41 years) and R: Reference sites (Mature forest).

2.2.3 Data collection and analysis

Plant community composition in each site was determined by identifying all trees, shrubs and lianas (≥2.5 cm diameter at breast height [dbh]) in one 3 × 50 m plot embedded in a 10 × 50 m permanent transect where all trees ≥ 10 cm dbh were identified. I surveyed understorey plant community using ten $1m^2$ quadrats spaced at 5 m intervals along the permanent transect, where all plant species ≤1 m in height were counted and identified

To examine functional characteristics I categorized species according to the following functional traits: growth form, regeneration strategy, forest strata occupied when mature, seed dispersal mode, seed length and native/non-native status (Table 2.1). I used published literature (e.g. Cooper and Cooper 2004; Pohlman 2006) and online resources (e.g. Queensland Herbarium) to assign each species to each category. The functional traits chosen address attributes that have been used in previous studies on secondary succession (Tabarelli and Peres 2002; Piotto et al. 2009; Katovai et al. 2012; Mayfield et al. 2013; Santo-Silva et al. 2013), and provide valuable information on successional patterns and the development of secondary forests in terms of diversity and structure.

Table 2.1 Functional traits and categories used to classify the understorey and adult plant communities in secondary and mature forest sites in tropical Australia

Trait	Categories	Source
Growth form	Grasses & Sedges, Ferns & Herbs, Shrubs & Small trees, Trees, Vines,	Queensland Herbarium
Successional stage	Early, Intermediate, Late	Queensland Herbarium; Pohlman 2006
Forest strata occupied when mature	Understory, Subcanopy, Canopy, Emergent	Queensland Herbarium; Cooper & Cooper 2004; Pohlman 2006
Seed dispersal mode	Abiotic, Biotic	Queensland Herbarium; Cooper & Cooper 2004
Seed length	Small (< 0.6 cm in length), Medium (0.7 - 1.8 cm), Large (> 1.9 cm)	Queensland Herbarium; Cooper & Cooper 2004
Origin	Native, Non-native (exotic)	Queensland Herbarium

Species diversity of the understorey plant communities was assessed using Fisher's alpha. I used ANOVA models and post-hoc Games-Howell tests to assess differences between age classes. Comparisons between the understorey and the adult plant community included shrubs, trees and vines only. I calculated Jaccard's similarity coefficient was calculated and used ANOVA models and post-hoc Games-Howell tests to assess differences between age classes.

To explore trait and species similarities among plant communities, I used non-metric multidimensional scaling (NMDS) ordination. To interpret species or functional trait correlations with ordination axes, Pearson correlation coefficients were used. Finally, I tested for differences between age categories using

PerMANOVA models. Differences in the proportions of functional traits in the understorey were explored using Kruskal-Wallis tests, and post-hoc Mann-Whitney U tests to establish the differences between secondary and mature forests. Rao's quadratic entropy (FD_Q) was employed to measure trait diversity (Lepš et al. 2006), a suitable measure when several functional traits are considered (Rao 1982; Botta-Dukát 2005; Mason et al. 2005). Kruskal-Wallis tests and post-hoc Mann-Whitney U tests were used to establish the differences among the calculated trait diversity and forest age categories. Statistical analyses were performed using PC-ORD Version 6.08 and IBM SPSS Statistics Version 21. Rao's quadratic entropy (FD_Q) was calculated using Lepš et al. (2006).

2.4 RESULTS

2.4.1 Species diversity and species composition

A total of 3429 individuals (209 species, 144 genera and 77 plant families) were recorded in the understorey plant communities across all of the study plots. I found almost four times (1926) as many individuals per area sampled in young secondary forests (4 - 12 years) than in other forest age classes, all of which had similar numbers of individuals (range: 456 - 521). Species counts in the understory of secondary forests were much lower than in mature forest sites with young, medium and old secondary forest values of 58, 62 and 76 species (respectively) compared with 112 species recorded in mature forests. The total number of plant families and genera were lower in secondary forest (range: 34 - 38 families and 48 - 55 genera), compared with 55 families and 89 genera found in mature forests. Further, 73 of the 112 species recorded in mature forests were found only at these sites.

Forest age significantly affected plant diversity in the understorey plant communities (One Way- ANOVA: $F_{[3, 20]} = 7.1$, $p < 0.01$). Old secondary forests had higher diversity and differed significantly from intermediate-aged secondary forests (Games-Howell test: $p < 0.05$). Not surprinsingly, mature forests had the highest diversity across all forests and differed significantly from young and intermediate-aged secondary forest sites (Games-Howell test: $p < 0.01$), but not from old secondary forests (Figure 2.2)

I recorded a total of 222 species of shrubs, small and large trees, and vines across both the understorey and overstorey plant communities in the study sites. These records included 51 species exclusive to the understorey, 87 species recorded only in the overstorey communities (dbh > 2.5 cm), and 84 species occurred in both understorey and overstorey plant communities. Of the species that were exclusive to the understorey, ~40% were only detected in secondary forests. Most of these were shrubs or small trees (55%) that dominate the early to intermediate successional stages (86%). Interestingly, species exclusive to the understorey of mature forests (24 species) were mainly late successional (62%) and were mostly vines (50%), shrubs and small trees (33%), and trees (16%). Of the 84 species present in both understorey and overstorey plant communities only 4 spp. occurred across all age categories. I recorded 25 species exclusive to secondary forests, which were mainly early successional (60%) and small-seeded (80%), whereas, the 24 species exclusive to mature forest sites were mostly late successional (71%) and large-seeded (54%).

When comparing species composition between the understorey and the overstorey plant communities, young and intermediate-aged secondary forests showed the highest similarity with a Jaccard similarity index of ~27% (range: 16 - 36%, Figure 3.3). Mature forest sites sites showed the least floristic similarity between strata with a average Jaccard similarity index value of 14% and differed significantly from young and intermediate-aged secondary forests (ANOVA: $F_{[3, 20]} = 6.1$, $p < 0.01$; Games-Howell test: $p < 0.05$).

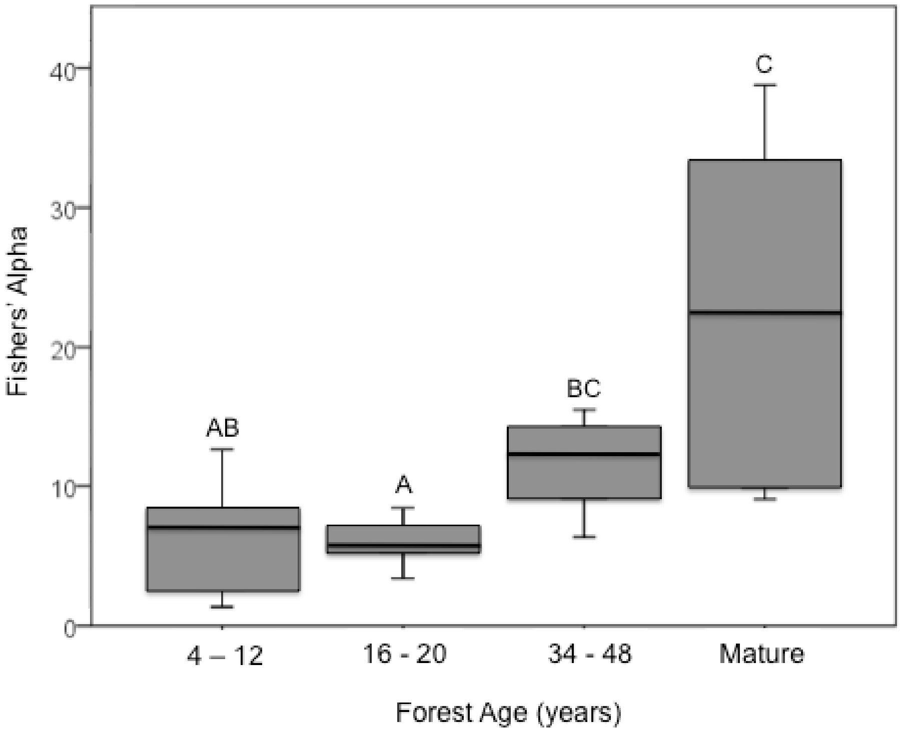

Figure 2.2 Diversity of the understory plant community in secondary and mature forests in tropical Australia. Letters shared in common between or among groups indicate no significant difference.

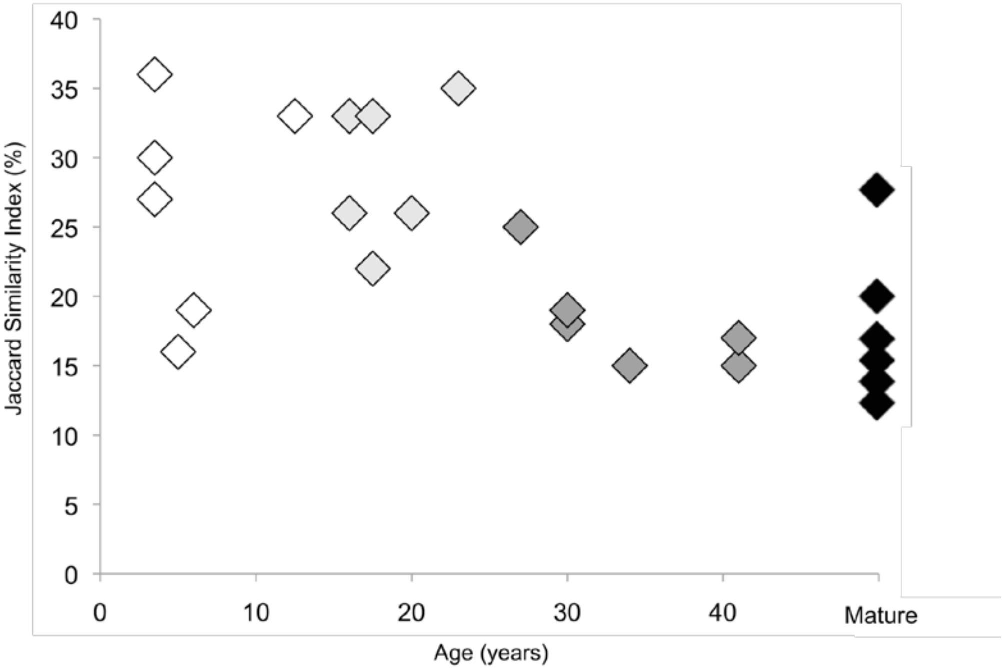

Figure 2.3 Jaccard similarity coefficients (%) between the species of the understorey and the adult communities for each study site. Sites represented by white symbols are forests of 4 - 12 years of age, light shaded ~16 – 23, dark shaded ~ 27 – 41, and black mature forest sites.

2.4.2 Trait composition and trait diversity

Forest age influenced plant trait composition in the understorey (PerMANOVA analysis: F = 8.55, df = 3, $p< 0.05$). The ordination explained 92% of the variation in the data (stress = 10.1, two-dimensional solution; Figure 2.4). Axis 1 which explains most of the variation (86%) described a successional gradient. It was negatively correlated with non-native species, grasses and sedges, small-seeded and understorey species, all common features of early stages of succession. Further, this axis was positively correlated with functional traits associated with later stages of succession such as medium-seeded species, with biotic dispersal, and growth forms such as trees and vines that will eventually form the upper canopy layers. Old secondary forests and mature forests showed greater similarity (clustering) within their age categories compared to younger secondary forests which were more variable in their trait association. This variation in young and intermediate forests along Axis 1 may reflect different rates of recovery in these forest categories. Similarly, Axis 2, which explained only a small amount of the variation in the data (6%), was positively correlated with the presence of ferns and other species with abiotic dispersal. This axis was negatively correlated with species relying on biotic vectors for their seed dispersal.

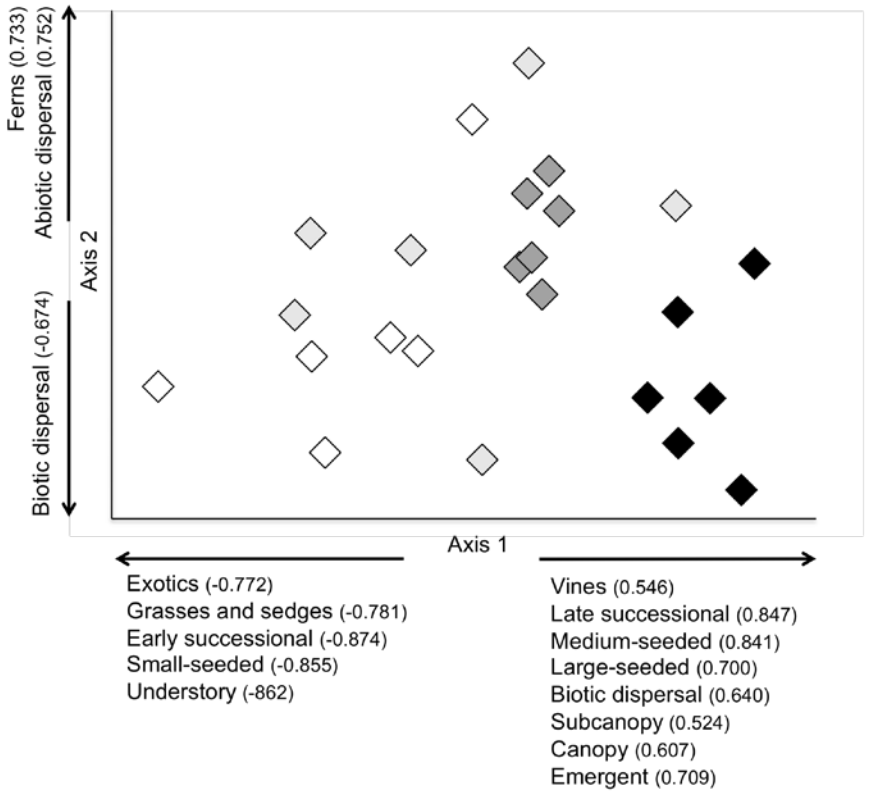

Figure 2.4 NMDS ordination in plant trait space of secondary and mature forest sites from tropical Australia. Sites represented by white symbols are forests of 4 - 12 years of age, light shaded ~16 – 23, dark shaded ~ 27 – 41, and black mature forest sites. Numbers in parenthesis are significant Pearson correlations using a Bonferroni-corrected alpha value (P = 0.00375).

Common plant species recorded in the understorey of these forests represent the functional traits identified by the ordination. For example, young secondary forests were dominated by species associated with early successional functional traits (small seeds and/or abiotic dispersal mechanisms), such as the exotic species *Ageratum conyzoides L. subsp. conyzoides* (Asteraceae). In mature forests, medium- to large-seeded species that form the upper canopy layers, such as *Argyrodendron trifoliolatum* (Sterculiaceae), *Castanospora alphandii* (Sapindaceae) and *Cryptocarya mackinnoniana* (Lauraceae) dominated. These late successional species are common in the understorey and tree communities of mature forests, but are practically absent from secondary forests, with only three seedlings and one adult tree of *Cryptocarya mackinnoniana* (Lauraceae) recorded in these regenerating forests (Figure 2.5).

When analyzing trait diversity between forests, I found differences in terms of seed length, forest strata occupied when mature, and native/non-native status (X^2 = 18.21, X^2 = 18.06 and X^2 = 13.9, respectively, df = 3 and $p< 0.01$ for all; Table 2.2). Intermediate-aged forest sites had significantly less diversity for forest stratum than old secondary forest sites (U = 1.0, p = 0.006). Mature forest sites had the highest trait diversity for forest stratum and seed length, and differed significantly from all secondary forests ($p< 0.008$ and p = 0.004, respectively for all Mann-Whitney comparisons). Additionally, mature forests had the lowest abundance of non-native species and were significantly different from all secondary forest sites ($p< 0.008$ for all Mann-Whitney comparisons).

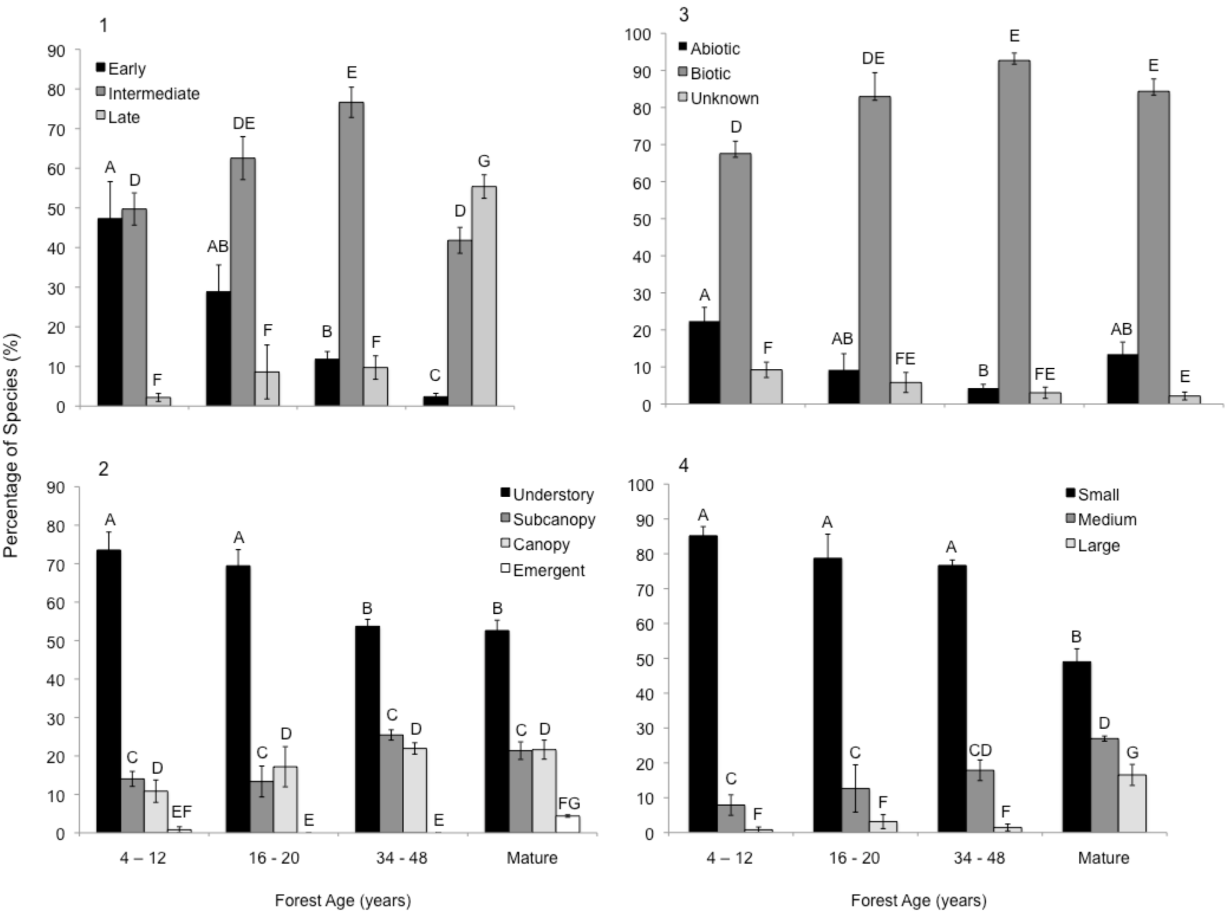

Figure 2.5 Traits composition of the understory plant community in secondary and mature forest sites in tropical Australia. (1) Proportion of early, intermediate, and late successional species; (2) proportion of species with abiotic, biotic, and unknown seed dispersal mechanisms; (3) proportion of understory, subcanopy, canopy, and emergent species; and (4) proportion of species with small (< 6 mm in length), medium (7 - 18 mm) and large (> 19 mm) seeds. Letters shared in common between or among groups indicate no significant difference.

