PATTERNS OF SECONDARY FOREST RECOVERY IN TWO SOIL TYPES

PhD Thesis

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Patterns of secondary forest recovery in two soil types

By

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"Passava os dias ali, quieto,
no meio das coisas miúdas.
E me encantei"
Manoel de Barros, Brazilian poet

Dedication

I dedicate this thesis to my parents Roberto and Rosa and my brothers Chico and Álvaro.

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Many people have contributed to the completion of this PhD thesis, in many ways. This work was possible thanks to my principal supervisor Dr Susan Laurance. She gave me the opportunity to come to Australia for my doctorate studies. During the entire time, she has trusted me and she has given me enough liberty to follow my ideas. Nonetheless, she has been watching my steps and guiding me to better pathways. I really appreciate her honesty and generosity. Dr Miriam Goosem has been absolutely crucial for the completion of my thesis, professionally and personally. Her kindness and hard work are endless. A big thank you also to Dr Sandra Abell, who accepted to collaborate in one of the chapters, becoming a great advisor for the whole process. I thank Michael Bird for being available when I needed and for providing relevant guidance in the early stages of this project.

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Patterns of secondary forest recovery in two soil types

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Michael Bird

Statement of contribution

Chapters 2-5 included in this thesis have been prepared for submission or are currently in review in ecological journals. Different researchers have made contributions to this thesis.

Chapter 2 in this thesis is a literature review on the patterns of woody community regeneration in secondary forest. This chapter is being prepared to be published in collaboration with Susan Laurance. Claudia P. Paz conceived the main idea and reviewed the literature. Susan Laurance and Claudia P. Paz analysed the data and wrote the manuscript.

Chapter 3 is my first data chapter where I investigate the woody plant community change in the secondary forests. This manuscript has been prepared for submission in *Plant Ecology and Diversity* as: "Paz CP, Goosem M, Tng D, Fensham RJ, Goosem S, Preece ND and Laurance SGW. Does soil type affect woody plant community recovery during secondary forest succession?" Claudia P. Paz, Susan Laurance and Miriam Goosem conceived the main ideas and carried out fieldwork. David Tng provided the species list with their functional traits and helped discussion and editing on early drafts. Claudia P. Paz analysed the data and wrote the manuscript with contributions from Susan Laurance and Miriam Goosem. Miriam Goosem analysed satellite images and historical photographs to determine site ages. Rod Fensham, Steve Goosem and Noel Preece, helped with discussions and editing the manuscript.

Chapter 4 is focused on the arbuscular mycorrhizal communities in secondary and mature forests. This chapter had been prepared for submission in *Oecologia* as: "Paz CP, Abell S, Goosem M, Öpik M, Fensham RJ, Goosem S, Preece ND and Laurance SGW. The effects of soil types on arbuscular mycorrhizal communities during tropical forest succession". Claudia P. Paz,

Sandra Abell, Susan Laurance and Miriam Goosem conceived the main idea and carried out fieldwork. Maarja Öpik discussed ideas and performed molecular analysis. Claudia P. Paz analysed the data and wrote the manuscript with Susan Laurance, Sandra Abell and Miriam Goosem. Rod Fensham, Steve Goosem and Noel Preece helped with discussions and in editing the manuscript.

Chapter 5 investigates the accumulation of soil organic carbon in active pastures, secondary and mature forests. This chapter has been submitted to *Forest Ecology and Management* as: "Paz CP, Goosem M, Bird M,, Preece ND, Goosem S, Fensham RJ and Laurance SGW. Soil types influence soil carbon stock recovery in tropical secondary forests". Claudia P. Paz developed the idea, conducted fieldwork, analysed the data and wrote the manuscript. Miriam Goosem and Susan Laurance helped with developing the idea, they collected vegetation data, and assisted with writing and editing the manuscript. Michael Bird, Rod Fensham, Steve Goosem and Noel Preece helped in discussing, editing and writing the manuscript.

Susan G W Laurance guided all the work that made this thesis possible and read the entire thesis. Miriam Goosem and Michael Bird also read and helped with editing all the chapters.

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General Abstract

Tropical forests are biologically diverse and vital for their contribution to global biogeochemical cycles. However, agricultural expansion has led to the devastation of more than half of forests worldwide. In order to accelerate forest regeneration to provide habitat and ecosystem services, we need to observe what limits natural recovery in order to understand the regeneration process. In that context, secondary forests provide a means to increase forested area. Here, I refer to secondary forests as the spontaneous regrowth of vegetation after major disturbances without human intervention. By studying the regeneration of degraded lands, ecologists should be able to observe patterns of changes, make predictions and determine the potential for recovery and, if necessary, propose interventions to accelerate the recovery process.

Soil condition is one major factor expected to limit forest recovery. However, the resilience of different types of soil to disturbance is still a matter of uncertainty. Chemical, physical and biological alteration could result in negative impacts on plant growth, as well the structure and composition of plant communities, with potential consequences for pathways of secondary forest recovery. In this context, my doctoral thesis investigates the patterns of secondary forest recovery in two contrasting soil types nearby the Australian Wet Tropics bioregion. Along a total 45 sites (33 secondary forest, 6 pastures and 6 mature forest sites), I documented changes in soil properties, woody plant vegetation, soil organic carbon stocks and arbuscular mycorrhizal communities and asked whether the different substrates affect the pathways of secondary forest recovery. To achieve my goals, I prepared a literature review where I observed that numbers of species in long chronosequences (>40 years) tended to plateau following a rapid increase in the first 20 years after land abandonment, but found only nine

chronosequences that were older than 45 years that fitted the selection criteria. Even though the number of species tended to increase with forest age, more than half of the studies (56%) reported low floristic similarity between the oldest secondary forest and mature phase forests. Soil fertility and parent material were only directly investigated in four studies, indicating the scarcity of evidence on the relationship between soil properties and secondary forest regeneration.

To answer my research questions, I collected extensive field data to address questions on the above- and below-ground changes in the biophysical environment after pasture abandonment. Firstly, I used as response variables, nine measures of woody vegetation recovery, representing structural, functional and compositional parameters to demonstrate that species diversity and species dominance showed distinct patterns of recovery in the two soil types. The community composition was also significantly different between basalt and granite soils. I conclude that time since abandonment is crucial for secondary forest recovery, however, soil types may influence the composition of the community that is able to reestablish. Spatial distribution of surrounding mature forest may also affect the rate of recovery. Contrary to my expectation, the poorer and sandier granite-based soil showed faster rates of species recovery compared with the more nutrient-rich basalt soils. Increasing woody species diversity was associated with increasing dominance, which may indicate a positive effect of the early establishment of dominant species on later successional species. The effect of soil type suggested that soil condition was important for the rate of forest recovery, yet in needs to be considered in context with the greater landscape as in a parallel study my collaborators and I found that distance to mature forests was also important for the forest recovery rates.

Secondly, I was interested in the below-ground recovery of secondary forests, with a special focus on the most common plant mutualist: the arbuscular mycorrhizal fungi. In this chapter, I investigated changes in the arbuscular mycorrhizal fungi (AMF) community of

secondary forests and their association with edaphic and vegetation properties. Despite the importance of AMF for plant nutrition and soil structure, little is known about their diversity in successional forests and the environmental factors that shape AMF communities during succession. I found that mature forest on the poorer soil had significantly higher AMF richness than mature forests on the more fertile soil. However, secondary forests on the more fertile soil tended to present higher AMF richness compared to the secondary forests on the poorer soils. The relatively greater species richness in mature forest on granite derived soils agrees with predictions that plant communities in less fertile soils are more dependent on mycorrhizal associations, however in secondary forests the trend did not hold. Soil pH and total phosphorous were the best environmental predictors of AMF richness and community composition.

Thirdly, I investigated another below ground component, which represents an important ecosystem function played by forest soils: the soil organic carbon stocks. For this study, I estimated soil carbon stocks in the two soil types to allow comparisons before and after pasture abandonment. Secondary forests around the world have been found to recover above-ground biomass stocks relatively fast compared with species diversity and composition. However, soil organic carbon stocks do not always replicate stand age or above-ground biomass accrual. I asked whether soil and vegetation parameters are better predictors of soil carbon stocks than secondary forest age and if soil type influenced these relationships. I found that, in comparison with basalt soils, granite soils tend to accumulate SOC stocks and recover their isotopic composition at faster rates during forest succession. However, basalt soils tend to maintain higher SOC stocks after pasture abandonment. SOC variation was best explained by a model that included soil pH, woody species diversity and soil type, with significant changes mostly driven by sites on granitic soils. These results support the idea that predictions of SOC stocks can be improved with the inclusion of basic information on vegetation cover and soil type.

To summarise, I found that nutritional and textural differences between soil types remain during forest succession, indicating that the major edaphic properties of some parent materials remain little or unaffected after long-term agricultural use. As expected, woody plant communities, mycorrhizal fungi, and soil carbon stocks seem to respond to such soil type differences at local scales, even though the variability within sites and successional categories suggest a strong idiosyncratic nature to secondary forest regeneration processes. Continued investigation of the interactions of plants, fungi and the mechanisms that stabilise C in the soil will likely produce further theoretical and practical ecological evidence to improve the understanding of secondary forest regeneration. Although primary forests may be irreplaceable, abandoned lands have a great capacity to become biologically and functionally rich systems again.