Table 2.2 Average of Rao's quadratic entropy (FDQ) for each trait and forest age category

Forest age	Growth form	Successional stage	Height when mature	Seed dispersal mode	Seed length	Origin
Young	0.68	0.38	0.36	0.45	0.05	0.37
Intermediate	0.47	0.37	0.31	0.2	0.07	0.23
Old	0.63	0.34	0.56	0.22	0.3	0.18
Mature	0.57	0.48	0.73	0.42	0.57	0

2.5 DISCUSSION

Secondary forests in abandoned grazing pastures of tropical Australia show a slow successional transition in species and trait composition along a forest chronosequence. Plant recruitment in young secondary forests was dominated by existing species with similar functional traits, while old secondary forests showed higher species diversity and a broader range of functional traits. Increasing species diversity through time is a common pattern in forest succession (Denslow and Guzman 2000; Capers et al. 2005; Chazdon et al. 2010; Dent et al. 2013; Yeo and Fensham 2014). Likewise, an increase in trait diversity is generally associated with later stages of succession (Hooper et al. 2005; Chazdon et al. 2010; Asanok et al. 2013; Santo-Silva et al. 2013). However, I found that even old secondary forests have lower plant trait diversity regarding forest strata occupied when mature, and large-seeded species than mature forests. This could be the result of constraints on seed dispersal as most large-seeded species in the tropics are dispersed by frugivorous vertebrates (Howe and Smallwood 1982), which are often absent from young secondary forests and fragmented landscapes (Moran et al 2009).

In tropical forests, both seed dispersers and predators influence seed recruitment patterns and the plant demographic processes that shape forest composition (Terborgh et al. 2008; Terborgh 2012). Secondary forests are often highly disturbed and fragmented, affecting animal communities and plant recruitment processes (Tylianakis et al. 2008), which may result in differentiated species and functional trait composition from mature forests, despite similar species diversity. This pattern has been found elsewhere (Peña-Claros 2003; Capers et al. 2005; Piotto et al. 2009; Mullah et al. 2012), and reflects our findings in tropical Australia. As succession progressed, I also observed the expected increase in species diversity in the understorey, which differed significantly from the overstorey plant community only in mature forests. Although old secondary and mature forest sites did not differ significantly in species diversity; species composition and some functional traits (seed length, forest strata occupied when mature and native/non-native status) remained different. Further, large-seeded and late successional species were an important component only in mature forest sites; where more than 30% of the total species registered in the understorey were large-seeded and unique to these forests. In contrast, species with large seeds comprised less than 5% of the total species recorded in all secondary forests combined. These marked differences in species composition and functional traits between the understories of secondary and mature forests may be due to seed dispersal and recruitment limitations (van Breugel et al. 2007) and to the impacts of forest fragmentation on forest dynamics (Melo et al., 2010; Haddad et al. 2015). In secondary forest fragments, seedling dynamics may also be faster than in mature forests, with seeds arriving and germinating, but perhaps dying rapidly due to unfavourable site conditions.

Forests dynamics may also vary between regions, and different patterns can be the results of multiple factors. For instance, regenerating forests in the Neotropics are characterized by high abundance of lianas that rapidly colonize these forests (DeWalt et al. 2000; Letcher and Chazdon, 2009; Barry et al. 2015; Letcher 2015), while my studied chronosequence did not show this pattern. Young secondary forest had only a few liana species (9 ssp), while old secondary and mature forest sites registered a higher number of species (15 and 20, respectively). This different pattern in the colonizing of lianas is most likely the result of study site proximity to mature forests. Lianas spread vegetatively through basal branches and underground tubers (Putz and Mooney, 1991) my study sites were purposely not adjacent to mature forest and as a consequence lianas could only colonize the site via seed dispersal. Most liana species in tropical Australia have biotic seed dispersal (Gallagher et al. 2011), hence dispersal limitations may play and important role in slowing liana colonization in these forests.

Overall, recovery of species and functional trait diversity along the chronosequence varied among forest age categories, young and intermediate forests had lower diversity of species and functional traits. This may be due to the higher percentages of grasses and other exotic plants in these younger sites, which may slow down their natural recovery (Vieira et al. 1994; Holl et al. 2000; Garcia-Orth and Martinez-Ramos 2008; Chazdon 2014). Along the chronosequence, species with biotic dispersal were an important component even in young secondary forests, highlighting the importance of seed dispersers in tropical forest dynamics and their recovery.

As succession progressed, recruiting species were more likely to occupy subcanopy and canopy positions upon maturity. This successional pathway indicates that with time, young forests may reach a similar composition to old secondary and mature forest sites (Norden et al. 2009). However, the high abundance of non-native species and grasses in young and some intermediate-aged forest sites may arrest or delay succession in these sites with respect to species composition, functional traits and forest structure.

Our results suggest that secondary forests in this landscape take more than 50 years to develop an understory community similar in diversity of species and functional traits to mature forests, if not in actual species composition. The recovery of canopy species and species with large seeds is slow, and even older secondary forests differed significantly in their functional diversity from mature forests. Active restoration efforts might be necessary to overcome dispersal and recruitment limitations and increase biodiversity in these secondary forests, if forest compositions similar to the original landscape are desirable.

3.6 ACKNOWLEDGMENTS

Special thanks to Stephen McKenna and Rigel Jensen for their assistance in identifying rainforest plants. I also thank the landholders and owners of the different properties for granting access and allowing continuous fieldwork. Nandini Velho, Natalia Norden, Robin Chazdon and Jorge Meave made useful comments and suggestions on earlier versions of the manuscript.

Chapter 3: Limitations in dispersal and recruitment along a secondary tropical forest chronosequence[*]

3.1 ABSTRACT

Secondary forests are expanding rapidly in tropical regions. As a result, secondary forests may play an important role in the conservation of biodiversity. The recovery rate of plant communities in secondary forests varies considerable due to limiting by mechanisms associated with seed dispersal and seedling recruitment. I explored the presence and strength of these mechanisms through a comparison of plant species in soil seed banks, seedlings and adult plant communities. I estimated species composition and used functional traits to characterize emerging seedlings from soil samples, and compared them to the understorey and adult plant communities along a chronosequence of secondary forests in tropical Australia. I collected 1280 soil seed bank samples (5 cm diameter, 5 cm deep), and used 160 (1 x 1 m) seedling quadrats and 16 permanent plots (50 m x 10m) to assess species diversity and composition. I estimated soil seed bank densities and calculated similarities with the standing vegetation (understorey and adults). Young (4 - 12 years) and intermediate-aged (16 - 20 years) forests had significantly lower species diversity and higher seed densities than mature forest sites. Their soil seed banks were dominated by early successional species such as herbs, grasses, and exotics. Soil seed banks of old (23 - 34 years) secondary forests and mature forest sites had more trees and late successional species with large seeds (> 19 mm length). Soil seed banks of these secondary forests, particularly <20 years of age, support only a minor subset of the local species' pool. There was greater overall similarity between plant communities in

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[*] This chapter is based on the paper prepared for submission to Oecologia by Palma A.C., Goosem, M and Laurance S.G.W with minimal changes in format and content.

the soil seed bank and the understorey, compared to soil seed bank and adult plants. These results suggest that secondary forests in the region assemble slowly with dispersal limitation constraining their recovery. Further, I found that there were greater similarities in floristic composition within forest age classes (young versus old) than between different demographic stages (e.g. seed bank versus seedlings), which suggested stronger patterns of recruitment limitation between demographic stages than forest age.

3.2 INTRODUCTION

The recovery and conservation of tropical secondary forests are necessary to preserve biodiversity and restore ecosystem services (Chazdon 2014). Soil seed banks are the first seed source to initiate forest succession; estimating its size and composition in disturbed areas is essential to determine their natural regeneration potential (Aerts et al. 1995; Bakker and Berendse 1999; Butler and Chazdon 1998; Hopfensperger 2007). Over the course of succession, some secondary forests show convergence with the plant community composition of mature forests (Norden et al. 2009). However, changes in the ecosystems and altered succession trajectories can lead to the formation of novel ecosystems, where the species composition differs from the original assemblage (Hobbs et al. 2009).

Seeds are added to the soil seed bank through dispersal mechanisms and removed through germination, predation or pathogens (Schupp and Fuentes 1995). In tropical forests, seeds of late successional species do not form a persistent soil seed bank (Chazdon 2014), and seed longevity is generally low (Khurana and Singh 2001); nonetheless, seeds of some pioneer species can germinate after more than a decade in the soil (Dalling and Brown 2009). Soil seed banks influence vegetation dynamics and provide information to understand regeneration processes (Castillo and Stevenson 2010; Graham and Hopkins 1990).

In tropical secondary forests the soil seed bank is usually composed of a subset of the available species (Cubina and Aide 2001) and can show low similarity to the standing vegetation (Oke et al. 2006). Often, soil seed banks of regenerating forests are dominated by herbs, exotics and other early successional species (Bonilla-Moheno and Holl 2010; Kalesnik et al. 2013; Mukhongo et al. 2011; Oke et al. 2006) that potentially inhibit the recruitment, growth and survival of native species (Dupuy and Chazdon 1998; Esaete et al. 2014). Studying soil seed banks across secondary forest chronosequences may help to understand temporary changes in species composition and similarities to the standing vegetation (Dalling and Denslow 1998).

Soil seed banks in secondary tropical forest chronosequences gradually gain diversity and woody species as succession unfolds (González-Rivas et al. 2009; Maza-Villalobos et al. 2011). However, pathways of succession, and the species composition of soil seed banks can vary widely in secondary forests due to legacies of past land use that alter soils, seed dispersal mechanisms, and plant community assembly processes (Cramer et al. 2008). For instance, some sites may have arrested succession, may have shifted towards novel ecosystems, or may have very low densities of tree species and could require active restoration to achieve a forested condition (González-Rivas et al. 2009; Hobbs et al. 2009; Zahawi and Augspurger 1999).

Seed dispersal and recruitment limitations are crucial processes in tropical forests, involving different filters and stages constantly determining species composition (Figure 3.1). This chapter aims to evaluate the regeneration potential of secondary forests by examining limitations in dispersal and recruitment across a secondary tropical forest chronosequence. Using the emerging seedlings from soil seed bank samples and floristic data on the standing vegetation, I calculated species diversity and plant trait distributions. I used species and plant trait similarities between forest age categories and demographic stages to explore how limitations in seed dispersal and recruitment may be influencing the recovery of these forests. If seed dispersal and recruitment limitations lessen as succession unfolds, I expected species and functional traits composition between demographic stages (seed bank, understorey, adults) to have a higher similarity within young age classes, where early successional species, herbs, and exotics would dominate. Old secondary forest sites would have higher diversity and a wider range of functional traits across demographic stages. Additionally, if as succession unfolds more species reach secondary forests sites, the species and functional trait composition of old secondary forests would be similar to mature forest sites.

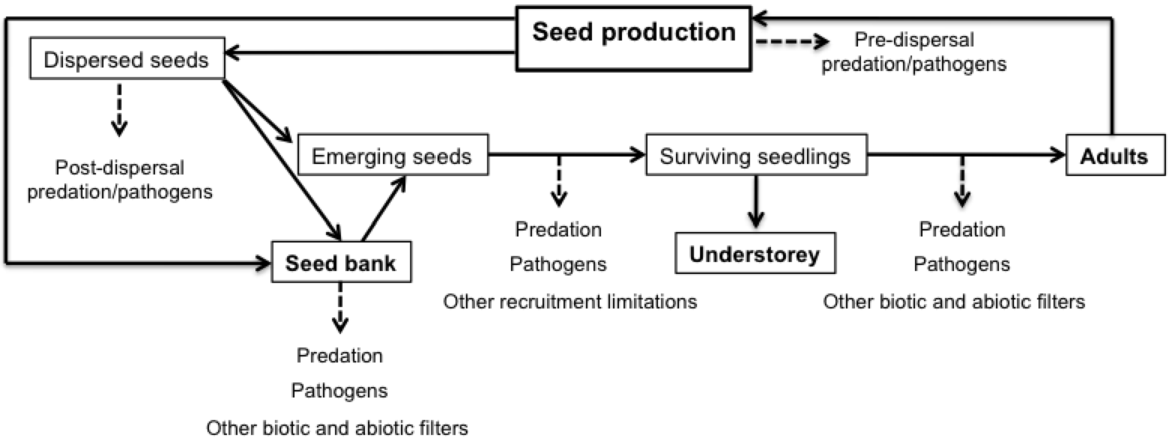

Figure 3.1 Diagram for seed dispersal, recruitment limitations and other key processes that shape forest composition.

3.3 METHODS

3.3.1 Study area and site selection

The study was carried out on the southern Atherton Tableland (17°23.3’S 145°35.8’E - 17°27.0’S 145°38.2’E), a highly fragmented landscape in north-eastern Australia. The climate is tropical, with mean annual rainfall ranging from 1700 to 2600 mm, and a distinct dry season from July to October (BOM 2014). Mean monthly temperatures range from a mean minimum of 10ºC in the drier months to a mean maximum of 29ºC during the wet season.

In the 1920s much of the region was cleared of continuous rainforest and converted to pasture for the dairy industry (Frawley 1987; Gilmore 2005). Some pastures were abandoned in the 1940s and others in the 1980s as economic conditions changed (Gilmore 2005). Following pasture abandonment, forest regenerated and now secondary forests of different ages dominate the landscape. Interpreting a time-series of aerial photographs and satellite imagery, different sites were selected that comprised the range of ages of secondary forests available. This study encompasses 12 secondary forest and 4 mature forest sites, none adjacent to mature continuous forest (Figure 3.2).

Chronosequence studies have been criticized because calculating age since abandonment and determining previous land uses are major challenges (Chazdon 2014), and because the explanatory power of age and land use history varies largely depending on the attributes analysed (Chazdon 2008; Dupuy et al. 2012; Lebrija-Trejos et al. 2008). I have attempted to address these challenges through replication of independent sites that are within the same climatic region and share similar past land use. Additionally, by using age since closed-canopy formation as a proxy of forest age I have limited the variation between the initial conditions of different sites.

3.3.2 Site ages and categories

The age of each site was determined using a time series of Queensland State Government aerial photography, satellite images from Google Earth (© 2014 Google Image, ©2014 DigitalGlobe), and imagery from Queensland Globe (©State of Queensland 2013, ©CNES 2012, Spot Image S.A. France, ©2013 Pitney Bowes). Each image was examined for any vegetation other than pasture, using stereo-pairs of images where available. Otherwise, aerial photographs were scanned at high resolution and successive pairs of digital images were compared side-by-side on-screen. Age since abandonment was calculated to be the mid-point between consecutive images where pasture had been replaced by other vegetation. Age since canopy formation was determined as the mid-point between successive images where visual estimate of canopy cover in the more recent image was at least 70% and canopy height greater than 5 metres. I classified secondary forests into three age categories using the number of years since canopy formation as a proxy of forest age. Age categories: Young: forests of 4 to 12 years, Intermediate: forests of 16 to 20 years, and Old: forests of 23 to 34 years. I selected 4 sites for each age category and an additional 4 mature forest sites as reference.

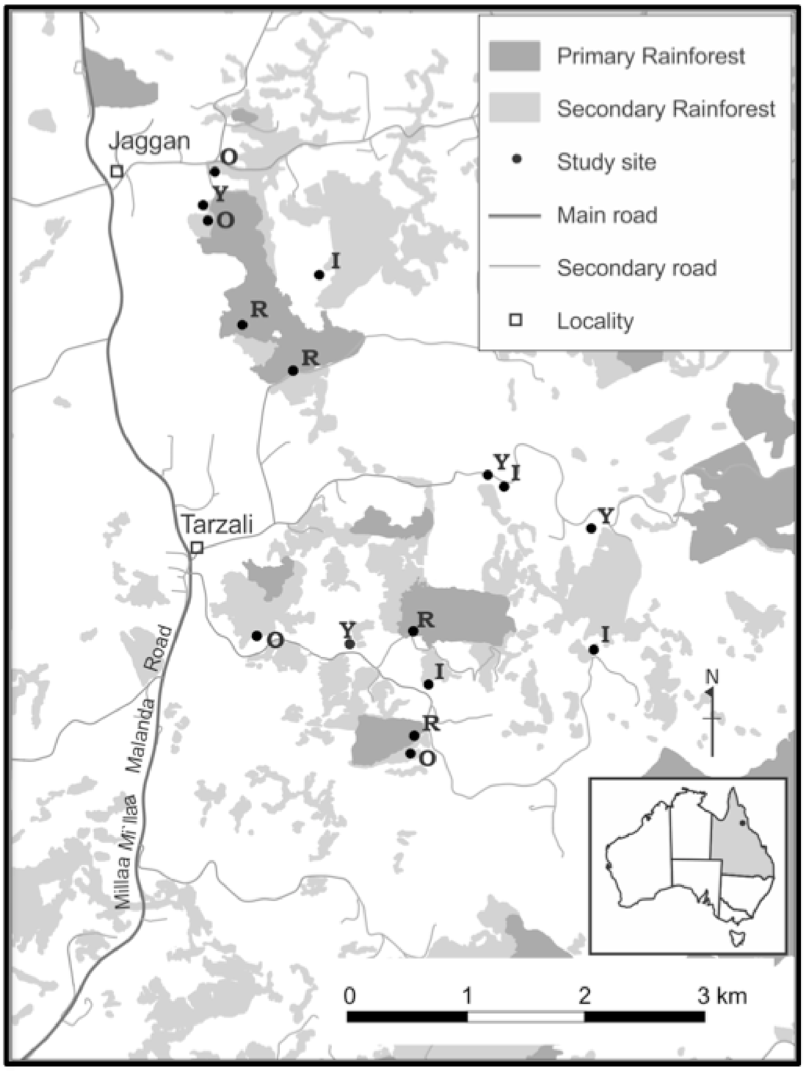

Figure 3.2 Map of the study area, southern Atherton Tableland, North Queensland, Australia. Different letters represent the different secondary and the mature forest sites. Y: Young secondary forests (4 – 12 years), I: Intermediate-aged (16 – 20 years), O: Old (23 – 34 years) and R: Reference sites (Mature forest).

3.3.3 Data collection and analysis

I estimated the soil seed bank composition by collecting soil samples (5 cm diameter, 5 cm deep) at 1.25 m intervals along two 50 m transects which totalled 80 samples per site. Soil samples were transported in plastic bags, and spread evenly to a depth of 4 to 5 cm in plastic trays inside a greenhouse. Germination was recorded every two weeks until no new seedlings appeared in the trays (10 months). After each census, all identified seedlings were removed, and the soil was loosened to promote germination. All unidentified seedlings were transplanted for later identification. To detect any contamination, one tray was filled with a commercial potting mix and placed among the sample trays. Seedlings of species that germinated in the control and other seedlings observed growing on the floor of the greenhouse were considered contaminants and therefore excluded from further analysis.

To examine functional traits, I categorized the germinating species into different functional groups including: growth form, successional stage, forest strata occupied when mature, seed dispersal mode, seed length and exotic or native status (Table 3.1). I used published literature (Cooper and Cooper 2004; Pohlman 2006) and online resources (e.g. Queensland Herbarium) to assign each species to each group.

I evaluated species diversity using Fisher's alpha and tested for differences between age categories using Kruskal-Wallis and post-hoc Mann-Whitney U tests. Using non-metric multidimensional scaling (NMDS) ordination I explore a) taxonomic similarity and b) trait similarity among sites and demographic stages. Pearson correlation coefficients and Bonferroni-corrected alpha values were used to interpret species or trait correlations with ordination axes. Using Sorenson (Bray-Curtis) distance the similarity/dissimilarity matrix was calculated, and PerMANOVA models were employed to test for differences between age categories. Additionally, I explored differences in the proportion of functional traits recorded using Kruskal-Wallis tests and post-hoc Mann-Whitney U tests.

Table 3.1 Functional traits and categories used to classify the emergent seedlings from secondary and mature forest seed bank samples in tropical Australia.