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Chapter 1

General Introduction

Tropical forests are biologically diverse and vital for their contribution to global biogeochemical cycles (Bunker *et al*. 2005, McGroddy and Silver 2011). However, increasing human populations and the need for agricultural expansion have led to the devastation of more than half of forest ecosystems worldwide (Blaser *et al*. 2011). Deforestation is the main driver of habitat loss and contributes to the elevated rates of CO_2 emissions in the atmosphere. This has raised concerns globally for the future of forests especially in the light of global climate change (Laurance *et al*. 2012, FCCC 2015). Currently, primary forests comprise approximately 50% of their original area in the tropics, with degraded and logged forests rapidly dominating the landscapes (Blaser *et al*. 2011). Understanding regeneration processes becomes, therefore, crucial to overcoming the ecological and economic issues related to forest loss (Lamb *et al*. 2005, Chazdon 2008, 2014).

Secondary forests play a key role in recovering habitats and providing essential ecosystem services. By definition, secondary forest refers to the spontaneous regrowth of vegetation after major disturbances (*e.g.* forest clearing or agricultural use), and such forests are proliferating as land abandonment increases (Corlett 1994, Cramer *et al*. 2008). A common cause of land abandonment is a reduction in soil productivity (Munroe *et al*. 2013). In the tropics soils tend to be highly weathered and less fertile, which can lead to land abandonment after only a few years of use (Benayas *et al*. 2007, Verheye 2008). This shifting cultivation results in more forest clearing as farmers move to new areas with more fertile soils. Continuous forest clearing and abandonment have contributed to the expansion of secondary forests, which currently occupy an estimated 5 hundred million hectares across the tropics

(ITTO 2002, Chazdon 2014). Despite increasing interest in secondary forests, successional changes in these forests are rarely studied over the long term, and this applies particularly to soils (Chazdon *et al*. 2007, Marín-Spiotta and Sharma 2013, Poorter *et al*. 2016) and to the Australasian region.

Alterations in soil condition are one of the factors that can limit forest recovery (Hooper *et al*. 2005, Holl *et al*. 2000, Cramer *et al*. 2008, Flynn *et al*. 2010). However, despite evidence showing that forest clearing and agriculture alter soil fertility and structure (Lal 2004, Defries *et al*. 2004, Cameron and Moir 2013), the resilience of different types of soil to disturbance is still a matter of uncertainty (Holl 1999, Fortini *et al*. 2010). The negative effects of a degraded soil could continue to influence plant growth from seed to adulthood. For instance, high soil compaction reduces soil porosity and moisture holding capacity, which can be detrimental for nutrient cycles and root penetration, affecting plant establishment and growth (O´Sullivan and Simota 1995, Greacen and Sands 1980). At the community level, alterations in soil moisture and nutrients affect the balance of competition and facilitation between and within species (Callaway and Walker 1997, Connell and Slatyer 1977) with potential consequences for pathways of secondary forest recovery (Cramer *et al*. 2008).

1.1 Thesis scope and structure

This doctoral thesis investigates the patterns of secondary forest recovery in two contrasting soil types within the Wet Tropics bioregion of Australia, much of which has been listed as a World Heritage Area (Fig. 1), as a hotspot for conservation (Mittermeier *et al*. 2011, Goosem *et al*. 1999). Along secondary forest chronosequences, I have documented changes in soil properties, woody plant vegetation, soil organic carbon stocks and arbuscular mycorrhizal communities. Due to the occurrence of two major soil types (Fig. 2), I have queried whether different substrates affect pathways of secondary forest recovery (Fig. 3). Based on ecological

theory and empirical data I believe my research will contribute to a deeper understanding of natural succession of secondary forests and some of the factors related to this process. This thesis is organized into six chapters: this introduction, a literature review, three empirical chapters that have been prepared for submission to peer-reviewed ecological journals, and a general conclusion chapter. The data chapters have been planned as stand-alone manuscripts for publication and may contain some repetition in methods. Supplementary data or results are presented at the end of each chapter, when necessary, whereas the appendix contains the copies of previously published work that used part of the data from this thesis. Below, I present a synthesis of the major findings of each chapter.

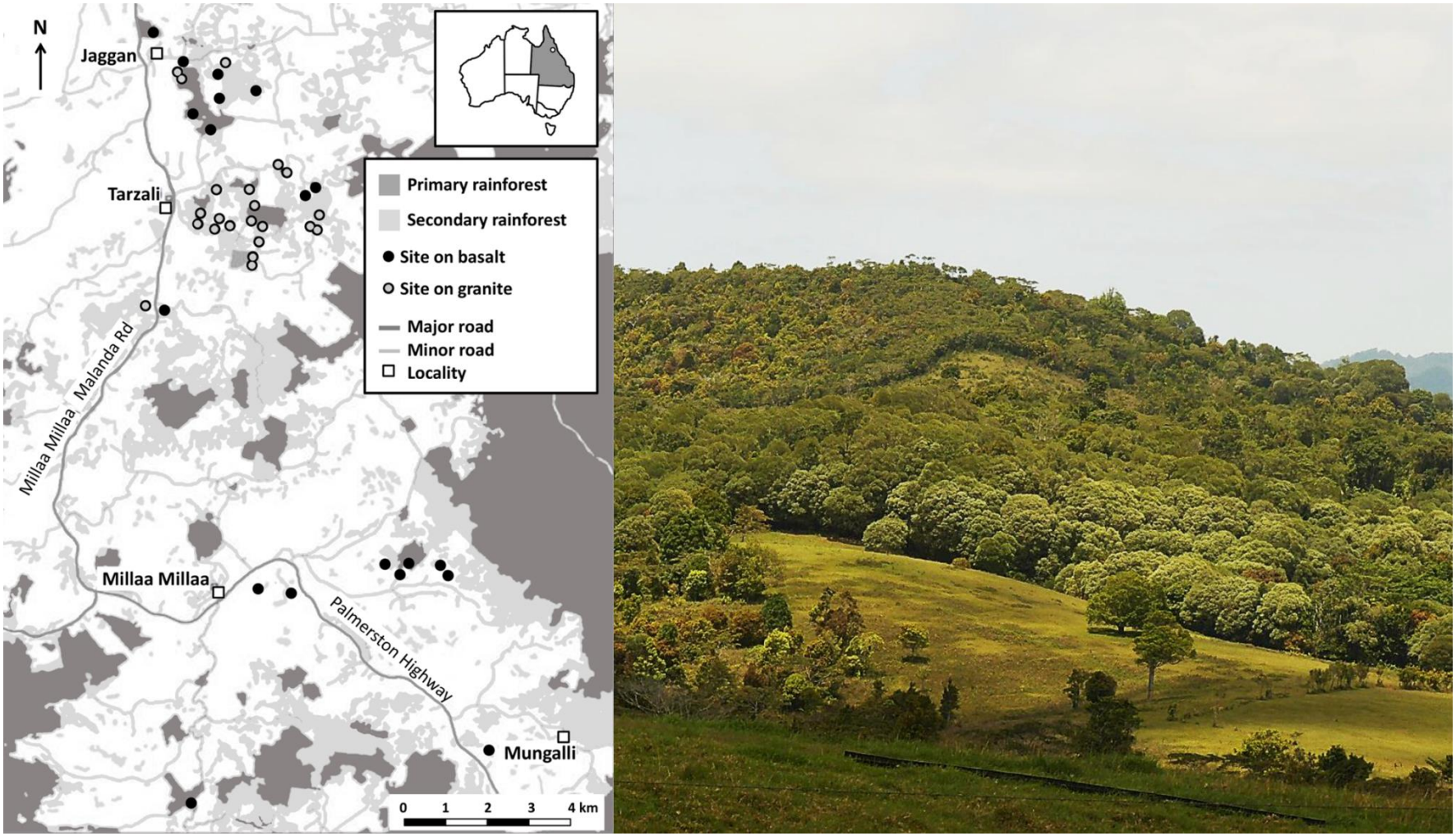

Figure 1. Distribution of study sites in the landscape and overview of active pastures and secondary forests at different successional stages in Atherton Tableland, North-eastern Queensland, Australia. Photo: CP Paz.

Figure 2 Soil samples (10- 30 cm depth) from secondary forest sites on basalt soil (top row) and granite (bottom row) in Atherton Tableland, North-eastern Queensland, Australia. Samples are organized by stand age, whereas the last three samples in each row are from mature forest stands. Photo: CP Paz.

1.2 Summary of Chapter 2: Secondary forest regeneration across the tropics: successional pathways and drivers

This chapter is a literature review on secondary forest chronosequences across the tropics to be submitted for publication. Chronosequences, also known as space-for-time substitution approach, have been a useful tool to investigate secondary forest dynamics (Walker *et al*. 2010). My main goal was to review published studies that have documented patterns of woody plant changes after land abandonment taking into account the rate of species accumulation, convergence in floristic composition and factors that were found to influence the patterns of regeneration.

The review highlighted some important ecological patterns and also detected gaps in our understanding of rainforest succession that could be explored in the future. Based on the

data from 17 publications, selected by specific criteria, I found that the majority (88%) of chronosequence studies were located in the Neotropics, indicating several gaps in knowledge, including the Australian tropical forests.