Trait	Categories	References
Growth form	Grasses & Sedges, Ferns, Herbs, Shrubs & Small trees, Trees, Vines	Australian Tropical Rainforest Plants; Queensland Herbarium
Successional stage	Early, Intermediate, Late	Pohlman 2006; Queensland Herbarium
Forest strata (Height when mature)	Understorey, Subcanopy, Canopy, Emergent	Australian Tropical Rainforest Plants; Cooper & Cooper 2004; Pohlman 2006; Queensland Herbarium.
Seed dispersal mode	Abiotic, Biotic	Australian Tropical Rainforest Plants; Cooper & Cooper 2004; Queensland Herbarium
Seed length	Small (< 0.6 cm in length), Medium (7 - 1.8 cm), Large (> 1.9 cm)	Australian Tropical Rainforest Plants; Cooper & Cooper 2004; Queensland Herbarium
Status (origin)	Exotic, Native	Australian Tropical Rainforest Plants; Queensland Herbarium

I calculated seed densities by dividing the total germinating seedlings per site by the total area of soil sampled. Differences between age classes were assessed using Kruskal-Wallis tests, and post-hoc Mann-Whitney U tests. To compare the similarity of the soil seed banks to the aboveground vegetation (understorey and adult community) I calculated the Jaccard’s similarity coefficient (Anderberg 1973).

ANOVA models and post-hoc Games-Howell tests were used to assess differences between age classes. I sampled the understorey plant community of each site using 10 1m^2 quadrats spaced at 5 m intervals along a 50 m transect. All plant species ≤1 m in height were counted and identified. The adult plant community composition in each site was determined by identifying all trees, shrubs and lianas (≥ 2.5 cm diameter at breast height [dbh]) in a 3 x 50 m plot embedded in a permanent 10 x 50 m transect where all trees ≥ 10 cm dbh were identified. Statistical analyses were performed using PC-ORD Version 6.08 and IBM SPSS Statistics Version 21.

3.4 RESULTS

3.4.1 Species diversity, species composition and functional traits

A total of 2615 individuals germinated from the soil seed banks across all of our study sites. These individuals included a total of 72 species, 60 genera and 38 plant families. Almost four times more individuals (1436 stems) germinated in young secondary forests samples (4 - 12 years) than in other forest age classes, all of which had similar numbers of individuals (range: 373 - 420). Numbers of plant families and genera were lower in secondary forests (range: 16 - 22 families and 26 - 31, genera), compared with 25 families and 35 genera germinating from mature forest sites samples.

Forest age significantly affected plant diversity in the soil seed bank samples (Kruskal-Wallis test: 8.21, df = 3, $p < 0.05$). Old secondary forest had a higher diversity than young secondary forest (Mann Whitney U test: U= 0.00, 2-tailed $p < 0.05$). Mature forest had the highest diversity and differed significantly from young and intermediate-aged forest samples (Mann Whitney U test; U= 2.00, 2-tailed $p < 0.05$), but not from old secondary forests.

Unexpectedly, forest age did not have a significant influence on common species composition in seed banks (PerMANOVA analysis: F = 1.64, df = 3, p = 0.09). However, herbs and exotic species dominated the seed bank of young secondary forest samples, while tree species and shrubs became more abundant as succession progressed. The ordination explained 76% of the variation in the data (stress = 17.2, two dimensional solution; Figure 3.3). Axis 1, explained 38% of the variation and was positively correlated with the presence of *Alpinia caerulea* (Zingiberaceae, herb), *Dendrocnide moroides* (Urticaceae, shrub) and *Trema tomentosa* (Ulmaceae, shrub/small tree). These native species were only recorded in the soil seed bank of old secondary and mature forest samples. Further, this axis was negatively correlated with the presence of *Ageratum conyzoides subsp. conyzoides* (Asteraceae) an exotic herb that dominated the soil seed bank of young secondary forest samples. Similarly, Axis 2 (38% of the variance), was negatively correlated with the presence of *Gahnia sieberiana* (Cyperaceae) a native sedge found across all age categories, but more abundant in young and intermediate-aged forest samples.

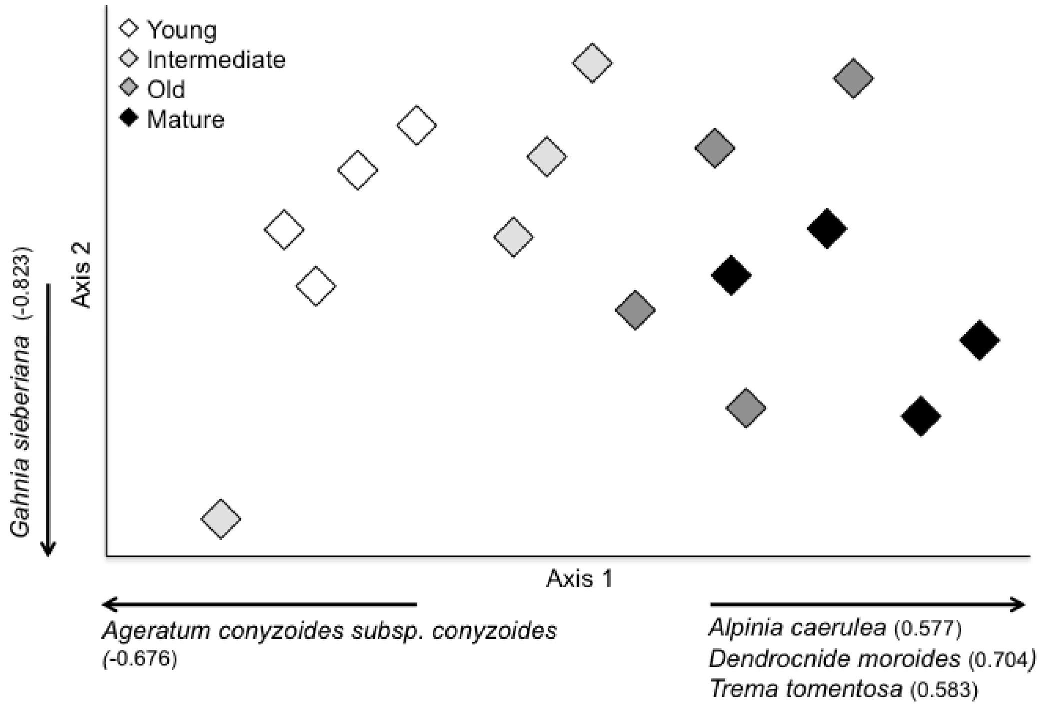

Figure 3.3 NMDS ordination in plant species space of soil seed banks samples from secondary and mature forest sites in tropical Australia. Sites represented by white symbols are forests of 4 - 12 years of age, light shaded ~16 – 20, dark shaded ~ 23 – 34, and black mature forest sites. Numbers in parenthesis are significant Pearson correlations using a Bonferroni-corrected alpha value (P = 0.00104).

Contrary to what I expected, forest age also did not have a significant influence on functional trait composition of plant species in the soil seedbank (PerMANOVA analysis: F = 1.74, df = 3, p = 0.19). Nonetheless, some successional trends are evident, with soil seed banks of young secondary forest dominated by functional traits associated with early stages of succession (e.g. abiotic dispersal, understorey species) whereas late successional traits (e.g. large seeds, trees) became more abundant as succession unfolds. The ordination explained 93% of the variation in the data (stress = 13.6, three-dimensional solution; Figure 3.4).

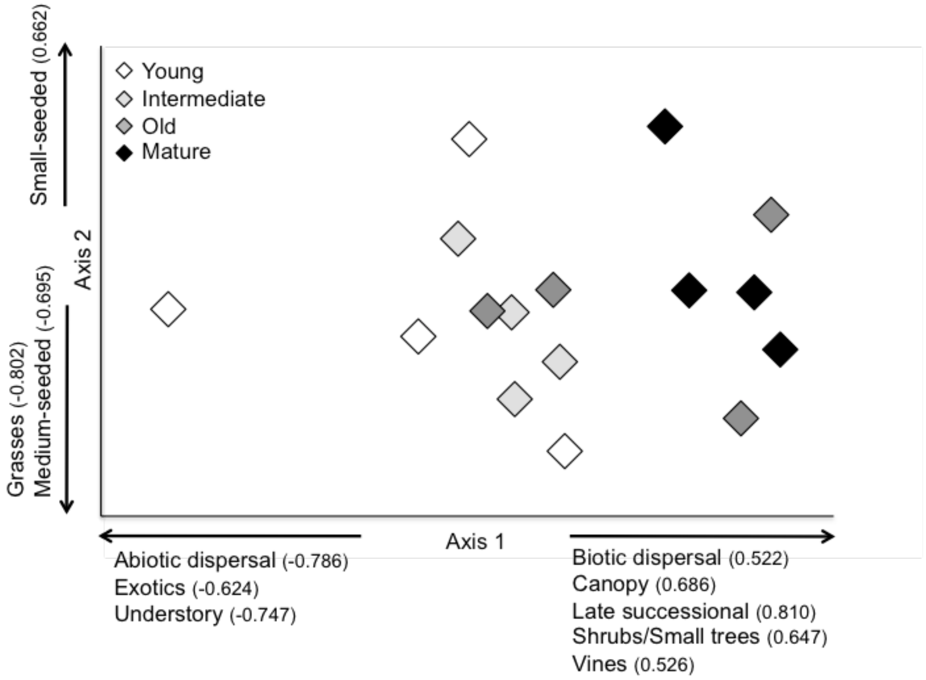

Figure 3.4 NMDS ordination in functional traits space of soil seed bank samples from secondary and mature forest sites in tropical Australia. Sites represented by white symbols are forests of 4 - 12 years of age, light shaded ~16 – 20, dark shaded ~ 23 – 34, and black mature forest sites. Numbers in parenthesis are significant Pearson correlations using a Bonferroni-corrected alpha value (P = 0.0041)

Axis 1 of the ordination in functional traits space of the soil seed bank samples (Figure 3.4), explains most of the variation (53%) described a successional gradient. It was negatively correlated with the proportion of species with abiotic seed dispersal, exotics, and understorey species, all features of the early stages of succession. Further, this axis was positively correlated with late successional species, with biotic dispersal, and growth forms such as shrubs, small trees and vines that will eventually form the upper canopy layers. Axis 2 (30% of the variance) was negatively correlated with the presence of grasses and medium-seeded species, and positively correlated with the presence of small-seeded species. Axis 3 (not shown in figure), explained only a small amount of the variation in the data (10%), was positively correlated to the presence of trees, intermediate successional species and species that will form the canopy layers. This axis was negatively correlated with the presence of early successional species and species with abiotic seed dispersal.

Overall, exotic species comprised 45.6% of the total species registered in the soil seed bank samples of young secondary forests. Exotics were also present in mature forest samples but in lower proportions (19.8% of total registered species). Grasses, sedges and herbs were more abundant in young and intermediate-aged soil seed bank samples. Shrubs and small trees dominated old secondary and mature forest soil seed bank samples, where vines were also more abundant. Ferns germinated only in old secondary and mature forest soil samples (Figure 3.5).

The distribution of functional traits along the chronosequence illustrates the trends identified by the ordinations. Late successional species were only present in old secondary and mature forest samples, with significantly higher numbers in mature forests ($U= 0.00$; $p< 0.01$ for young vs. mature and intermediate vs. mature). Understorey species were more abundant in young and intermediate-aged secondary forests; however, high numbers of understorey species were also registered in the other forest age categories. The lowest proportion of canopy species occurred in young forests whereas mature forest samples showed the highest proportion of these species.

Finally, the dominant dispersal mechanisms of plant species identified in the soil samples was also found to vary with secondary forest age. Young and intermediate-aged secondary forest soil samples had the highest proportion of plant species relying on abiotic mechanisms for their seed dispersal (31% and 29 %, respectively), whereas old secondary and mature forest soil samples had greater numbers of species with biotic dispersal. Seedlings from large-seeded species (> 19 mm) were only recorded in mature forest samples. Overall species with small seeds accounted for more than 95% of all records.

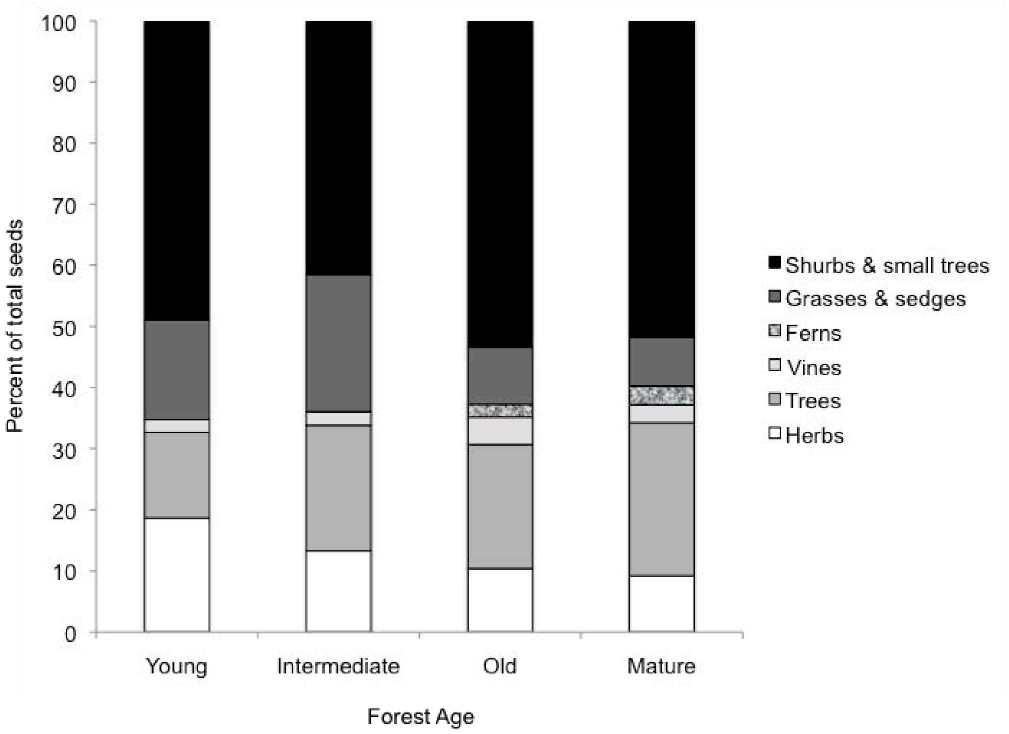

Figure 3.5 The proportions of different growth forms among soil seed bank samples in tropical Australia according to forest age category.

3.4.2 Distribution of functional traits amongst demographic stages

An ordination in plant functional traits space of soil seed bank samples, understorey and adults plant communities showed that forest age had a significant influence on trait composition between demographic stages across the chronosequence (PerMANOVA analysis: F = 2.80, df = 3, p = 0.04). This ordination explained 94.7% of the variation in the data (stress = 10.1, two-dimensional solution; Figure 3.6). Soil seed banks and understorey communities along the chronosequence are dominated by functional traits associated with early stages of succession (e.g. abiotic dispersal, exotics, understorey species), whereas adult plant communities are characterized by functional traits linked with later stages of succession (e.g. large seeds, trees). Axis 1 which explains most of the variation (83.4% of the variation) described a successional transition. It was positively correlated with the proportion of species with abiotic seed dispersal, exotics, herbs, grasses, sedges and small-seeded understorey species, all features of the early stages of succession. This axis was negatively correlated with the proportion of late successional species, medium to large-seeded species with biotic dispersal, and trees that will form the upper canopy layers. Axis 2 (11.3% of the variance) was negatively correlated with the proportion of vines and intermediate successional species, and positively correlated with the proportion of early successional species.

Interestingly, all seed bank samples were cluster together regardless of forest age, indicating high trait similarity between age classes. Similarly, the understorey and seed banks of young and intermediate-aged secondary forests were cluster together. While adult plant communities were scattered demonstrating a lower similarity in trait composition between age classes for this demographic stage.

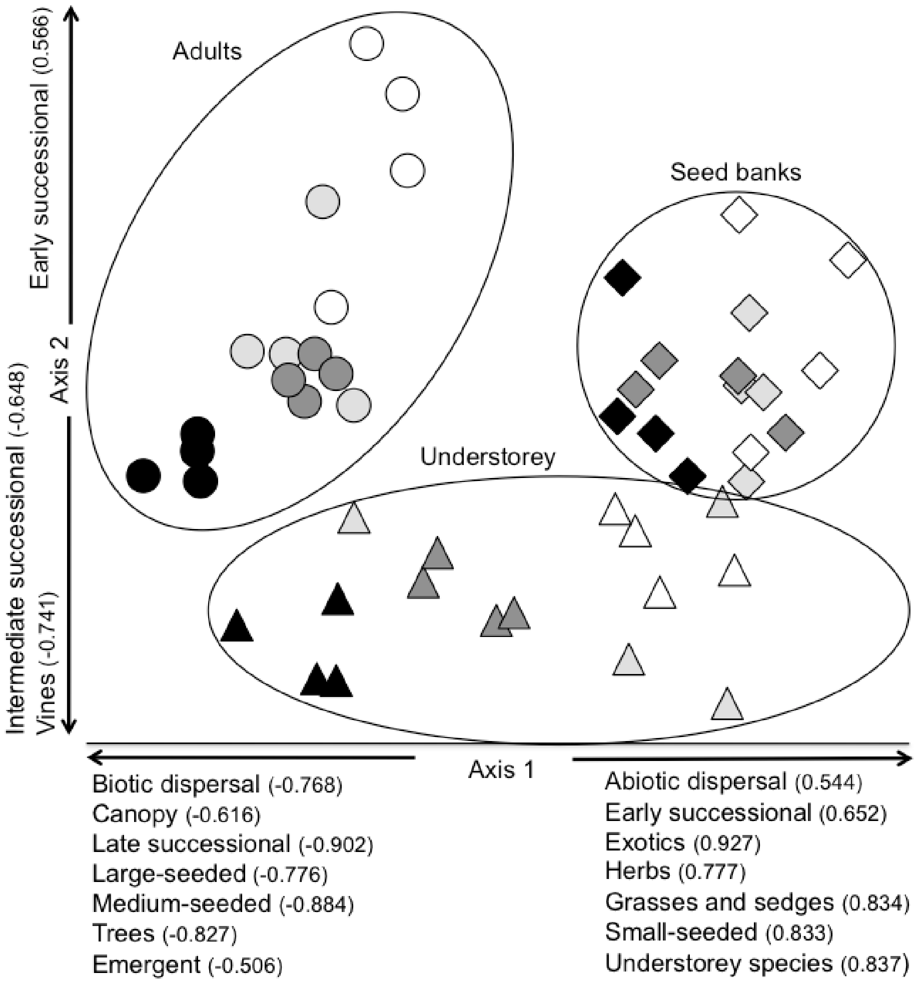

Figure 3.6 NMDS ordination in functional traits space of soil seed bank samples, understorey and adults plant communities from secondary and mature forest sites in tropical Australia. Sites represented by white symbols are forests of 4 - 12 years of age, light shaded ~16 – 20, dark shaded ~ 23 – 34, and black mature forest sites. Diamonds represent seed bank, triangles understorey and circles adult plant communities. Numbers in parenthesis are significant Pearson correlations using a Bonferroni-corrected alpha value (P = 0.00375).

3.4.3 Soil seed bank densities and species similarities between demographic stages.

Forest age significantly influenced soil seed bank densities (Kruskal-Wallis test: 8.65, df = 3, $p < 0.05$). Young secondary forests showed the highest calculated seed densities (range: 4379 - 14987 seeds/m^2) and were significantly different from all other age categories (Mann Whitney U test; U = 0.00, 2-tailed $p < 0.05$ for all comparisons). Mature forest sites had the lowest calculated seed densities (range: 1215 - 3341 seeds/m^2).