1.3 Summary of Chapter 3: Does soil type affect woody plant community recovery during secondary forest succession?

This is an original data chapter that has been prepared for submission to *Plant Ecology and Diversity*. Two collaborative publications were generated using part of the dataset from this chapter (Tng *et al*. 2015, Goosem *et al*. 2016; copies of the full articles in Appendix). This chapter presents novel information on the research of secondary forest recovery patterns, where the effects of soil types and their properties are explored. My aim was to investigate secondary forest recovery patterns in the two dominant, contrasting soil types in the study area (basalt- and granite- derived soils). I have analysed nine measures of woody vegetation recovery, representing structural, functional and compositional parameters to examine the influences of soil type and stand age on secondary forest recovery.

Figure 3. Interior of secondary forests at different successional stages. From 12.5 years since pasture abandonment (A), 20 years (B and C), 34 years (D-F), 41 years (G) to mature phase, forests (H and I) in Atherton Tableland, North-eastern Queensland, Australia. Photo: CP Paz

1.4 Summary of Chapter 4: The effects of soil types on arbuscular mycorrhizal communities during tropical forest succession

In the next two chapters, I shift the focus away from vegetation recovery to explore two aspects of below-ground recovery in secondary forests. In this fourth chapter, I investigate changes in the arbuscular mycorrhizal fungi community of secondary forests and their association with edaphic and vegetation properties. This is an original data chapter that has been prepared for submission to *Oecologia*. Despite the ecological importance of AMF, little is known about their diversity in successional forests and the environmental factors that shape AMF communities during succession (Davison *et al*. 2015).

1.5 Summary of Chapter 5: Soil types influence soil carbon stock recovery in tropical secondary forests

In the last data chapter, I investigate an important ecosystem function played by forest soils: the sequestration of organic carbon. For this study, I estimated soil carbon stocks in the two soil types to allow comparisons before and after pasture abandonment. A version of this original data chapter is in review at *Forest Ecology and Management*. Tropical forests are major carbon (C) sinks both above- and below-ground. Secondary forests have been found to recover above-ground biomass stocks to historical levels in a few decades (Poorter *et al*. 2016). However, changes in soil organic carbon (SOC) stocks do not consistently follow stand age or above-ground biomass accrual (Marin-Spiotta and Sharma 2013). I asked whether soil organic carbon (SOC) stocks and dynamics change with secondary forest age in two contrasting soil types analysing soil and vegetation parameters (*e.g.* soil texture and acidity, woody species diversity and basal area) to determine the best predictors of SOC stock changes.

1.6 Summary of Chapter 6: General conclusion

In this last chapter I summarise and integrate the main findings from the data chapters. Based on my own data and previous studies I discuss some of the implications of this research for forest management and suggest future directions for investigation.

Chapter 2

Secondary forest regeneration across the tropics: successional pathways and drivers

Abstract

Secondary forests are now a dominant feature of tropical landscapes with approximately 500 million ha distributed globally. These regenerating forest communities are expected to recover to mature forests, however, despite numerous studies, the time and trajectories to recovery are still unpredictable, and may depend upon many biotic and abiotic factors. Here I review the published literature to provide an overview of our current knowledge on the regeneration of woody plant species in secondary forests with respect to the rate of species accumulation, convergence in floristic composition and factors found to influence the patterns of regeneration. I searched for articles that documented woody species accumulation in secondary forests with different ages since land abandonment and compared them with local mature phase forests. I focused on the following study characteristics, which was also the criteria to include articles in my review: secondary forest ages, location, number of sites/replicates, sampling criteria for vegetation inclusion (*i.e*. all trees ≥ 10 cm dbh), number of woody species per forest age category, floristic similarity between older secondary and reference forests as well as the biotic and abiotic factors that were found to be affecting woody species recovery. From 211 published articles which mentioned these factors, I considered 67 and included 17 publications that met all criteria. Secondary forest chronosequences ('space-for-time substitution' approach) ranged in length from 8 to 80 years

with the majority (88%) located in the Neotropics. The number of woody plant species increased with time in most forest chronosequences, regardless of the type of previous land-use, the initial number of woody species in the youngest stand or the length of chronosequence age. Species gain in long chronosequences (>40 years) tended to plateau following a rapid increase in the first 20 years after land abandonment. However, only nine selected chronosequences were older than 45 years. More than half of the studies (56%) reported low floristic similarity between the oldest secondary forest and reference sites. The environmental drivers of such patterns remain less well explored in these studies, as only 47% analysed changes through time. Distance from forest fragment was the most-studied factor, showing a small influence on species number increase and community composition convergence. Although often mentioned as influential factors, environmental features, such as soil fertility (*e.g.* nutrient limitation) or the soil type (*e.g.* parent material) were directly investigated in only four studies. This gap in the understanding of rainforest succession should be explored in the future.

Keywords: *literature review, regrowth forest, plant diversity, forest succession*

2.1 Introduction

Secondary forests are dominating the tropical landscape. Currently, over 60% of tropical forest area (*ca*. 500 million ha) is regenerating from different forest disturbances, such as logging, clearing and agricultural use, which are likely to affect their patterns of recovery (ITTO 2002, Blaser *et al*. 2011). For instance, forest clearings and abandoned agricultural fields are known to cause larger negative impacts as they transform the ecosystem completely, by removing the native vegetation and introducing foraging or crop species (Corlett 1994). The eventual abandonment of lands plays a crucial role for the recovery of above- and below-ground carbon stocks, the recuperation of water and nutrient cycles and return of biodiversity.

However, while some of these ecosystem components can be predicted across regions (*e.g.* above-ground biomass), the recovery of plant communities may follow different trajectories, as they are influenced by a range of environmental and biological factors (Johnson *et al*. 2001, Martin *et al*. 2013). It is broadly accepted that once cleared lands are abandoned, it is possible that the vegetation community may not return to the original composition, remaining in alternative or arrested states (Cramer *et al*. 2008, Lindenmayer *et al*. 2008, Lugo and Helmer 2004, Lugo 2009).

The type of land use and its management intensity are legacies of human land use that have been identified as important drivers of successional trajectories (Cramer *et al*. 2008, Buschbacher *et al*. 1988; Nepstad *et al*. 1991, Uhl 1987, Mesquita *et al*. 2001, Norden *et al*. 2011). Mesquita *et al*. (2001) made an important contribution in this field by determining that fire management of tropical pastures in central Amazon, significantly influenced the different regeneration pathways of pioneer species in secondary forests. Abandoned pastures that were unburnt were initially dominated by pioneer trees of the genus *Cecropia*, whereas burned pastures were dominated by *Vismia* spp. (Mesquita *et al*. 2001). These early differences in forest regeneration subsequently influenced recovery trajectories with the *Cecropia*-dominated forests accruing plant species at faster rate than *Vismia*-dominated forests (Mesquita *et al*. 2001, Norden *et al*. 2011). Despite taking different trajectories over time, these forests could in the long-term converge to a similar composition and become ecologically comparable to surrounding mature forest.

Secondary forest recovery can also be influenced by the area and distance to mature rainforest (Holl 2000, Chazdon 2008; Hooper *et al*. 2005, 2004, Dalling and Denslow 1998, Standish *et al*. 2007, Wijdeven and Kuzee 2000). The majority of plant species in rainforests are vertebrate-dispersed. Hence the capacity of these vertebrates to move through cleared landscapes can be a severe obstacle to seed dispersal and recruitment. As a result, a faster

rate of recovery has been observed in secondary forests close to larger areas of mature forest compared with secondary forests farther from mature forests (Sloan *et al*. 2015).

Soil alterations due to forest conversion and land-use can transform habitats by causing nutrient limitation, susceptibility to drought stress (Tilman, 1987) and low survival of the soil seed bank (Guariguata and Ostertag 2001). Cultivation practices can have different long-term responses on soil C and nutrient accumulation, which may reflect in the time required for forest biomass to recover (Fernandes and Sanford 1995, Hughes *et al*. 1999, Smith *et al*. 1999, Silver *et al*. 2000). A degraded soil condition caused by physical and chemical alteration together with invasion of exotic species can be highly negative for secondary forest regeneration (Peltzer *et al*. 2010). Dominance of exotic species, particularly grasses, at early stages of abandonment is expected to cause either successional delays or arrest the recovery process (Goldsmith *et al*. 2011). Exotic grass species are often highly competitive because they can be efficient resource users and they have escaped their natural predators (Bakker and Wilson 2004, Mitchell *et al*. 2006). These characteristics provide advantages that allow non-native species to grow, reproduce and suppress native species (Peltzer *et al*. 2010). Non-native trees, however, may be different, as Lugo (2004) reported that non-native trees can be essential for land regeneration where otherwise abandoned pastures remain in an arrested state of succession. Lugo suggests that often exotic species can tolerate the altered soil condition and therefore their establishment can facilitate the recruitment of late-successional native species. Native and non-native species may then coexist and develop a new category of ecosystem called 'novel ecosystems' (Hobbs *et al*. 2006, Cramer *et al*. 2008 Lugo 2009).

Despite increasing understanding of the local mechanisms driving secondary succession, the trajectories and final outcomes of community regeneration are still unpredictable. It is unclear whether environmental drivers have been satisfactorily explored in order to demonstrate strong association with such changes. In this context, secondary forest chronosequences (space-for-time substitution) have been used worldwide and offer a good

opportunity to investigate forest successional pathways when long-term monitoring plots are not available (Prach and Walker 2011).