When species composition between the soil seed banks and the understorey communities were compared, soil seed banks of mature forest were significantly less similar (average 2.5 %, Jaccard similarity index) than the soil seed banks from secondary forest sites (ANOVA: $F_{[3, 15]} = 8.4$, $p < 0.01$; Games-Howell test: $p < 0.05$ for mature vs. young samples). The highest similarity was found between the soil seed bank samples and the understorey plant communities of young sites with about 21% Jaccard similarity index value (range: 18 - 29%, Figure 3.7a). When the soil seed bank samples and the adult plant communities were compared, a similar pattern was found. Mature forest seed bank samples had significantly less similarity (average 1%, Jaccard similarity index) than secondary forest samples (ANOVA: $F_{[3, 15]} = 5.6$, $p < 0.05$; Games-Howell test: $p < 0.05$ for mature vs. young samples). The highest similarity between the soil seed bank samples and the adult plant communities was also found in young sites with about 11 % similarity (range: 7 - 17 %, Figure 3.7b).

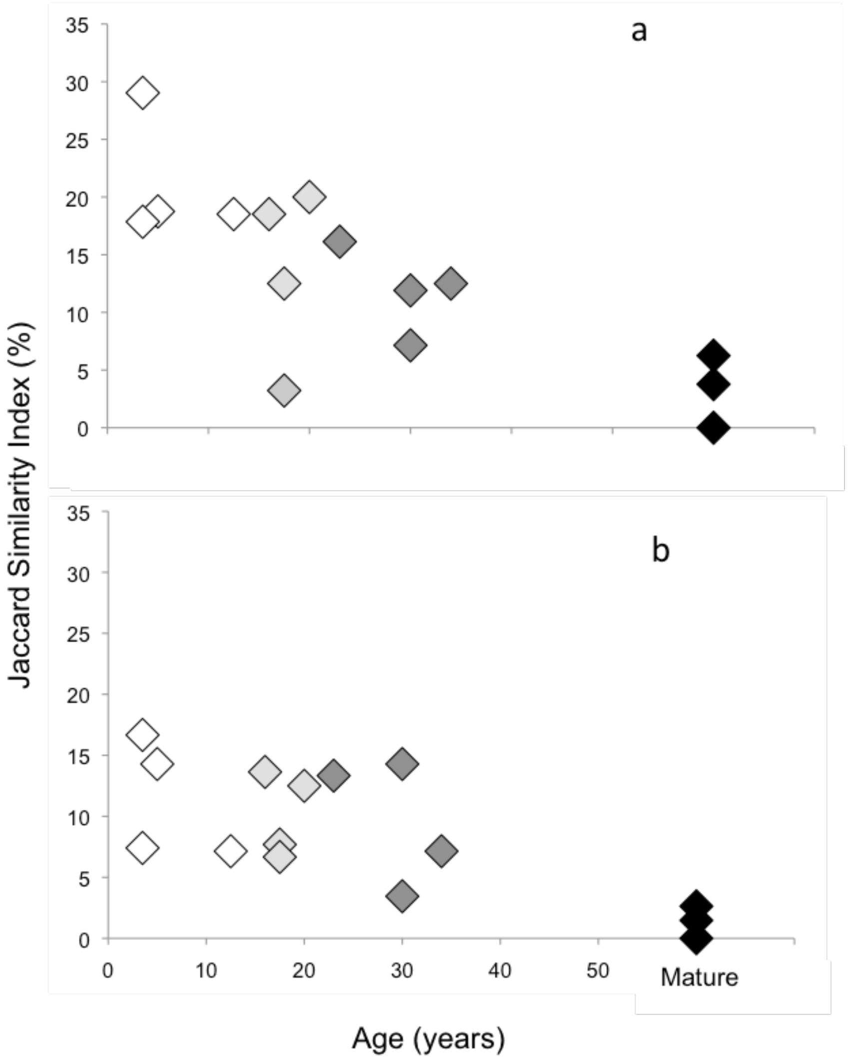

Figure 3.7 Jaccard similarity index (%) between species found in the understory (a), the adult communities (b), and the germinating seedlings from secondary and mature forest seed bank samples in tropical Australia. Sites represented by white symbols are forests of 4 - 12 years of age, light shaded ~16 – 20, dark shaded ~ 23 – 34, and black mature forest sites.

3.5 DISCUSSION

3.5.1 Species diversity, species composition and functional traits

Secondary forests in tropical Australia show a slow successional transition in diversity, species composition and functional traits. Existing herbs, grasses, sedges and exotic species with similar functional traits dominated soil seed bank samples and seedling communities in young and intermediate-aged forests. These taxa in general are small-seeded species with high seed yields and hence have a higher dispersal capacity to colonize disturbed sites (Levine and Murrell 2003; Lugo 2004). Exotics, in this study comprised 45.5% of the total species detected in the soil seed bank of young forests and 31% of species in old secondary forests. Similar patterns of exotics dominating soil seed banks were reported by Hopkins and Graham (1983, 1984) across a range of lowland pastures, secondary and mature forest sites, and by Pullo (2005) in rainforest restoration sites. As expected, soil seed banks from old secondary forests showed higher species diversity and a broader range of functional traits. Trees and shrubs, including four late successional species, comprised the highest proportion of emerging seedlings in old secondary and mature forest samples.

Late successional species are of particular interest in secondary forest studies as they represent the floristic composition of mature tropical forests and their appearance is indicative of forest recovery. In this study, late successional species accounted for only ~5% of the 72 species detected in the seed bank of secondary forest, and ~8% of the species in mature forest sites. However, late successional species are usually scarce in soil seed banks, because their seed yield is lower (as normal for larger seeds), they do not usually form a persistent seed bank (Alvarez-Buylla and García-Barrios 1991; Dalling et al. 1997; Dalling et al. 1998), and typically suffer strong predation pressures (Hopkins and Graham 1983; Khurana and

Singh 2001). Previous studies that have assessed the availability of late successional species in soil seed banks have determined that they comprised <2% of species in regenerating tropical forest in Mexico (Quintana-Ascencio et al. 1996), and <1% or 0% of the registered species in mature and young secondary forests, respectively, in tropical Australia (Hopkins and Graham 1983; Hopkins and Graham 1984). Additionally, late successional species in this region usually have quick-germinating and short-lived seeds (Hopkins and Graham 1983), which may explain their limited presence in the seed banks of even old and mature forest sites. Therefore, assessing the abundance of late successional species in this demographic stage provides only limited insight into the recovery of secondary forests. Alternatively, if I consider how late successional species constitute the understorey communities of these regenerating forests, I detected a far greater species pool with ~ 20% of the total species for secondary forests and ~ 46% for mature forest sites. In the adult plant communities, late successional species comprised ~ 35% of total species recorded in secondary forests, while in mature forest sites most species (~73%) were late successional. These values do not just reflect the species pool so much as the longevity of these species compared to the shorter-lived herbs and pioneers.

Contrary to what I expected, forest age did not have a significant effect in the composition of the soil seed banks. However, a slow transition from exotics and herbs in younger sites to shrubs and trees as succession unfolds was evident. The absence of late successional species in young and intermediate-aged seed bank samples could be a direct consequence of stand age, with younger forests either having unfavourable conditions for the survival of seeds in the soil seed bank (recruitment limitation), or because these young forests do not support a wide range of dispersers and therefore these seeds do not reach these sites (dispersal limitation).

3.5.2 Community assembly in secondary forests- a comparison between demographic stages

Interestingly, there were stronger patterns of recruitment limitation between demographic stages than between age classes. Functional traits were more similar within demographic stages (seed bank, understorey, adult) despite differences in forest age, than within sites. Soil seed banks showed a higher functional trait similarity between age classes than other demographic stages, even for mature forest sites. These similarities further indicate the limitations in recruitment for some species that are present in all soil seed banks but are absent from other demographic stages. It is important to note that soil seed banks were similar in composition because exotics, herbs and grasses dominated all samples, with exotics being present even in mature sites. Shaded environments that develop with age might be limiting the recruitment of these taxa which generally demand higher light conditions (Poorter et al. 2004). However, it is likely that dispersal limitation might be playing a key role slowing down the recovery of these forests, as only a few large-seeded rainforest species that belong to late successional stages (shade tolerant) were recorded in the understorey of this secondary tropical forest chronosequence.

As succession unfolds seed bank dynamics and recruitment processes change. Young secondary tropical forests tend to have higher seed densities and lower similarity between seed banks and the standing vegetation (Dupuy and Chazdon 1998; González-Rivas et al. 2009; Maza-Villalobos et al. 2011; Quintana-Ascencio et al. 1996). I found a similar pattern, higher viable seed densities in young secondary forest samples and lower seed densities as succession progressed. However, seed densities in intermediate-aged, old and mature forest samples did not differ significantly. It is possible that age-related effects are more important in younger secondary forests, but once a significant decrease in light availability in the forest understorey is reached, herbs, weeds and pioneers decline and are not able to produce new seed crops, causing a decrease in their seed bank stocks (Baider et al. 2001) and stabilizing seed densities.

Measuring similarities between seed bank samples and other demographic stages separately may help elucidate dispersal and recruitment limitations in secondary forests. In our study, mature forests had the lowest floristic similarity across demographic stages compared to secondary forests. It is common to find little similarity between seed banks and the standing vegetation (González-Rivas et al. 2009; Hopkins and Graham 1983; Tekle and Bekele 2000; Zahawi and Augspurger 1999), and not surprising as studies frequently compare seed banks only with tree communities (e.g. Dalling and Denslow 1998), or group saplings and adults in one category (e.g. González-Rivas et al. 2009). When I compared the understorey with the soil seed bank there were higher similarities for all age categories, than when comparing seed banks and adult plant communities. As expected, young secondary forests showed higher correspondence with both the understorey and adult plant communities.

In conclusion, soil seed banks in these secondary forests support only a small fraction (52 spp) of the local plant diversity and assemble slowly. Recruitment limitations are preventing the establishment of exotics in old secondary and mature forest sites because the seed bank is overwhelmingly dominated by these species but fortunately they are not regenerating. Further, late successional species are in low numbers in all seed banks and their regeneration is twice as high in mature forest seedling and adult communities compared to secondary forests. Field experiments using seeds and seedlings of native rainforest species might help us determine the influence of dispersal and recruitment limitations in the recovery of these forests.

3.6 ACKNOWLEDGMENTS

Special thanks to Stephen McKenna for his assistance in identifying rainforest seedlings and Dr Ashley Field for his help identifying ferns. I also thank the landholders and owners of the different properties for granting access and allowing continuous fieldwork. Pablo Stevenson made useful comments and suggestions on the manuscript.

Chapter 4: A review of the use of direct-seeding and seedling plantings in restoration, what do we know and where should we go?*

4.1 ABSTRACT

To select the most appropriate method to facilitate the restoration of an ecosystem requires an understanding of the various outcomes commonly achieved through different restoration techniques. What method results in the most timely and cost-effective means of reinstating biodiversity and restoring ecosystem functions and services? In this chapter, I explored the efficacy and costs of two revegetation techniques widely used in ecosystem restoration: direct seeding and planting of seedlings. The analysis focussed on 120 scientific peer-reviewed publications reporting on experiments using seeds or seedlings, and encompassed a range of ecosystems such as wetlands, savannas and forests. I examined current restoration issues including species diversity, survival, species selection, costs, and how future climate change may influence restoration efforts.

The results showed that direct seeding experiments used more species than seedling studies yet had lower survivorship. Species availability is the major constraint in the selection of which species were used, regardless of the approach employed. Although costs are extremely important when planning a restoration project, few published findings report on the economic aspects of ecosystem restoration. Further, none of the studies addressed the impacts of global climate change on restoration programs or how we should consider future shifts in the environment. Results from this chapter

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[*] This chapter is based on the published paper by Palma A.C and Laurance S.G.W, with minimal changes in format and content.
Palma A.C and Laurance S.G.W 2015. A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? Applied Vegetation Science, 18(4):561-568. doi: 10.1111/avsc.12173. Appendix 1.1

highlight the need for restoration experiments to explore more species. Additionally, restoration efforts are in need of detailed reporting that includes time frames and costs. Future studies need to consider future climate scenarios that will affect restoration efforts.

4.2. INTRODUCTION

Humans have transformed and modified almost all of the world's ecosystems. Currently, about 77 per cent of the earth's ice-free surface is used for agriculture, urban settlements or is embedded within these transformed lands (Ellis et al. 2010). Habitat loss resulting from ecosystem transformation and deforestation are major drivers of global changes in biodiversity, carbon storage, and ecological connectivity (Foley et al. 2005; Butchart et al. 2010). These losses are putting many ecosystems and the services they provide at risk.

Natural landscapes transformed for agriculture may be used for centuries or abandoned after only a short period due to declining productivity or socio-political changes (Thomlinson et al. 1996; Rey-Benayas 2005). Agricultural fields are subject to erosion (Long et al. 2006) and when abandoned are often prone to invasion by exotic species (Florentine & Westbrooke 2004). All types of cultivation leave a legacy of past land use such as altered soils and plant communities (Cramer et al. 2008), in some cases these legacies may slow down the natural recovery of ecosystems making active restoration necessary.

As ecosystems around the world are degraded and transformed by human activity, their ecological restoration is desirable and plays a central role in maintaining biodiversity and re-establishing essential ecosystem functions and services (Funk et al. 2008; SCBD 2010; TEEB 2010). Ecological restoration is a process that initiates or accelerates recovery of an ecosystem that has been degraded, damaged or destroyed, with respect to its structure (species composition, abiotic requirements and physiognomy); functional properties (productivity, energy flow, nutrient cycling); and exchanges with surrounding landscapes (SER 2004).

Worldwide, natural and assisted regeneration processes have restored more land and at a lower cost than active efforts (Rey-Benayas 2005). However, natural recovery in some original ecosystems (e.g. tropical forests) can be arrested or slow, taking ~ up to 500 years for systems to recover (Kartawinata 1994; Guariguata & Ostertag 2001). Therefore, reintroduction approaches involving techniques such as planting or direct seeding are often desirable to accelerate recovery if mature-phase habitats are to be attained in the rapid timeframes required for conservation, or where abandoned lands are so degraded that natural vegetation cover cannot recover unaided (Rey-Benayas 2005). Such revegetation techniques may also accelerate litter-fall and nutrient inputs (Celentano et al. 2011), and the restoration of soil microbial processes might accelerate the overall recovery of an ecosystem.

Considerable money, time, and energy have been spent globally on restoring degraded and/or abandoned lands using mainly two revegetation techniques: (i) direct seeding and (ii) the planting of seedlings (Florentine & Westbrooke 2004). There are many published scientific studies and numerous technical reports considering these techniques. Practitioners have used both techniques, building up local knowledge, capacity and expertise. However, to our knowledge this is the first review that synthesizes the findings of scientific peer-review studies and analyses restoration results and trends across ecosystems. I reviewed the global published literature covering field experiments that used seeds and seedlings to restore ecosystems and included key information that can help evaluate current outcomes and plan future efforts.

Restoration programs may have a broad range of goals, from restoring ecosystems and its functions to include historical, cultural and social aspects (Higgs 1997; Wortley et al. 2013). However, amongst these goals, five factors can be identified, and are the focus of our review.

1. *Species Richness*. Similarity of species diversity to the reference community and the presence of different functional groups are attributes of restored ecosystems (SER 2004). I compared the number of species used in different restoration experiments (seeds or seedlings).

2. *Germination, survival and mortality rates*. I evaluated whether the percent of germinated seeds or surviving seedlings reported by the studies differed according to the restoration technique (seeds or seedlings). I also report the causes of mortality given by each study.

3. *Seed Size*. Seed size is a plant functional trait that is considered to confer both advantages and limitations to species' germination and recruitment potential (Dalling & Hubbell 2002). I examined if seed size influences survival in direct seeding experiments by considering studies that included data on seed size (mass) and survival (per species).

4. *Costs*. High deforestation rates, land abandonment and degradation mean that there is an urgent need for low cost methods of restoration (Doust et al. 2008) that can be applied on a broad landscape scale. Although not consistently reported in these studies, when available I discuss the relative costs of different restoration methods.

5. *Future climate*. Rising temperatures and extreme weather events that result in droughts, floods or heat waves, will have important implications for the planning of restoration projects. I report the criteria used to select species and identify if

restoration experiments have considered implications of climate change on species selection and restoration planning.

4.3 METHODS

This review is based on the results of an ISI Web of Knowledge search conducted in March 2013 for literature published between 1965 and 2013 that used combinations of two or more of the following key words: seed/ seedlings/ reforestation/ restoration/ direct seeding/ direct seedling/ seedling planting/ and sowing. Articles were only included in the review if they met the following criteria: i) The article was published, peer reviewed and written in English; ii) The article included at least one field experiment using seeds or seedlings for restoration or native ecosystem reforestation purposes.

I found 120 papers that fulfilled the criteria. The selected papers were classified according to ecosystem and type of restoration technique used (seeds, seedlings, tree cuttings or rhizomes). The selected studies were organized into six ecosystem categories: Mangroves, Shrublands, Savannas, Wetlands, Grasslands, and Forests. I divided experiments according to the revegetation technique used, and - since 21 of the selected papers had experiments that employed both seeds and seedlings - I divided experiments according to the restoration approach used. This resulted in 145 experiments, for each experiment I summarized the number of species studied, success (germination, survival and mortality rates,), species selection criteria used, mortality causes and costs (Appendix 1). I converted all costs to US dollars corresponding to the average exchange rate for the year published, and standardized them to either cost per seedling or cost per hectare restored (depending on the data provided).

I used a Chi-square test to test for differences between the numbers of experiments using the different restoration technique (seeds or seedlings) across ecosystems. Independent T tests were used to assess differences between: numbers of species used, success (defined as the per cent of germinated seeds or surviving seedlings reported by the studies), and the restoration technique used. I applied ANOVA models to analyze for differences between seed size and germination/survival. Seed size categories: Small: seeds 0-99 mg; Medium: 100-2000 mg; Large: >2000 mg. All statistical analysis and graphs were performed using IMB SPSS Statistics Version 21.

Although not all papers dealing with use of direct-seeding and planting of seedlings in restoration projects were found, since other keywords and combinations were possible. I selected the search keywords for being the most representative and used in the literature.

4.4 RESULTS

When I classified the experiments according to ecosystem type and the restoration technique employed, I found that forests dominated published studies. Collectively, temperate and tropical forests accounted for 67 % of field experiments ($n = 97$), followed by grasslands (20 per cent), savanna and wetlands (8.3 per cent) and mangrove and shrublands (4.2 per cent) (Table 2.1). The proportion of seed and seedling experiments differed significantly between experiments in these ecosystems ($\chi^2 = 22.75$, $df = 5$, $p < 0.01$), with more direct seeding occurring in grasslands than in forested ecosystems.

Table 4.1 Ecosystems, number of studies and restoration experiments using seeds or seedlings for restoration/reforestation.

Ecosystem	**Number of Studies**	**Number of Experiments**	**Experiments Using Seeds**	**Experiments Using Seedlings**	**Experiments Using Cuttings**	**Experiments Using Rhizomes**
Mangroves	3	3	0	3	0	0
Shrublands	3	3	3	0	0	0
Savannas	5	5	3	2	0	0
Wetlands	6	7	2	4	1	0
Grasslands	25	30	24	4	1	1
Forests	78	97	40	53	4	0
TOTAL	**120**	**145**	**72**	**66**	**6**	1

4.4.1 Species Richness

Direct seeding experiments, on average, used twice the number of species than seedling experiments. This was a highly significant result (Independent T-test: $t= 2.3$, $df = 115$, $p < 0.01$) (Figure 4.1), with direct seeding experiments averaging about 10 species per study (mean: 9.5 ± 11.3, $n = 67$), and seedling studies averaging 5 (mean: 4.8 ± 5.3, $n = 63$). For this analysis I excluded three studies that used more than 50 species of seedlings, because these were exceptional projects larger in scale than the majority (ranging from 9 to 100 restored hectares).

4.4.2 Germination, survival and seed size

Across all ecosystems and experiments examined, the success percent survival of planted seedlings was significantly greater than that achieved by direct seeding (Independent T-test; $t = -8.5$, $df = 83$, $p < 0.01$, $n = 84$). On average, survival of planted seedlings was three times higher at 62% compared to the 18% percent germination/survival of seeds (Figure 4.2). Furthermore, when examining the effects of seed characteristics on survival, species with larger seeds tended to have higher germination/survival rates than species with small seeds (ANOVA; F= 5.0 $df= 2$, $p < 0.01$, $n= 49$) (Figure 4.3).

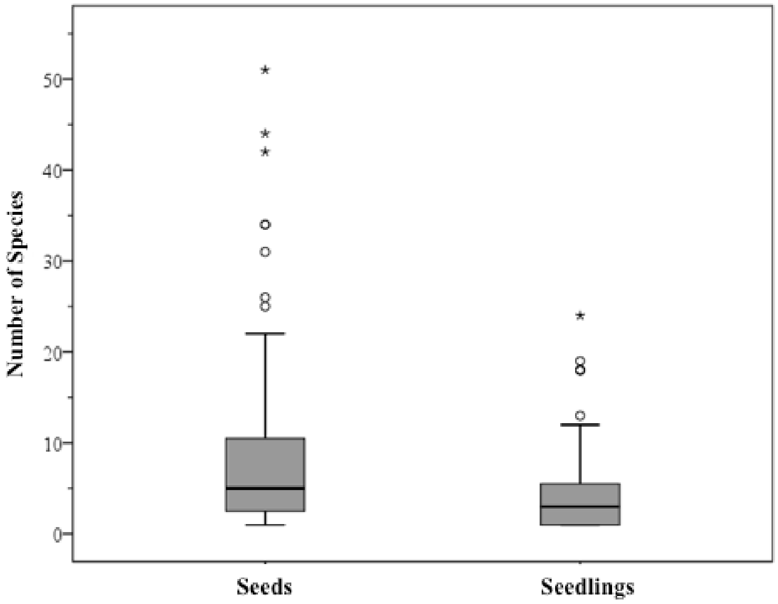

Figure 4.1 Number of species used in restoration experiments for each restoration approach: seeds (n = 67) and seedlings (n = 63). Independent T-test: t= 2.3, df = 115, p < 0.01). The tick line represents the median, the outer limits of the box the first and third quartiles. Whiskers extend to cover any data point < 1.5 times the interquartile range. Circles represent outliers and asterisks are far outliers.

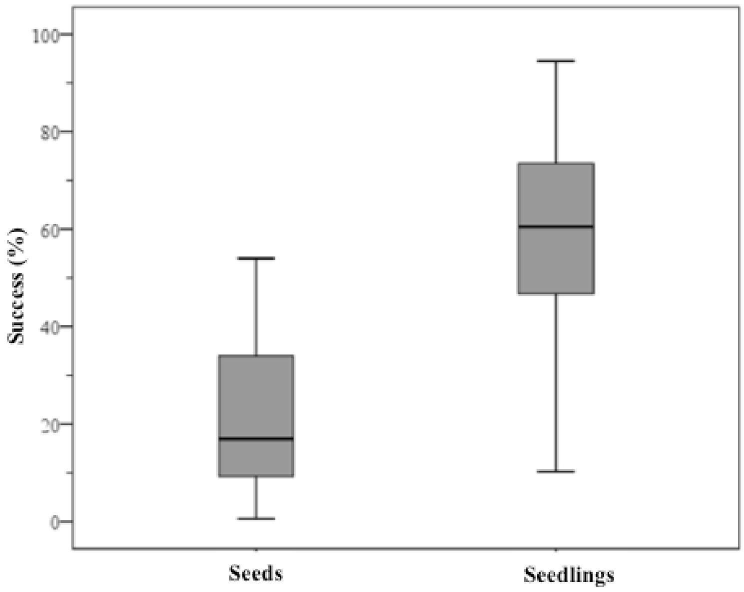

Figure 4.2 Successful Germination/Seedling Survival (%) of experiments for each restoration approach: seeds (n = 31) and seedlings (n = 54). Using reported data for individual species planted and sown. Independent T-test; *t* = -8.5, *df* = 83, *p* < 0.01. The tick line represents the median, the outer limits of the box the first and third quartiles. Whiskers extend to cover any data point < 1.5 times the interquartile range. Circles represent outliers and asterisks are far outliers.

Although mortality and/or lack of germination are major constraints in restoration efforts, only half (n = 60) of the experiments reported the direct causes of death. Environmental variables accounted for most mortality events, with droughts, desiccation, or floods as the major reported causes of death (n = 24 studies). Microsite conditions, substrate quality and/or composition were also important (n = 11), and species interactions including predation, herbivory, disease and competition accounted for mortality in 19 experiments. Other causes of death included fire, frost, seedling size, lack of nutrients, shade or fungus (Appendix 1).

4.4.3. Species selection

While species selection is a fundamental consideration when restoring ecosystems, I found that seed or seedling availability is the major experimental constraint. Most studies (n = 84) reported species availability as one of the principal criteria for species selection, with four experiments listing it as the only criterion. Surprisingly, 30 per cent of experiments did not report the reason for using the selected species. Apart from availability, functional traits such as seed size and shade tolerance were considered in 13 per cent of experiments. Finally, species selection was also motivated by economic value of the species, (n = 11 studies), rare or threatened status (n = 7), wildlife resources (n = 5), mine site and other degrading land uses (n = 8), or common occurrence (n = 4). None of the reviewed experiments evaluated species tolerance to drought, flood, temperature extremes, or other climatic events that might occur under climate change scenarios.

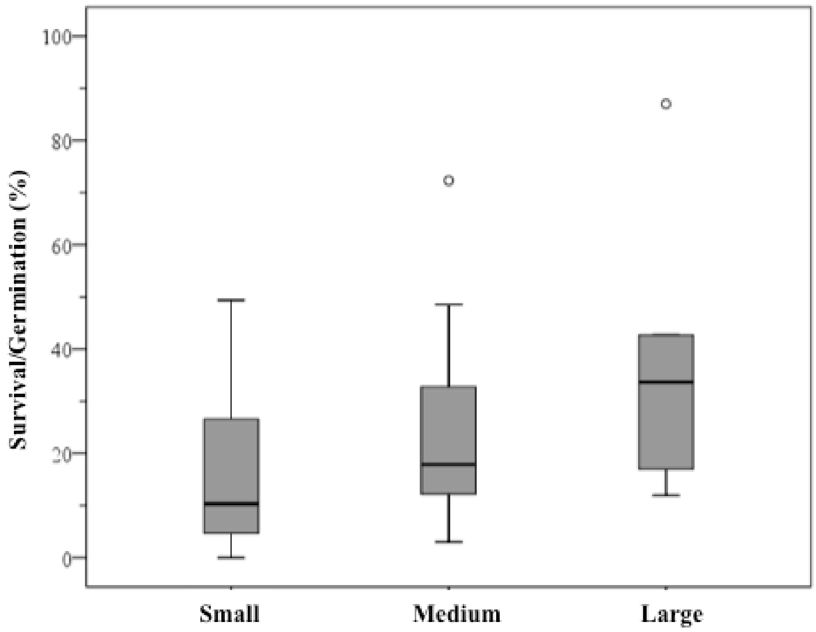

Figure 4.3 Survival/Germination according to seed size (mass) in direct seeding experiments. Seed mass categories: Small: seeds 0-99 mg (n = 29); Medium: 100-2000 mg (n = 14); Large: >2000 mg (n= 6). ANOVA; F= 5.0 *df*= 2, $p < 0.01$. The tick line represents the median, the outer limits of the box the first and third quartiles. Whiskers extend to cover any data point < 1.5 times the interquartile range. Circles represent outliers and asterisks are far outliers. Circles represent outliers

4.4.4. Restoration costs

As ecological restoration projects become more common and necessary, cost-effective methods to recover ecosystems are needed. Of the 120 studies reviewed, 17 stated the importance of developing economically achievable restoration but only nine experiments provided actual costs (Appendix 1).

Assessing the costs of restoration experiments was challenging because studies calculated expenses by either 1) the area planted or 2) the cost per seed/seedling planted. Without the presentation of additional data on the total stems planted or seeds sowed it was difficult to make direct comparisons between the two datasets.

I found that direct seeding is cost-effective, with prices determined by the species diversity. For example, in grassland ecosystems in Germany the costs of seed mixtures ranged from $ 500 USD/ha (3 species) to $ 4.300 USD/ha (51 species). Although, using seed mixtures of multiple species is significantly more expensive than applying mixes of a few species, diversity might accelerate vegetation development and biomass production (Kirmer et al. 2012) due to niche complementarity (Tilman et al 2001). In Brazilian tropical forest, seeding costs of five native species ranges from $ 747 to $ 912 (USD) per hectare (including: soil preparation, seeds, manual seeding, irrigation, fertilizer and formicide). Alternatively, planted seedlings in Brazilian forest costs between $ 1.200 and $ 5.500 (USD) per hectare (Engel & Parrotta 2001; Sampaio et al. 2007), with different planting techniques and the presence of invasive grasses greatly influencing costs.

In Costa Rica, planting costs of tropical forest seedlings (20 cm initial height) in abandoned pastures was higher than using unrooted 2 - metres tree cuttings (initial height). Costs ranged up to $ 182.55 per 100 seedlings versus $ 66.50 per 100 stakes (Zahawi & Holl 2009). Although stakes are considerable cheaper, not all species can be propagated this way. Additionally, their transportation and handling are more challenging than when dealing with seedlings (Zahawi & Holl 2009). Planting expenses in the black pine forests of NE Spain reported costs ranging from $ 1.122 to $ 1.980 USD per hectare (Espelta et al. 2003), with site preparation such as ripping greatly increasing seedling survivorship and planting costs.

These initial establishment costs serve as important guidelines, yet it is the post-planting site maintenance costs which really need to be elucidated in the literature, and how different planting techniques can influence these expenses. For example, maintenance of plantings in abandoned pastures costs \$ 80 - 120 per 100 seedlings (Zahawi & Holl 2009), while planting in plantations and secondary forests usually needs less or no maintenance (Zahawi & Holl 2009; Holl et al. 2011). Further, wetland plantings in Australia were estimated to cost \$ 0.60 per seedling when planting into uncleared areas of vegetation. When planting in degraded wetlands that required mulch application and where seedlings were protected by staked plastic guards, costs increased to \$ 60 per seedling (including 2 years monitoring) (de Jong 2000). Clearing and burning of shrublands in South Africa alone cost around \$ 79 (USD) per hectare, while clearing, burning and sowing seeds cost \$ 413 (USD) per hectare (Gaertner et al 2012).

4.5 DISCUSSION

Forests were the most frequently studied ecosystem for restoration experiments. Direct seeding experiments were more common in grasslands than in forests where planted seedling experiments dominated. Importantly for the restoration of biodiversity, direct seeding experiments were able to trial more plant species than seedling experiments. The selection of plant species in both types of experiments was significantly limited and potentially impaired by seed availability, which may bias studies towards species that produce frequent and abundant seed crops. Although the availability of seeds and seedlings will continue to be a decisive factor when choosing species to plant, the inclusion of species with a wide range of functional characteristics is necessary to promote diversity and ecosystem function (Naeem et al 2012). Restoration efforts should also include rare species (where possible) to reduce their vulnerability to extinction. Furthermore, by promoting the spread and establishment of available species or species with similar functional traits we need to consider if we are inadvertently homogenizing the plant communities in our restoration plantings.

Although confounding factors (climate or/and species) influence the performance of the techniques and need to be taken into consideration, general trends can be elucidated. The survival rates of planted seedlings were higher than in direct seeding experiments. The mechanism causing failure of species due to seed/seedling mortality was only diagnosed in half of the studies reviewed, despite this being one of the most important constraints in restoration. When causal mechanisms for mortality were reported, drought and desiccation were the most common. Seedlings of large-seeded species had greater survivorship than small – a finding that has been supported in previous plant functional trait reviews (see Moles & Westoby 2002). The greater resource provisioning of the larger seeds (Westoby et al. 1996) may facilitate drought tolerance (Gilbert et al. 2001; Khurana & Singh 2004; Hallett et al. 2011) and increase survival. However, under extreme drought conditions, this advantage appears to be lost (Edwards & Krockenberger 2006; Arellano & Peco 2012).

Older seedlings survive better than younger seedlings, and nursery conditions appear to be an important part of developing resilience. For example, drought stress in the nursery through water limitation can increase drought resistance (Vandendriessche 1992). This drought stress “hardening off” period can thicken the leaf cuticle so that the leaves lose less water. For certain species, seedlings of drought-stressed grandparents or parents, produced larger, deeper root systems that grow faster than seedlings from the same genetic lineages whose grandparents and/or parents did not suffer drought stress (Herman et al. 2012). These studies demonstrate that there is considerable plasticity in both phenotypic and genotypic response to environmental stress. Understanding this plasticity will be important to foresee how plantings will survive under climate change scenarios.

Plant establishment and recruitment in highly degraded lands are limited by seed dispersal and seedling survival (predation & desiccation) (Aide & Cavelier 1994; Holl 1999; Holl et al. 2000). Although direct seeding is cheaper than planting, using seedlings yields better results in terms of greater survivorship, and possibly accelerating structural recovery as well. If planting seedlings is not feasible, seed burial to depths ideal for the species involved will lessen desiccation and protect against predation (Doust et al. 2006). An alternative approach would be to deliver seeds with hydromulch and seed coatings that limit desiccation and provide nutrients to facilitate germination (Brofas & Varelides 2000; McCullough & Endress 2012). Since drought is a major cause of mortality, a seed coating that increases drought resistance may facilitate plant diversity in recovering landscapes. Future experiments examining different seed coatings, the ability of different species to germinate after their application, and its financial feasibility are necessary.

Many restoration projects lack formal reporting and monitoring of their challenges, costs, and outcomes. This is due to limited funds and the lack of expertise among practitioners and volunteers (Chazdon 2014). However, detailed reporting in restoration is important to guide future projects. Studies need to demonstrate why they think their timeframe is appropriate to demonstrate successful restoration. Although establishing a general framework for calculating restoration costs highly challenging, not only because the costs depend on the country, the landscape and the scope of the restoration effort, but also because there is no standardized reporting of costs and maintenance of restored areas. It is, however, extremely important because environmental degradation is an “external cost” to a country’s economy. At present it is poorly priced if priced at all (Mullen 2001). If we can determine a price to repair a degraded habitat then this “externality” (in economists’ terms) can be dealt with in a country’s economic balance sheet either through the pricing of restoration programs or by avoided activities that lead to ecological degradation.

Restoration experiments should explore both climate change scenarios and land management policies to optimize restoration success and long-term performance. Water stress, already a major source of plant mortality in restoration programs, may intensify under elevated temperature regimes (Cheesman & Winter 2013) and drought scenarios predicted by many global climate models (IPCC 2014). Of the two restoration techniques direct seeding may be more vulnerable to climate extremes, particularly in tropical ecosystems, and could be restricted to sites with existing vegetation. From a land management perspective, the increasing human population will boost the need for lands devoted to agriculture (Tilman et al. 2001), creating additional pressures on already vulnerable ecosystems (e.g. secondary forests, buffer zones, and restoration sites).

Given the high levels of anthropogenic degradation and fragmentation of tropical forests, the conservation of their biodiversity depends on managing and understanding how secondary forests reassemble (Dent et al. 2013). To fully comprehend the pathways of forest regeneration it is not only important to understand key ecological processes, but also to define the potential of recovery following disturbance (Whitmore 1998). Using different restoration techniques in secondary forests of different ages can provide information on how to manage these lands and increase plant biodiversity.

Future restoration efforts should expand in three main themes. First, explore the range of site preparation techniques that may improve water-holding capacities and plant productivity (e.g. ripping, biochar). Second, consider the roles of phenotypic and genotypic plasticity in plant selection and nursery preparation prior to planting. Third, identify whether the inclusion of species with wider geographic distributions that span large environmental gradients will improve the overall resilience of the vegetation community to climate extremes.

4.6 ACKNOWLEDGMENTS

We would like to thank J. Hill, M. Goosem, S. Goosem, A. Cheesman, W. Edwards, P. Stevenson, T. McDonald, and two anonymous reviewers for comments and feedback on the manuscript.

Appendix 1.1 Palma A.C and Laurance S.G.W 2015. A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? Applied Vegetation Science, 18(4):561-568. doi: 10.1111/avsc.12173.

Appendix 1.2 Data and studies included in the review.

Chapter 5: Seed and seedling experiments in secondary forests: the roles of dispersal and recruitment limitations[*]

5.1 ABSTRACT

Dispersal and recruitment limitations are crucial processes shaping forest composition. In secondary forests these mechanisms may operate differently than in mature forests, because early-aged and isolated secondary forests may suffer stronger limitations due to a lack of suitable dispersers and harsh environmental conditions (e.g. elevated competition with exotics and grasses). To assess dispersal and recruitment limitations in these forests, I used experiments involving seeds and seedlings along a chronosequence of secondary forests in tropical Australia. The experiments included 6 species that varied in seed size (6 to 50 mm in length) and successional status. Seeds of five species were placed in one of three treatments: 1) exposed seeds, 2) fenced seeds and 3) buried seeds. After 14-17 months, seed of all species germinated in all ages of secondary forests, however in young secondary forest sites (4 - 12 years) fewer seeds survived. The greatest survival rates were observed when seeds were buried (27.25%), compared to the low survival of exposed seeds (6%). Planted seedlings (6 spp) had the greater overall survival (63.08%) and recorded higher growth rates in old secondary forests. I found that species identity was important for growth and survival in both experiments, but detected no effect of successional status or seed size. As all species germinated irrespective of variation in site conditions, I suggest that dispersal limitation may be the greater barrier to

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[*] This chapter is based on a paper prepared for submission to Forest Ecology and Management by Palma A.C., Goosem, M and Laurance S.G.W with minimal changes in format and content.

recovery of secondary forests in the region than the recruitment limitations imposed by environmental conditions experienced during our experiment.

5.2 INTRODUCTION

Rapid transformation of mature tropical forests puts at risk the high biodiversity and the diverse ecosystem services these forests provide. Approximately 70% of the tropical rainforest biome has been modified into a matrix of mature forest remnants, agricultural fields, and secondary forests of different ages (Dent et al. 2013; van Breugel et al. 2013). Secondary forests and altered habitats are essential to biodiversity conservation, carbon sequestration and landscape connectivity. Understanding limitations to their recovery is vital to ensure best-practice management in the future (Chazdon 2014; Dent et al. 2013; Faria et al. 2009).

Models of forest succession explain and predict changes in species composition specifying interactions among species, and how plant traits affect such interactions through time (Pickett et al. 1987, Pulsford et al. 2014, Meiners et al. 2015). Some models focus on the physiological and morphological traits of the first colonists (e.g. Egler 1954, and Connell and Slatyer 1977) and highlight that most of the species that will dominate later in succession are present since the onset of succession (Egler 1954). These species will either prevent or facilitate the colonization of other species according to their life-spans and stress tolerances (Drury and Nisbet 1973, Connell and Slatyer 1977). Other models propose that changes in species composition depend on tradeoffs between life history traits, that differentiate species in their ability to acquire resources (Pulsford et al. 2014). Another model that explains tropical succession is the tolerance-fecundity tradeoff (Muller-Landau 2010). This model assumes that species vary inversely in fecundity and stress-tolerance; species with high fecundity and small seeds are unable to tolerate environmental stress (e.g. low soil moisture) whereas species with low fecundity and large seeds are able to tolerate environmental stress. Nonetheless, small seeded species tend to dominate early in succession because they are highly fecund and can be dispersed widely (Coomes and Grubb 2003). However, species with larger seeds present at the onset of succession should outcompete small seeded plants because larger seed reserves provide higher recruitment and survival (Moles and Westoby 2004).