To evaluate trends in secondary forest succession research and detect knowledge gaps, I performed a review of publications on secondary forest chronosequences across tropical and subtropical regions. To my knowledge, this is the first attempt to systematically examine the empirical evidence available from secondary forest changes in tree communities, taking into account the successional pathways and drivers that have been considered relevant. More specifically I asked three questions: (1) What are the patterns of woody plant species accumulation in secondary forests? (2) Are woody plant communities converging towards a mature forest composition? and (3) Which environmental drivers are associated with accumulation of woody plant species in secondary forests?

2.2 Methods

I searched for peer-reviewed indexed publications from the last 30 years (1985 to 2015) on Web of Science (www.webofknowledge.com) using keywords that would capture the maximum number of studies across the wet/moist tropics. Combinations of keywords included the following terms: 'secondary forest', 'regrowth forest', 'successional forests*', 'tropic*', 'recovery', 'succession*', 'pathway', 'trajectory' and 'chronosequence'. As my questions were related to patterns of woody plant species accumulation and community convergence, I systematically reviewed the publications that reported in their abstract some ecological measure of these parameters, such as species number, species richness and comparisons among community assemblages. Once selected the articles, I took note of the length of the chronosequence, region/country, criteria for inclusion of vegetation (*e.g.* all trees ≥ 10 cm dbh), number of sites/replicates, number of tree species per age category, floristic similarity between older secondary forests and mature forests as well as the factors that were found to be affecting tree species recovery. I also recorded the environmental factors that were

considered to be driving such changes in tree species accumulation, convergence or similarities in floristic composition. Studies that included other measures of forest development (*e.g.* above-ground biomass accumulation) were considered, however only species number/richness was reported, as variables of interest for this review. For this review we did not include studies on tree plantations or enriched secondary forests, regeneration in forest gaps or regeneration from low impact forest disturbances (Lamb 2011).

To address my first question on the patterns of accumulation of woody plant species through time, I determined species richness at each secondary forest stand or category, based on the time (years) since land abandonment. Number of species was standardized by stem number and when data were extracted directly from rarified species curves, the smallest number of stems was used. When secondary forest sites were classified into age categories I used the mean age for each category, otherwise I considered the actual stand age. I plotted number of species against time since abandonment and compared fitted curves among forest chronosequences.

To investigate the woody plant community convergence during the regeneration process, my second question, I asked whether the oldest secondary forest sites were similar to reference forests (referred to in these studies as mature forest, primary forest or old-growth forest). I sought indices of dis/similarity or percentage of shared species to obtain a quantitative measure of community convergence. When a similarity value was not accessible, I obtained a "low" or "high" similarity/convergence index, based on the authors' interpretation. To answer the third question about the environmental factors that could be influencing accumulation of woody plant species, I noted the type of predictor/driver in question and whether it was positive, negative or neutrally associated with the response variable in question.

2.3 Results

From 211 articles selected by the keywords I selected to review 67 papers and included 17 publications to my final analysis. Three of the publications had analysed two distinct chronosequences, which were considered separately in my comparisons. The length of secondary forest chronosequence (difference between the youngest and oldest secondary forest sites) ranged from 8 to 80 years. Most of the published research was undertaken in the regions of South and Central America (88.2%, n=15). Secondary forest chronosequences occurred predominantly on abandoned lands that were used as grazed pastures (64.7%), or sugarcane, rice, beans and corn, which were mostly cultivated in slash-and-burn systems (Table 1).

Table 1. List of studies included in the literature review on chronosequences (space-for-time substitution approach) of secondary forests in tropical and subtropical regions. Full citations are provided in References. Species similarity refers to tree community similarities between oldest secondary forests and reference sites (*e.g.* mature forest). Drivers analysed refers to environmental drivers other than stand age (years since land abandonment) that were investigated in each study. Drivers with an asterisk indicate the ones that were considered as relevant/significant for secondary forest regeneration. 'L' refers to 'low similarity' and 'H' refers to 'high similarity'.

ID	Reference	Country/ Region	Youngest stand (years)	Oldest stand (years)	Previous land-use	Total Nr Plots	Similarity (%)	Drivers analysed
1	do Nascimento *et al*. 2012	Brazil/NE	12	20	sugarcane	9	47	soil nutrients, soil texture*
2	Zanini *et al*. 2014	Brazil/S	6	45	slash-burn system	28	37	topsoil (texture, nutrients), relief, space
3	Dent *et al*. 2013	Panama	20	100	Pasture and fruit production	10	38	
4	Long *et al*. 2012	China/S	3	60	rice	6	26	soil nutrients (P*)
5	Klanderud *et al*. 2010	Madagascar	1	26	slash-burn system	28	L	number of slash-burn cycles*, distance, altitude, slope
6	Letcher *et al*. 2009	Costa Rica	10	44	pastures, rice	30	H	time of pasture use*
7	Norden *et al*. 2009	Costa Rica/NE	12	29	pasture	6	~40	
8	Piotto *et al*. 2009	Brazil/NE	10	40	slash-burn system	14	62	
9	Marin Spiotta *et al*. 2007	Puerto Rico	10	80	pasture	18	57	