Multiple mechanisms also affect and shape forest regeneration in both mature and altered ecosystems (Benitez-Malvido and Martinez-Ramos 2013). Dispersal and recruitment limitations are two key processes that shape forest composition. Dispersal limitation is the "failure of the propagules of a given species to arrive at an available site" (Terborgh et al. 2011), while recruitment limitation is the failure of a species to be present in all sites favourable for its growth and survival (Hubbell et al. 1999). Therefore, although overcoming dispersal allows species to reach different sites, recruitment limitations may prevent the germination and/or survival of the species. Both mechanisms not only play a fundamental role in maintaining the high biodiversity of mature tropical forests (Terborgh 2012), but also affect the recovery of regenerating forests, where long distances to seed sources and harsh or unfavourable environmental conditions may delay forest recovery (Guariguata and Ostertag 2001; Norden et al. 2009). Although recruitment cannot occur without seeds, seeds are no guarantee of recruitment (Clark et al. 2013). Therefore studying both processes in tropical secondary forests can provide insights into the barriers for the recovery of these ecosystems. Although multiple factors preventing forest recovery are well known, increased knowledge regarding the strength of the processes that influence recovery in different landscapes is required. Experimental research may assist in providing the necessary information to understand natural regeneration in secondary forests and develop management strategies to aid their recovery (Bentos et al. 2013). Direct seeding and planting of seedlings have been widely investigated in different ecosystems to examine the potential of species in forest restoration, their potential economic value to forestry, their use by wildlife or to investigate how functional traits (e.g. seed size) influence performance (Palma and Laurance 2015). Using both techniques, we investigated whether limitations either to dispersal and/or recruitment cause barriers to forest succession and recovery.

My experiments tested two main hypotheses: 1) dispersal limitation is the major barrier to forest recovery; 2) recruitment limitation plays the major role in slowing down succession. I predicted that if dispersal limitation were the major barrier, seeds from all study species would germinate in all sites from our secondary forest chronosequence, regardless of forest age. Alternatively, if recruitment limitation plays the major role, some or all of the studied species would fail to germinate, and/or both seeds and planted seedlings would show low survivorship. Additionally, I predicted that large-seeded species would be more successful in all secondary forests, with larger seeds increasing resource provisioning (Westoby et al. 1996) and stress tolerance (Muller-Landau 2010) improving seedling performance (Moles and Westoby 2002; Moles and Westoby 2004).

The different seed treatments (exposed, fenced, buried) help understand recruitment limitations in the different sites. If predation and/or desiccation were limiting recruitment, buried seeds would be more successful in all age categories. Alternative, if these recruitment limitations do not constraint the germination of exposed or fenced seeds, all treatments would have equal germination, and just placing seeds directly in the soil would be a fast easy alternative to aid biodiversity recovery in these regenerating forests.

The planted seedlings provide insight on how the environment could limit growth and survival. If high rates of herbivory and mortality are found in all forests, recruitment limitations could be strongly preventing the recovery of these ecosystems.

5.3 METHODS

5.3.1 Study area and site selection

The study was carried out on the southern Atherton Tableland (17°23.3’S 145°35.8’E - 17°27.0’S 145°38.2’E), a highly fragmented landscape in north-eastern Australia. The climate is tropical, with mean annual rainfall ranging from 1700 to 2600 mm, and a distinct dry season from July to October (BOM 2014). Mean monthly temperatures range from a mean minimum of 10ºC in the drier months to a mean maximum of 29ºC during the wet season.

In the 1920s much of the region was cleared of continuous rainforest and converted to pasture for the dairy industry (Frawley 1987; Gilmore 2005). Some pastures were abandoned in the 1940s and others in the 1980s as economic conditions changed (Gilmore 2005). Following pasture abandonment, forest regenerated and now secondary forests of different ages dominate the landscape. Interpreting a time-series of aerial photographs and satellite imagery, we selected different sites that would provide us with a chronosequence of secondary forest age from 4 – 34 years since canopy formation. This study encompasses 12 secondary forest sites, none adjacent to mature continuous forest (Figure 5.1).

Chronosequence studies have been criticized because calculating age since abandonment and determining previous land uses are major challenges (Chazdon 2014), and their explanatory power may depend on the scale of study design (Chazdon 2008; Dupuy et al. 2012; Lebrija-Trejos et al. 2008). We have addressed these challenges through extensive aerial photography interpretation, replication of independent sites that are within the same climatic region and share similar past land use. Additionally, we used age since closed-canopy formation as a proxy of forest age to limit variation between the initial conditions of different sites.

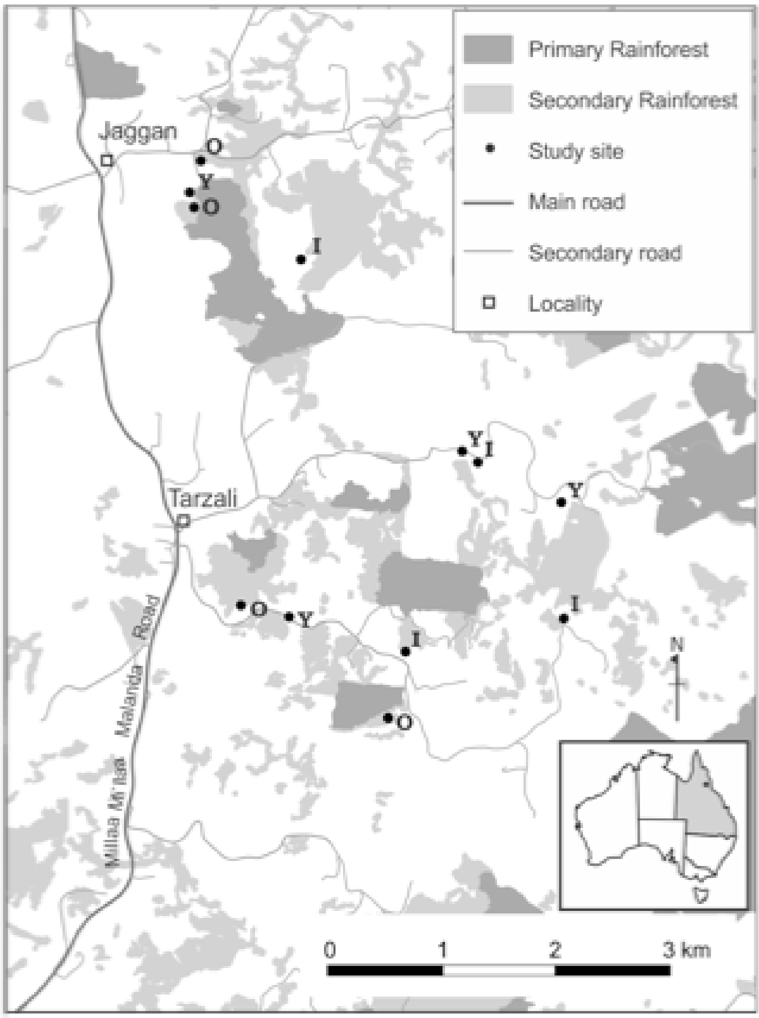

Figure 5.1 Map of the study area, southern Atherton Tableland, North Queensland, Australia. Letters represent the age of secondary sites. Y: Young secondary forests (4 – 12 years), I: Intermediate-aged (16 – 20 years) and O: Old (23 – 34 years).

5.3.1.2 Site ages and categories

Using a range of Queensland State Government aerial photography, satellite images from Google Earth (© 2014 Google Image, ©2014 DigitalGlobe), and imagery from Queensland Globe (©State of Queensland 2013, ©CNES 2012, Spot Image S.A. France, ©2013 Pitney Bowes), study sites were selected. Each image was examined for any vegetation other than pasture, using stereo-pairs of images where available. Otherwise, aerial photographs were scanned at high resolution and successive pairs of digital images were compared side-by-side on-screen. Age since abandonment was calculated to be the mid-point between consecutive images where pasture had been replaced by another vegetation. Age since canopy formation was determined as the mid-point between successive images where visual estimate of canopy cover in the more recent image was at least 70% and canopy height greater than 5 metres. Secondary forests were classified into three age categories using the number of years since canopy formation as a proxy of forest age: Young: forests of 4 to 12 years; Intermediate: forests of 16 to 20 years; and Old: forests of 23 to 34 years, including 4 sites for each age category.

5.3.2 Species selection

Six rainforest tree species were selected, based on previous information regarding the species composition of secondary and mature forest sites in this region (Goosem et al. 2016; Palma et al. in review). For the direct seeding experiments, I chose three large-seeded (> 20 mm in length) rainforest tree species (*Beilschmiedia tooram*, *Cryptocarya oblata* and *Endiandra bessaphila*), which were **absent** from our regenerating forest but **present** in mature forest sites in the region; and two small-seeded (< 15mm in length) rainforest tree species (*Litsea leefeana* and *Guioa lasioneura*) that are present in both secondary and mature forest sites in the region.

For the planting experiment an additional small-seeded late successional species (*Synima cordierorum*) was included, this species is present in both secondary and mature forest sites in the region, but was unavailable as seed for seed experiments. I collected seeds of *C. oblata*, *E. bessaphila*, *L. leefeana* and *G. lasioneura* from at least four rainforest remnants and parental trees scattered within the region and bought seeds of *B. tooram* and seedlings of *S. cordierorum* from local nurseries.

5.3.3 Seed experiments

I established the seed experiments during the wet season (November 2013-February 2014). After collection, seeds were soaked in water for 48 hours, the pulp removed and then placed in the secondary forests within 60 - 72 hours. The three seed treatments included: 1) exposed seeds (litter removed and seeds placed on the soil); 2) fenced seeds (litter removed, seeds placed on the soil within a plastic fence, 50 cm in height; and 3) buried seeds (litter removed, seeds sown to a depth of 2 cm). I used five species and 20 seeds per treatment per site for a total of 3600 seeds. In each site I established a seed experimental plot (3 m x 2.5 m) divided into 15 (1 m x 0.5 m) quadrats, randomly allocating one of the three different direct seeding treatments and species to each quadrat.

5.3.4 Seedling experiments

All seedlings were germinated and grown for 1-3 months in a greenhouse, with 1 month of “hardening” outdoors with no extra watering (except *S. cordierorum,* bought at 8 months of age). Seedlings were planted during the wet season (March of 2014) at the same sites used for the direct seeding experiments. I planted six species and 30 seedlings per species per site (except *C. oblata,* 24 seedlings per site) for a total of 2088 seedlings. Species were randomly allocated into 6 (3 m x 3 m) quadrats within a (9 m x 6 m) experimental planting plot at each site.

5.3.5 Data collection and analysis

5.3.5.1 Seed experiments

All seeds were monitored weekly during the initial five to 10 weeks after placement in the secondary forest sites. During each census I recorded seed number, status (e.g. eaten, removed, dry, rotten, germinated) and height of each uniquely-tagged germinated seedling. After week 10, seeds were monitored once a month for three months and then every three months until April 2015. I calculated the relative growth rate of seedlings (RGR) in mm per day from the difference between initial and final heights of each seedling divided by the growth period ((ln(height final) − ln(heigh tinitial))/(growth period in days)). The total height of each seedling was measured from the ground to the most distant part of the main stem. All negative values were discarded.

I assessed the effects of two treatments: secondary forest age and direct seeding method and their interactions on seed germination (survival) and growth using nested analysis of variance models (ANOVA), with site nested within forest age. Data were transformed using the arcsine transformation (Zar 1999) to reach normality and Tukey’s test were used for post-hoc analysis.

5.3.5.2 Seedling experiments

Planted seedlings were monitored two weeks after planting and all individual seedlings tagged with a unique number. Subsequently, seedlings were monitored every three months for 13 months. In each census I recorded seedling number, status (e.g. eaten, removed, dry, dead) and height. I calculated relative growth rate (RGR) using the same method described for seeds.

I assessed the effect of secondary forest age and its interaction on seedling survival, growth and species using nested analysis of variance models (ANOVA) with site nested into forest age. Data was transformed using the arcsine transformation (Zar 1999) to reach normality and Tukey's test were used for post-hoc analysis. Statistical analyses were performed using IBM SPSS Statistics Version 21.

5.4 RESULTS

5.4.1 Seed experiments

5.4.1.1 Growth and survival

Seed survival was very low in young secondary forests (Figure 5.2a) compared to intermediate and older sites but variable enough that forest age was not significantly different when tested ($F_{(2, 9)}= 1.03$, $p = 0.39$). The seeding treatments did have a significant effect on seed survival ($F_{(2, 126)}= 45.85$, $p< 0.0001$), with the greatest survival rates recorded when seeds were buried compared to both exposed and fence treatments ($p< 0.0001$ for both comparisons, figure 5.2b).

Species identity was also important for seed survival ($F_{(4, 126)}= 25.71$, $p< 0.0001$). The highest survival was recorded for *B. tooram* and *L. leefeana* both of which differed significantly from *C. oblata* and *G. lasioneura* ($p< 0.0001$ for all comparisons, figure 5.2c). Seeds of *L. leefeana* also survived better than seeds of *E. bessaphila* ($p= 0.029$). Although the effect was not large, seeds in old secondary forest sites showed higher survival (average: 17.75%) compared to seeds in young (average: 10.33%) and intermediated-age secondary forest sites (average: 14.91%). I found interaction effects between secondary forest age, direct seeding method, and species identity on seed survival ($F_{(16, 126)}= 1.82$, $p= 0.034$). Overall, seed survival was greater in old secondary forests than in young forest for all species and treatments.

Survival for *B. tooram*, *E. bessaphila* and *L. leefeana* was greater when seeds were buried in old secondary forests (43.75 ± 27.51; 33.75 ± 16.52 and 53.75 ± 19.31, respectively), whilst *C. oblata* and *G. lasioneura* were more successful if sown in intermediate-aged forests (12.5 ± 15.54 and 8.75 ± 6.29, respectively).

Neither secondary forest age, nor direct seeding method significantly affected the growth of germinated seeds ($F_{(2, 17)}$= 1.49, p= 0.25, and $F_{(2, 23)}$= 0.12, p = 0.88, respectively, Figures 5.2d and 5.2e). In contrast, species identity was important ($F_{(4, 23)}$= 6.69, p=0.001), with highest growth in *G. lasioneura* and *L. leefeana*, with *G. lasioneura* growing more than *B. tooram* (p=0.013) and greater growth in *L. leefeana* compared to *B. tooram*, *C. oblata* and *E. bessaphila* (p< 0.0001; p= 0.006 and p= 0.015, respectively, Figure 5.2f). Overall, germinated seeds in old secondary forest sites had higher growth rates (average: 0.0068 mm/day) than germinated seeds in young (average: 0.0047 mm/day) and intermediate-aged secondary forest sites (average: 0.0048 mm/day). I did not find interaction effects between secondary forest age, direct seeding method, and species identity on growth of the germinated seeds ($F_{(2, 23)}$= 0.57, p = 0.57).

5.4.1.2 Failure to germinate and seed loss

Across all age categories and treatments (Figure 5.3a) the highest loss of seeds was due to seed removal (seeds that were no longer found, average: 65.09%); followed by rotten seeds (14.51%), eaten (13.75%), desiccated (4.21%) and finally seeds with visible fungi (2.44%). For the germinated seedlings, the highest cause of death was also removal (seedlings that were no longer found, average: 63.12%), followed by seedlings that were desiccated (29.01%), had fungi (5.67%), suffered from stem breakage (1.11%), showed clear signs of herbivory (0.72%) and finally seedlings that were unburied (0.37%).

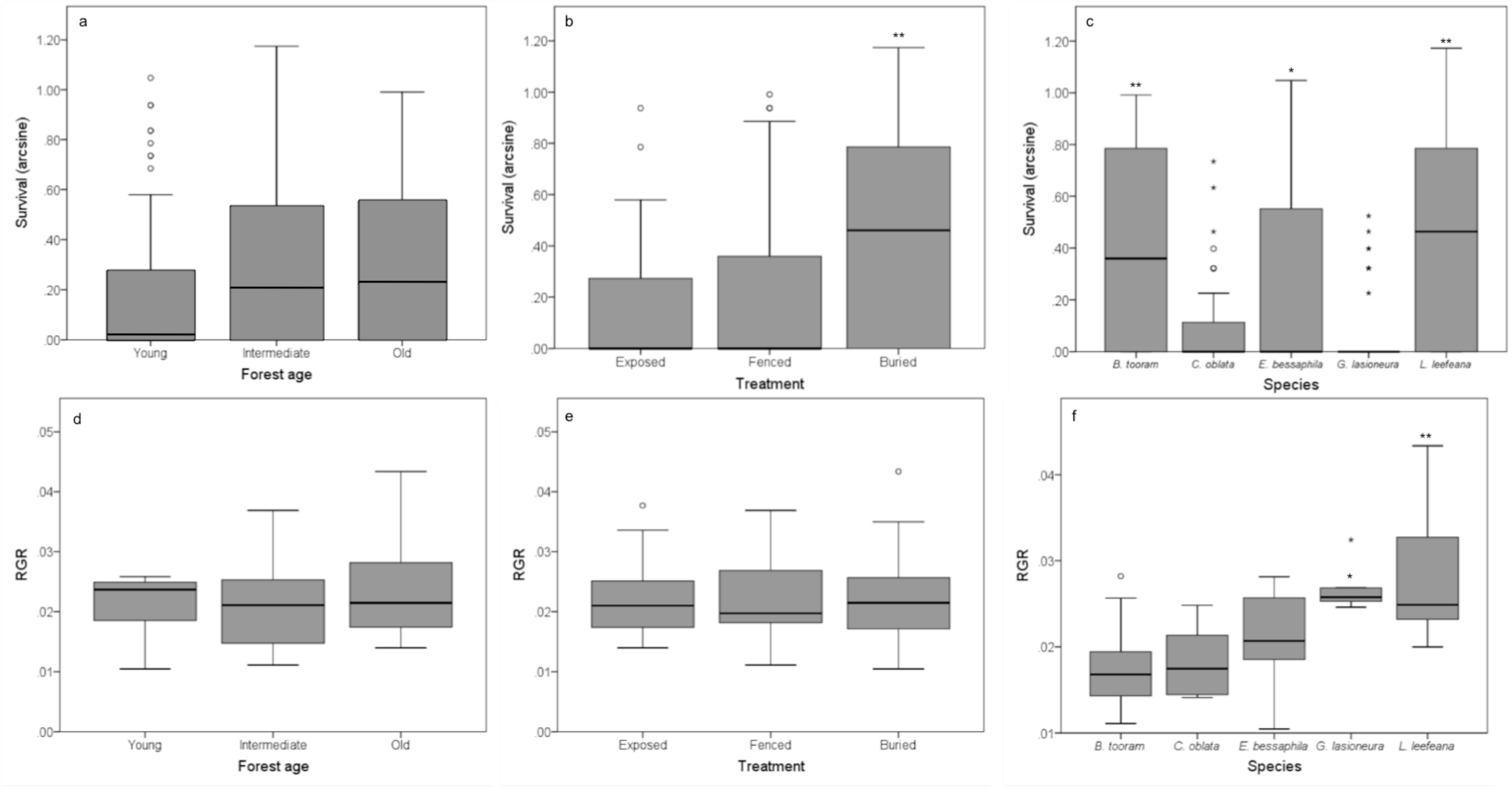

Figure 5. 2 Seeds that germinated successfully in seed experiments in three secondary forest ages. (a) Secondary forest age did not have a significant effect on seed survival ($F_{(2, 9)}$= 1.03, p = 0.39). (b) Direct seeding treatment affected seed survival ($F_{(2, 126)}$= 45.85, p<0.0001), buried seeds had highest survival than both exposed and fenced seeds (p<0.0001 for both comparisons).

(c) Species identity was important for seed survival ($F_{(4, 126)}$= 25.71, p< 0.0001) *B. tooram* and *L. leefeana* had the highest survival and both differed significantly from *C. oblata* and *G. lasioneura* (p< 0.0001 for all comparisons); seeds of *L. leefeana* also survived better than seeds of *E. bessaphila* (p= 0.029). (d) Secondary forest age did not affect the growth of germinated seeds ($F_{(2, 17)}$= 1.49, p= 0.25). (e) Seeding treatment did not affect growth either ($F_{(2, 23)}$= 0.12, p = 0.88). (f) Species identity was important ($F_{(4, 23)}$= 6.69, p=0.001), with highest growth in *G. lasioneura* and *L. leefeana*; *G. lasioneura* grew more than *B. tooram* (p=0.013) and *L. leefeana* showed higher growth when compared to *B. tooram, C. oblata* and *E. bessaphila* (p< 0.0001; p= 0.006 and p= 0.015, respectively). For all graphs, the tick line represents the median, the outer limits of the box the first and third quartiles. Whiskers extend to cover any data point <1.5 times the interquartile range. Circles represent outliers and asterisks significant differences.

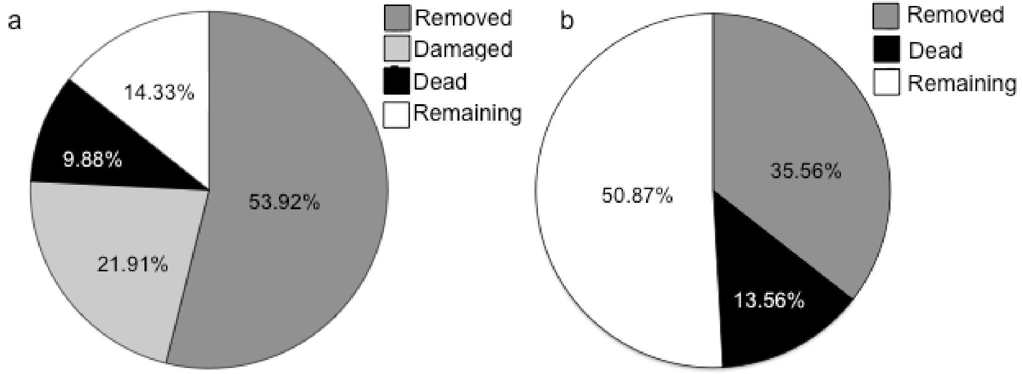

Figure 5. 3 Overall seed and seedling performance a) represents all direct seeding experiments combined across all forest age categories (young, intermediate and old) treatments (exposed, fenced and buried seeds) and species (*B. tooram*, *C. oblata*, *E. bessaphila*, *G. lasioneura* and *L. leefeana*) b) represents all seedling plantings combined across all forest age categories and species.

5.4.2 Seedling experiments

5.4.2.1 Growth and survival

Secondary forest age did not have a significant effect on seedling survival ($F_{(2, 9)}$= 4.28, p = 1.19). However, higher survival rates were found in seedlings planted in old secondary forest (average: 63.08%), compared to seedlings planted in young (average: 43.92%) and intermediate-aged secondary forest (average: 45.61%, figure 5.4a). Species identity influenced seedling survival ($F_{(5, 45)}$= 12.35, p< 0.00001, Figure 5.4b), with *S. cordierorum* showing the highest survivorship and surviving better than *B. tooram*, *E. bessaphila* and *G. lasioneura* (p= 0.029, p= 0.001 and p< 0.0001, respectively). Seedlings of *G. lasioneura* had the lowest survivorship and differed from *L. leefeana* (p= 0.042). I did not find interaction effects between secondary forest age and species identity on seedling survival ($F_{(10, 45)}$= 1.13, p = 0.35).

Secondary forest age did not influence growth in the planted seedlings ($F_{(2, 13)}$= 2.32, p = 0.13, Figure 5.4c) however, seedlings planted in old secondary forest sites showed higher growth rates (average: $7.3x10^3 \pm 3.3x10^3$ mm/day) than seedlings in young ($6.6x10^3 \pm 5.4x10^3$ mm/day) and intermediate-aged ($5.3x10^3 \pm 3.0x10^3$ mm/day) secondary forest sites. Species identity had a significant effect on seedlings growth ($F_{(5, 35)}$= 17.51, p< 0.0001) with *G. lasioneura* growing more than all other species (p< 0.0001 for all comparisons, Figure 5.4d). In contrast, *C. oblata* showed the lowest growth rate and differed significantly from *E. bessaphila*, *L. leefeana* and *S. cordierorum* (p= 0.00, p= 0.005, p= 0.026, respectively). I did not find interaction effects between secondary forest age and species identity on seedling growth ($F_{(10, 35)}$= 1.68, p = 0.12, Figure 5.3d).

5.4.2.2 Mortality

Across all age categories, removed seedlings (seedlings that were no longer found) accounted for the highest amount of mortality (71.69%), followed by desiccation (21.56%), signs of herbivory (2.75%), unearthed (2.09%) and finally broken stems (1.91%; Figure 5.3b).

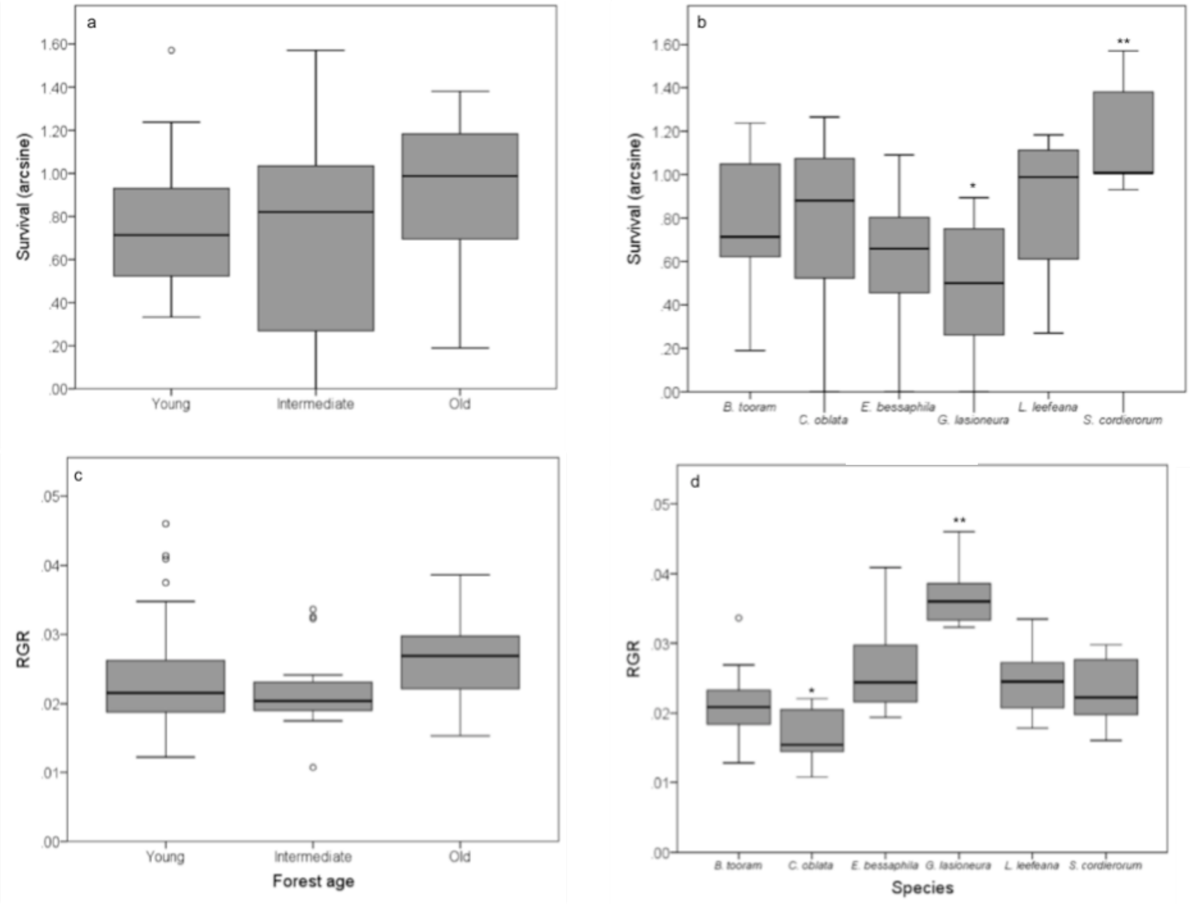

Figure 5.4 Planted seedlings in secondary forest of three different ages. (a) Secondary forest age did not have a significant effect on seedling survival ($F_{(2, 9)}$= 4.28, p = 1.19). (b) Species identity influenced seedling survival ($F_{(5, 45)}$= 12.35, p< 0.00001). *S. cordierorum* had the highest survival, differing from *B. tooram*, *E. bessaphila* and *G. lasioneura* (p= 0.029, p= 0.001 and p< 0.0001, respectively). Seedlings of *G. lasioneura* had the lowest survivorship and differed from *L. leefeana* (p= 0.042). (c) Secondary forest age did not influence seedlings growth ($F_{(2, 13)}$= 2.32, p = 0.13). (d). Species identity had a significant effect on seedlings growth ($F_{(5, 35)}$= 17.51, p< 0.0001) with *G. lasioneura* growing more than all other species (p< 0.0001 for all comparisons. *C. oblata* showed the lowest growth rate and differed from *E. bessaphila*, *L. leefeana* and *S. cordierorum* (p= 0.00, p= 0.005, p= 0.026, respectively).

5.5 DISCUSSION

Along a chronosequences of secondary forest, seed and seedling experiments provided important insight into processes that delay recovery of these forests. I found that three late successional species of mature rainforest, that were naturally absent from secondary forest germinated and grew once introduced. These results provide evidence that the absence of these species is due in part to the lack or limited dispersal opportunities for large seeded species in this old fragmented landscape. Furthermore, both seeds and seedling suffered from very high removal rates in my experiments, which I assume is due to predation or herbivory, and which in itself demonstrated the constraints to recruitment in these forests.

Species identity was more important than forest age for growth and survival but I did not find a clear pattern with respect to seed size or successional status. For example, *L. leefeana* and *B. tooram* showed the greatest survival for the direct seeding experiment. *L. leefeana* is a small-seeded early successional species that is common in all sites, whereas *B. tooram* is a large-seeded late successional species rarely encountered in secondary forests. Alternatively, in the same experiment survival was lowest for *C. oblata*, a big-seeded late successional species and *G. lasioneura* a small-seeded early successional species.

When planted as seedlings, *S. cordierorum*, a small-seeded late successional species survived the best. However, these seedlings were bought from a local nursery and they were 8 months older than all other seedlings. It is possible that *S. cordierorum* might actually survive better at these sites, or that their higher survival might just be an artefact of their greater age increasing their resilience (Herman et al. 2012; Vandendriessche 1992).

Not surprisingly, the small-seeded, early successional species *G. lasioneura* and *L. leefeana* showed the highest growth in seed and seedling experiments. These species are very common in these secondary forest sites and fast growth is a typical characteristic of early successional species are usually fast growing (Finegan 1996), while large-seeded, late successional species such as *B. tooram* and *C. oblata* have relatively lower growth rates.

Buried seeds had the greatest survivorship (average: 27.25%) with a three -to four-fold higher persistence than exposed (6%) and fenced (9.75%) seeds. Burial appears to protect seeds from predators, desiccation, heavy rains or movement of leaf-litter by foraging wildlife which may be important to increase germination in these forests. I assumed that removed seeds were eaten or damaged and did not germinate, but it is possible that they were cached by small mammals such as white-tailed rats (Harrington et al. 1997). Overall the direct seeding experiments showed a ca.14% survival of seeds which is a result very similar to other direct seeding experiments in different ecosystems which average an 18% survival (Palma and Laurance 2015).

Planting experiments provide further insight into recruitment limitations. I found the highest survival in old secondary forest sites (average: 63.08%) where fewer grasses and exotic species may favour establishment. As with the direct seeding experiment, the main cause of mortality was seedling removal. These removed seedlings could have been eaten whole or unearthed and then washed away during rainstorms. Desiccation was the next most common cause of mortality; droughts and desiccation being a commonly cited cause of death in planting experiments (Palma and Laurance 2015).

Previous studies on seed germination and seedling survival of species planted into secondary forests have also found that species identity is more important for survival than variations in habitat (Camargo et al. 2002; Cole et al. 2011). However, early growth and survival are not always an indicator of the species persistence in the long-term (Benitez-Malvido and Martinez-Ramos 2013). Extended monitoring of these experiments could provide more information on the success of each species and whether their relative success in establishment and growth changes over time and in response to changing biotic and abiotic environments (e.g. increased competition and decreasing light).

This study demonstrated that some of the missing plant species in the secondary forests of tropical Australia will germinate and grow when they are introduced as seeds and/or seedlings. With seed removal rates so high, direct seeding without burial is not recommended; sowing seeds might be an effective way to reintroduce much of the plant diversity that is currently missing from secondary forests. Planting of seedlings yields better results and older seedlings are more successful, however with the higher costs involved (e.g. greenhouses, transportation and more labour) this approach should be used for highly isolated sites, for lands with high conservation value such as wildlife corridors (Tucker 2000) or for the expansion of rare habitats.

Restoration efforts are important to accelerate biodiversity gains in isolated sites, or to introduce endangered plant species. However, we need to keep in mind that even if restoration efforts are successful 25 years after planting key features of mature rainforest are still lacking (Shoo et al. 2015). Although dispersal limitation lessens over the first years of recovery, with seed rain including more species, mature forest species continue to be limited (Reid et al. 2015), stressing the importance of actively restoring these species when possible.

In our experiments forest age did not have a significant effect on growth and/or survival. This demonstrates that once succession has started and some canopy has formed, reintroduction of different species to accelerate forest recovery can be successful even in young secondary forests. Since species identity was important, testing different species at small-scales before embarking in large-scale restoration projects is necessary.

These results highlight the significance of dispersal and recruitment limitations for the recovery of tropical secondary forests. I found that all the species included in the study germinated and grew even in young secondary forest sites. This shows that dispersal limitation may have a stronger influence than recruitment limitation for the recovery of these secondary forests. Direct seeding experiments and planting of seedlings are an effective way to assess dispersal and recruitment limitations in different habitats and for different species.

Planting clusters of different species has been a successful technique that enhances seed rain and seedling establishment with lower costs than tree plantations (Cole et al. 2010; Zahawi and Augspurger 2006; Zahawi et al. 2013). These small clusters can also be use to plant different species, include a broader range of functional traits and test their resilience to desiccation or heavy rains. These types of experiments are important as they may help us to plan restoration efforts for future climatic scenarios (Palma & Laurance 2015).

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Chapter 6: Synthesis

6.1 BACKGROUND

Tropical forests are the most productive and diverse ecosystems on Earth (Myers et al. 2000, Stegen et al. 2011), but are being rapidly transformed into a mixture of pastures and agricultural fields (Baccini et al. 2012). Additionally, human migration from former agricultural regions to urban areas in recent decades has produced an unprecedented increase in the area of abandoned tropical lands (Wright and Muller-Landau 2006, Hansen et al. 2013). These changes in land use have implications for conservation and forest management. As abandoned areas convert to secondary forests, their importance for biodiversity conservation increases. Further, these regenerating forests start providing some of the environmental services previously supplied only by mature forests (Pan et al. 2013).

Studying forest succession is fundamental to our understanding of how species composition changes after severe disturbances (Connell and Slatyer 1977, Begon et al. 2006). Multiple studies have addressed forest succession in Neotropical forests after human or natural disturbances (reviewed in Chazdon 2014). However, only a few studies have investigated secondary forest succession after human disturbance in tropical Australia (Yeo and Fensham 2014, Shoo et al. 2015, Goosem et al. 2016).

This doctoral thesis explored different themes relevant to secondary forests and their recovery in tropical Australia. In this final chapter the key findings from previous chapters (2-5) are integrated in the context of tropical secondary forest succession. The aim in this chapter is to synthesize the central findings of the thesis and possibilities for future research.

6.2 PLANT DIVERSITY AND FUNCTIONAL TRAITS RECOVERY

Overall, secondary forests in tropical Australia recover plant diversity and functional traits slowly. Results from Chapter 3, showed that young forests (4 - 12 years) and intermediate-aged secondary forests (16 - 23 years) had lower species diversity compared to old secondary and mature forest sites. These younger forests were also dominated by species with functional traits associated with the early stages of succession (e.g. small-seeded understorey species). Herbs, grasses and exotics dominated the understory communities of these regrowth forests. As succession unfolds, plant diversity increased and native rainforest trees and shrubs became more abundant, in both the understorey and adult plant communities, a common pattern in tropical forest succession (Denslow and Guzman 2000; Capers et al. 2005; Chazdon et al. 2010; Dent et al. 2013; Yeo and Fensham 2014).

In this study, young and intermediate-aged secondary forest differed significantly in species diversity and functional traits composition from mature forest sites. However, old secondary forest and mature forest sites did not differ significantly in species diversity. Yet, species composition and some functional traits (seed length, forest strata occupied when mature and native/non-native status) remained different. This result supports other studies that have found that plant diversity in tropical forest succession usually recovers at a faster rate compared to functional traits (Peña-Claros 2003, Capers et al. 2005, Piotto et al. 2009, Mullah et al. 2012). A key finding with important implications for the regeneration of these secondary forests is that late successional and large-seeded species were scarce even in old secondary forest (27 - 41 years). Low numbers of large-seeded animal dispersed seeds have also been found in enrichment plantings and other natural regenerating forests in this region (Yeo and Fensham 2014, Shoo et al. 2015) and elsewhere (Asanok et al. 2013, Lohbeck et al. 2013). These differences in species composition and functional traits between the understories of secondary and mature forests may be due to seed dispersal and recruitment limitations (van Breugel et al. 2007) and to the impacts of forest fragmentation on forest dynamics (Melo et al. 2010, Haddad et al. 2015).

Estimating species composition of soil seed banks, seedlings and adult plant communities provides further insight into the dispersal and recruitment limitations that may delay forest recovery. Results from Chapter 4, showed that exotic species comprised 45.6% of the total species registered in the soil seed bank of young secondary forests. Exotic species were also present in mature forest soil samples but in lower proportions (19.8% of sampled species). Grasses, sedges, herbs and functional traits associated with early successional stages were more abundant in the soil seed bank of young and intermediate-aged secondary forests. Shrubs and small trees dominated the old secondary and mature forest soil seed bank samples, where vines were also more abundant and ferns also germinated. Therefore, exotic species, grasses, sedges, herbs and early successional functional traits common in the understorey of young and intermediate-aged secondary forests were gradually displaced by shrubs, small trees and vines as succession progressed, however, exotic species were still prevalent even in old secondary and mature forest sites.

Soil seed banks, understorey and adult plant communities in these regrowth forests showed a slow transition towards the composition of mature forest. However, the high abundance of non-native species and grasses in young and some intermediate-aged forest sites may arrest succession in terms of species composition, functional traits and forest structure. However, results from chapters 3 and 4 suggest that in these regenerating forests, environmental conditions are limiting the recruitment of exotic species present in the soil seed bank in old secondary and mature forest sites, whereas the lack of seed availability or dispersers is constraining the arrival of late successional species throughout the chronosequence. Similar patterns of low numbers of large animal dispersed seeds in regenerating forests have been found in this region (Shoo et al. 2015) and the Neotropics (Melo et al. 2010; Lohbeck et al. 2013). However, secondary forests in close proximity to mature forest remnants, in a region with a high abundance of generalist species and efficient dispersal mechanisms can facilitate the establishment of diverse plant communities in just two or three decades (e.g. Denslow and Guzman 2000; Norden et al. 2009)

An interesting finding was the presence of only a few vines in both the understory and soil seed banks of young and intermediate-aged forests. In young regenerating forest in the Neotropics, vines usually colonize rapidly, reach high abundances and delay forest regeneration (Schnitzer and Bongers 2011, Barry et al. 2015). Since vines grow vegetatively from basal nodes and tuber, as well as from seeds, this colonizing pattern may be strongly influenced by the proximity of mature forests. In Australia, the rate and area of secondary rainforest is influenced by the size and proximity of mature forests remnants (Sloan et al. 2015, Goosem et al. 2016) with 85% of the ~ 11,000 ha on the Atherton tableland found within 400 meters of mature forest remmants (Sloan et al. 2015). This pattern illustrates the important role of seed sources and in forest recovery.

6.3 DISPERSAL AND RECRUITMENT LIMITATIONS

To further examine dispersal and recruitment limitations, I used field experiments with seeds and seedlings of native rainforest species. Results from these experiments (Chapter 5) showed that species identity is more important than forest age for both growth and survival in both experiments (direct seeding and planting of seedlings). No effect of successional status or seed size was detected. For example, *Litsea leefeana* and *Beilschmedia tooram* showed the greatest survival in the seed experiments. *L. leefeana* is a small-seeded early-successional species that is common in all sites, whereas *B. tooram* is a large-seeded late successional species rarely encountered in secondary forests. Alternatively, in the same experiment survival was lowest for *Cryptocarya oblata*, a large-seeded late successional species and *Guioa lasioneura,* a small-seeded, early-successional species. As all species germinated and grew irrespective of variation in site conditions, it seems dispersal limitation may pose greater barrier to recovery of secondary forests in the region than the recruitment limitations imposed by environmental conditions experienced during the experiments. However, recruitment limitations still play a major role during the early stages of plant development with high removal rates detected for both seeds and seedlings.

Seed survivorship was very low in my experiments (~ 14%), with seed removal (~ 65%) observed as the most frequent cause of seed loss. Planting of seedlings yielded better results and older seedlings were more successful. The higher costs associated with the preparation of seedling for planting (e.g. requirements for greenhouses, transportation and more labour), suggest this approach in restoration should be used for highly isolated sites, for lands with high conservation value such as wildlife corridors (Tucker 2000) or for the expansion of rare habitats. The survival of seeds was enhanced by planting rather than leaving on the surface so, if this can be achieved relatively cheaply, it may be the better approach for increasing diversity more generally in secondary forests.

Restoration efforts are important to accelerate biodiversity gains in isolated sites, or to introduce endangered plant species. However, we need to keep in mind that even if restoration efforts are successful 25 years after planting some key features of mature rainforest are still lacking (Shoo et al. 2015). Although dispersal limitation lessens over the first years of recovery, with seed rain including more species, mature forest species continue to be limited (Reid et al. 2015). This observation stresses the importance of actively restoring these species when possible. Although active forest restoration is still viewed as a costly effort, passive restoration by comparison may have direct and indirect costs that should also be considered. In developing countries where land tenure is not always strictly enforced, and where economic circumstances change rapidly, passive restoration may result in the loss of young forest to "new" landholders or wandering cattle (Zahawi et al. 2014).

6.4 IMPLICATIONS AND FUTURE RESEARCH

Worldwide, tropical secondary forests account for the largest recent increase of live biomass (Pan et al. 2013). This rapid growth makes some of these secondary forests highly productive and resilient; sequestering carbon up to 11 times faster than mature forests (Poorter et al. 2016). These carbon stocks will likely have a significant contribution towards mitigating climate change and helping reach the goals of the COP2015 meeting (FCCC 2015). Forest restoration is also gaining significance with important international efforts to restore large areas of world’s deforested and degraded lands in multiple countries (e.g. Bonn Challenge 2011). Future research will help to provide the necessary information to allow development of management strategies that aid the process of forest succession (Bentos et al. 2013). An overall understanding of the diverse factors that limit and influence secondary forests recovery in different environments will be important to enable restoration that increases biodiversity and ecosystem functions in these systems.

Increasing awareness of the repercussions of forest loss in changing ecosystems functions and its implications for human-well being (MEA 2005) make forest restoration a key feature of future research. Results from this thesis show a slow recovery in tropical secondary forests and the lack of key functional groups (e.g large-seeded trees) even in 40 year-old forests. This finding makes restoration efforts necessary if we want to ensure the long-term survival of local biodiversity and enhance the resilience of these forests against future climate change.

Although tropical primary forests are essential to preserve biodiversity (Gibson et al. 2011) and their conservation needs to be a priority, our changing environment and the large areas of tropical secondary forests around the world present a unique opportunity to restore this ecosystem and protect biodiversity. However, restoration efforts need to take into account climate change and the challenges it imposes on the conservation of vulnerable species. A key finding in Chapter 2 was the lack of restoration studies addressing the impacts of climate change on restoration efforts or providing information regarding how studies should consider future shifts in the environment. Restoration approaches should also include realistic goals that match the local communities needs and expectations and prioritizing actions in a crowed world (Perring et al. 2015). Multidisciplinary efforts that match goals of conservation and communities needs will also help improve the outcomes of restoration (Chazdon 2015).

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Appendix 1.1 Palma A.C and Laurance S.G.W (2015). A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? Applied Vegetation Science 18: 561-568

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SYNTHESIS

A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go?

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Costs; Planting methods; Reforestation; Restoration; Seedlings; Seeds

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Abstract

Questions: To select the best method to restore an ecosystem requires an understanding of the various outcomes commonly achieved through different restoration techniques. What method results in the most timely and cost-effective means of reinstating biodiversity and restoring ecosystem functions and services?

Methods: We explored the efficacy and costs of two re-vegetation techniques commonly used in ecosystem restoration: direct seeding and planting of seedlings. Our analysis focused on 120 scientific peer-reviewed publications reporting on experiments using seeds or seedlings, and encompassed a range of ecosystems such as wetlands, savannas and forests. We examined current restoration issues, including species diversity, survival, species selection, costs and how future climate change may influence restoration efforts.

Results: Direct seeding experiments used more species than seedling studies, yet showed lower survivorship. Species availability is the major constraint in the selection of which species were used, regardless of the approach employed. Although costs are extremely important when planning a restoration project, few published findings report on the economic aspects of ecosystem restoration. Further, we did not find any study addressing the impacts of global climate change on restoration programmes or how studies should consider future shifts in the environment.

Conclusions: Our results highlight the need for restoration experiments to explore more species. Restoration efforts are in need of detailed reporting that includes time frames and costs. We need to consider future climate scenarios that will affect ecosystem restoration efforts.

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Appendix 1.2 Supporting Information to the paper Palma, A.C. & Laurance, S.G.W. A review of the use of direct-seeding and seedling plantings in restoration, what do we know and where should we go. Applied Vegetation Science**.**

Complete list of studies and data included in the review

Reference	**Ecosystem**[1]	**Country**	**Method**[2]	**#of species**	**Success**[3]	**Mortality**[4]	**Species selection criteria**	**Cost Δ**[5]
Aerts et al. 2006	S	Ethiopia	D	1	34	Desiccation	Endangered	N.A
Aert et al. 2007	S	Ethiopia	S	1	54	Drought	Endangered	N.A
Affandi et al. 2010	M	Malaysia	S	1	49	Sedimentation	N.A	N.A
Aide Cavelier 1994	F	Colombia	C/D/S	11	29 -- 44	N.A	N.A	N.A
Alvarz-Aquino et al. 2004	F	Mexico	S	4	46	Predation	N.A	N.A
Ammondt et al. 2013	F	United States	D/S	5	1 -- 53	N.A	N.A	N.A
Bard et al. 2004	W	United States	D	11	N.A	N.A	Key functional groups	N.A
Bischoff et al. 2006	G	Switzerland	D	4	31	N.A	Different successional stages	N.A

Bonilla-Moheno & Holl 2010	F	Mexico	D	3	12	N.A	Shade Tolerant/ Big Seeds	N.A
Brudvig & Asbjornsen 2009	S	United States	S	1	61	N.A	N.A	N.A
Bruun et al. 2010	F	Sweden	D	6	0.6	Predation	Common	
Budelsky & Galatowitsch 2004	W	United States	S	1	70	Water fluctuation	Low natural recruitment	N.A
Butterfield 1995	F	Costa Rica	S	84	68	N.A	Evaluate commercial/ plantation use	N.A
Cabin et al. 2002	F	United States	D/S	12	NA -- 56	N.A	Ability to establish	N.A
Calvo-Alvarado et al- 2007	F	Costa Rica	S	8	N.A	Drought	Farmer preference/ economic value/ previous results	N.A
Camargo et al. 2002	F	Brazil	D	11	21	Predation	Different successional stages	N.A
Carpenter et al. 2004a	F	Costa Rica	C/S	3	94	N.A	Uses for local farmers	N.A
Carpenter et al. 2004b	F	Costa Rica	S	7	46	Erosion	Valuable for timber	N.A
Ceacero et al. 2012	F	Spain	S	1	19	Drought	N.A	N.A
Chambers 2000	G	United States	D	11	2 -- 31	Drought+	Different seed categories	N.A

Cole & Spildie 2000	F	United States	D/S	7/19	NA -- 77	Drought+	N.A	N.A
Cole et al. 2011	F	Costa Rica	D	5	53	N.A	Availability	D: 4 to 18; S: 116 to 182 (per 100 individuals)
Cooper & MacDonald 2000	G	United States	C/D/S/R	8/1/4/6	NA -- 50	Drought	Ability to establish	N.A
De Chantal et al. 2005	F	Finland	D	1	5	Biotope variation	N.A	N.A
de Jong 2000	W	Australia	S	5	N.A	Water fluctuation	Common	1,800 (per 3,000 trees)
De Steven & Sharitz 2007	W	United States	S	3	N.A	N.A	Wetland dominants	N.A
De Steven 1991a	F	United States	D	6	9	Predation	Wind-dispersed	N.A
De Steven 1991a	F	United States	D	6	9	Predation	Wind-dispersed	N.A
De Steven 1991b	F	United States	D/S	6	NA -- 40	Drought	Wind-dispersed	N.A
Doust et al. 2006	F	Australia	D	18	16	Microsites	Successional stages	^
Doust et al. 2008	F	Australia	D	31	13	N.A	Successional stages	^
Elster 2000	M	Colombia	S	3	24	Water	N.A	^

						fluctuation		
Engel & Parrotta 2001	F	Brazil	D	5	10	Drought	Ability to establish	747 to 912 per ha
Eranen & Kozlov 2006	F	Russia	S	1	62	Soil Condition	Dominant	^
Espelta et al. 2003	F	Spain	D/S	1	NA -- 54	N.A	Low natural recruitment	1,122 to 1,980 per ha
Fields-Johnson et al. 2012	F	United States	S	13	71	N.A	N.A	N.A
Foroughbakhch et al. 2006	H	Mexico	D	10	73	Frost	Potential use for local population	N.A
Foster 2001	F	United States	D	34	N.A	N.A	N.A	N.A
Frischie & Rowe 2012	G	United States	D	7	N.A	N.A	Low natural recruitment	N.A
Fulbright et al. 1992	F	United States	S	5	N.A	N.A	Wild-life habitat	^
Gaertner et al. 2012	H	South Africa	D	4	N.A	N.A	Sustainable harvesting	79 to 413 per ha
Garcia-Orth & Martinez Ramos 2008	F	Mexico	D	4	8	Predation	Availability	N.A
Gerhardt 1993	F	Costa Rica	S	4	15	Drought	Different successional stages	N.A

Gonzalez & Fisher 1994	F	Costa Rica	S	11	91	Competition	Effects on soil	N.A
Gonzalez-Rodriguez et al. 2011	F	Spain	D/S	2	34 -- 57	N.A	Interest in specific species	N.A
Griscom et al. 2005	F	Panama	S	3	30	Drought	Different successional stages	N.A
Grossman et al. 2003	F	United States	D/S	1	N.A	N.A	Low natural recruitment	N.A
Hau & Corlett 2003	F	China	S	4	63	Drought	Successional stages	N.A
Hellstrom et al. 2009	G	Finland	D	8	5	Microsites	N.A	N.A
Hessing & Johnson 1982	F	United States	D	8	N.A	N.A	N.A	N.A
Holl 1999	F	Costa Rica	D	6	20	Desiccation	Small-seeded (collected in pasture seed traps)	N.A
Holl et al. 2000	F	Costa Rica	S	4	10	Predation	N.A	N.A
Holl et al. 2011	F	Costa Rica	S	4	81	N.A	High survival/ rapid growth	N.A
Holmes 2001	H	South Africa	D	UNK	N.A	N.A	N.A	N.A
Hooper et al. 2002	F	Panama	D	20	17	Fire	Seed size/ shade tolerance	N.A
James et al. 2011	G	United States	D	3	N.A	N.A	Previous use	N.A

Jaunatre et al. 2012	F	France	D	3	N.A	N.A	Palatability/rapid cover bare ground	N.A
Joshi & Tyagi 2009	F	India	S	2	27	Microsites	N.A	N.A
Keeton 2008	F	United States	S	7	56	Predation	Availability	N.A
Kinyua et al. 2010	S	Kenya	D	4	N.A	Soil Condition	High nutritional value/ palatability	N.A
Kirmer et al. 2012	G	Germany	D	3/51	N.A	N.A	Local provenance	500 to 4,300 per ha
Lai & Wong 2005	F	China	D	1	36	UNK	Low natural recruitment	N.A
Laliberte et al. 2008	F	Canada	S	3	N.A	N.A	Ability to establish	N.A
Larson et al. 2011	G	United States	D	34	N.A	N.A	N.A	N.A
Lawson et al 2004	G	United Kingdom	D	18	N.A	N.A	N.A	N.A
Leary & Howes-Keiffer 2004	F	United States	S	5	N.A	N.A	Successional stages	N.A
Li et al. 2011	F	China	S	2	53	Drought	Previous use	N.A
Lof et al. 2006	F	Sweden	S	1	82	Microsites	N.A	N.A
Lof et al. 2009	F	Sweden	D	1	N.A	N.A	N.A	N.A
Madsen & Lof 2005	F	Sweden-Denmark	D/S	1	42 -- 67	Predation	N.A	N.A
Martin & Wilsey	G	United States	D	25	N.A	N.A	Availability	N.A

2006								
Massad et al. 2011	F	Brazil	S	126	30	Predation	Different functional groups	N.A
McLeod et al. 2001	F	United States	S	4	82	Flood	N.A	N.A
Mitchell et al. 2008	G	England	D	1	N.A	N.A	Low natural recruitment	N.A
Moreira et al. 2009	F	Portugal	S	2	82	N.A	N.A	N.A
Munson et al. 2012	G	United States	D	6	N.A	N.A	Native vs Introduced	N.A
Muranaka 2009	F	Japan	D	1	18	N.A	Endangered	N.A
Nichols et al. 2001	F	Costa Rica	C/D/S	1/3/2	N.A	N.A	Timber use,/N-fixing/ edible	N.A
Nyamai et al. 2011	G	United States	D	5	N.A	Predation	N.A	N.A
O'Dwyer & Attiwill 2000	G	Australia	D/S	1	N.A	Competition	Habitat for wildlife	N.A
Oliet et al. 2009	F	Spain	S	1	60	Lack of Nutrients	Common	N.A
Orrock et al. 2009	G	United States	D	1	29	Predation	Low natural recruitment	N.A
Parrotta & Knowles 1999	F	Brazil	D/S	42/73	N.A	N.A	Common/Commercial use	N.A
Parrotta 1992	F	Costa Rica	S	1	N.A	N.A	Crop tree	N.A
Pereira et al. 2013	S	Brazil	D	7	N.A	N.A	Seed categories	N.A

Pinard et al. 1996	F	Malaysia	D	6	N.A	Soil Condition	N.A	N.A
Prach et al. 2013	G	Czech Republic	D	44	N.A	N.A	Traditional species	N.A
Preece et al. 2013	F	Australia	S	5	91	Planting method	N.A	º
Rasran et al. 2007	G	Germany	D	*	N.A	N.A	Hay transfer (no selection)	N.A
Renison et al. 2002	F	Argentina	S	1	70	Fungus (from greenhouse)	Endangered	N.A
Renison et al. 2005	F	Argentina	S	1	70	N.A	Endangered	N.A
Robinson & Handel 1993	F	United States	S	18	N.A	N.A	N.A	N.A
Rokich et al. 2002	F	Australia	D	26	N.A	N.A	Used in restoration	N.A
Ruthrof et al. 2010	F	Australia	D/S	5	68	N.A	Declining	N.A
Sampaio et al. 2007	F	Brazil	D/S	10/18	9 -- 73	N.A	Different growth rates	2,000 to 5,500 per hectare
Seabloom et al. 2003	G	United States	D	5	N.A	N.A	N.A	N.A
Slocum et al. 2006	F	Dominican Republic	S	18	79	N.A	Common/ Different successional stages	^
Smit et al. 2008	F	Spain	D	1	39 -- 18	Drought	Low natural recruitment	N.A
Soliveres et al.	F	Spain	S	6	49	Competition	Different	N.A

2012							successional stages	
Sovu et al. 2010	F	Laos	D	4	N.A	Desiccation	Different successional stages	N.A
Suding & Gross 2006	G	United States	D	22	N.A	N.A	N.A	N.A
Sun et al. 1995	F	Australia	D	1	10	Competition	N.A	N.A
Thaxton et al. 2012	F	United States	S	10	49	Soil Moisture	Used in restoration	N.A
Toledo et al. 2001	M	Mexico	S	1	74	N.A	N.A	N.A
Traba et al. 2003	G	Spain	D	*	N.A	N.A	In cattle dung	N.A
Twedt 2006	W	United States	C/S	1/1	47	Competition	N.A	N.A
Uhl 1987	F	Brazil	D/S	5/5	35	Lack of shade	Common	N.A
Urretavizcaya & Defosse 2013	F	Argentina	S	1	34	Drought	Low natural recruitment	N.A
van Breugel et al. 2011	F	Panama	S	49	73	Seedling size	Commercial use/ food for wild-life	N.A
Van der Valk et al. 1999	W	United States	D	5	N.A	Water fluctuation	Low natural recruitment	N.A
Van Uytvanck et al. 2008	G	Belgium	S	2	73	Predation	Palatable tree species	N.A
Vieira et al. 1994	F	Brazil	D/S	1	54 -- 92	N.A	Present and modifying the landscape	N.A

Wallin et al. 2009	G	Sweden	D/S	2	39 -- 90	Competition	N.A	N.A
Walmsley & Davy 1997	F	United Kingdom	D	5	13	Microsites	N.A	N.A
Warren et al. 2002	G	United Kingdom	D	14	N.A	N.A	N.A	N.A
Windsor & Clements 2001	G	Australia	D	1	N.A	N.A	Rehabilitation of mine sites	N.A
Wishnie et al. 2007	F	Panama	S	24	N.A	N.A	Rapid growth /agroforestry use	N.A
Yurkonis et al. 2010	G	United States	D	20	N.A	N.A	N.A	N.A
Zahawi & Holl 2009	F	Costa Rica	C/S	10/2	N.A	N.A	Develop from stakes	C: 18 to 66; S:116 to 182 (per 100 individuals)
Zahawi at al. 2013	F	Costa Rica	S	4	90	N.A	High survival/rapid growth/extensive canopy development	^
Zimmerman et al. 2000	F	Puerto Rico	D	11	30	N.A	Different life histories	N.A

[1] Ecosystem type; F = forest, G = grassland, H = shrubland, M = mangrove, S = savanna, W = wetland

[2] Method; D = direct seeding, C = cutting, S = Seedlings

[3] Success; Percentage of seedlings/seeds that survived or germinated by the end of the study period. For studies reporting success for both seeds and seedlings, the first number corresponds to seeds, second number for seedlings

[4] Mortality; main cause of death or lack of germination. $^{+}$ Treatments that increased soil moisture had better survival

[5] Cost; all costs converted to US dollars corresponding to the average exchange rate for the year published.

[*] Hay or dung transfer

º Provides information on the cost of some supplies, but not actual cost of the restoration effort.

^Mentions importance of economic restoration methods, the advantages of restoring at low cost or stated some approaches as being cheaper, but provided no data to support their assertions.

N.A; data not available. For Success: either data was not available because survival or mortality where not measured, or they were measured as plant cover, biomass, species richness, density, probabilities of survival, and/or data was not available for all species included in the study.

UNK: Unknown/Undetermined

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