10	Howorth *et al*. 2006	Venezuela	10	35	beans, corn	8	66	land-use types
11	Muniz Castro *et al*. 2006	Mexico	0.25	80	pasture	17, 17	-	distance from remnant edge
12	Peña-Claros *et al*. 2003	Bolivia/W	2	40	agriculture	7, 7	L	
13	Chinea *et al*. 2002	Puerto Rico	7	66	pastures, sugarcane	33	L	substrate types (parent material)
14	Aide *et al*. 2000	Puerto Rico	52	77	pasture	28, 22	L	
15	Pascarella *et al*. 2000	Puerto Rico/SE	4	80	pastures	7	L	land-use history, elevation, distance from remnant forest
16	Aide *et al*. 1996	Puerto Rico	9.5	60	pasture	28	L	elevation, distance, soil type
17	Kappelle *et al*. 1995	Costa Rica	8	32	grazing pasture	12	64	

In general, secondary forest chronosequences showed increasing trends in woody plant richness with time, but the trajectories varied (Fig. 4). Chronosequences with more than 40 years (considered here as long chronosequences) showed logarithmic trends of woody plant species accumulation (Fig. 4). In long chronosequences the highest rate of species accumulation occurred in the first 20 years after land abandonment, followed by a diminishing rate of species accumulation from 20 to 30 years and stabilization or even minor declines in species richness after around 40 years (Fig. 4). Shorter chronosequences (<40 years of age) were more variable. Exponential and linear trends in species accumulation were more likely to be detected in short chronosequences (Fig. 4). When I included reference sites, most chronosequences showed a plateau pattern of species accumulation (Fig. 5). Only one chronosequence demonstrated a slight decreasing tendency in species accumulation, where secondary forests contained a higher number of species than reference sites (Fig 5, case 17).

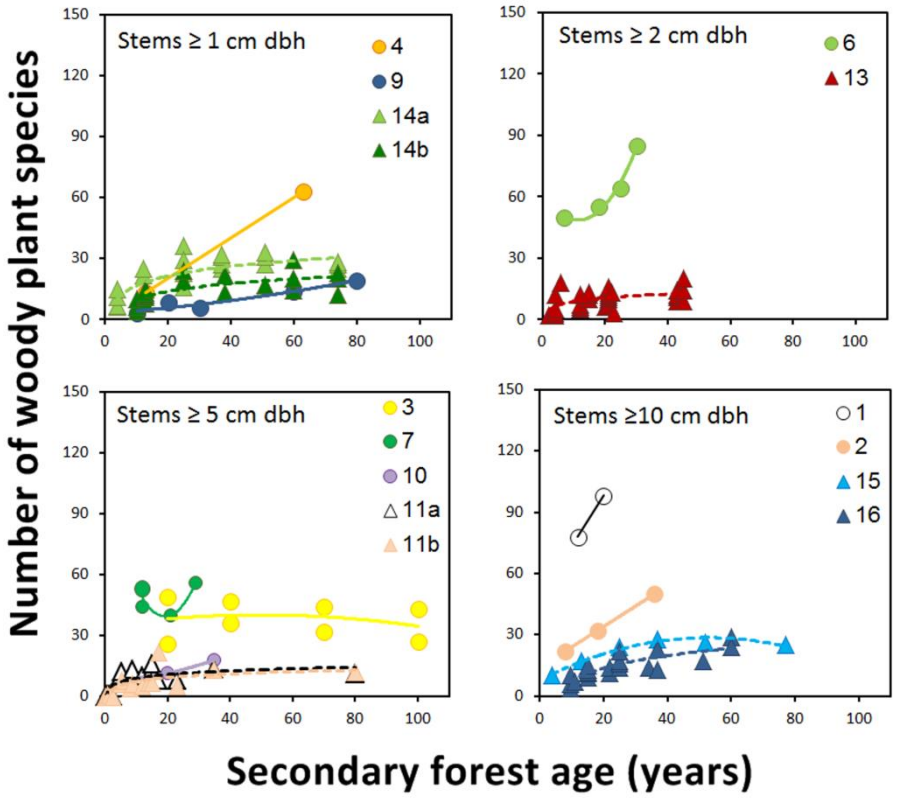

Figure 4. Number of tree species in relation to secondary forest stand age (years since land abandonment) in chronosequences across tropical and subtropical regions. Numbers in the legends refer to identification codes according to Table 1 – each number is a different study

considered in the review. Chronosequences were separated according to criteria for inclusion of stems (dbh= diameter at breast height). Solid lines refer to circles and dashed lines refer to triangles from the respective color.

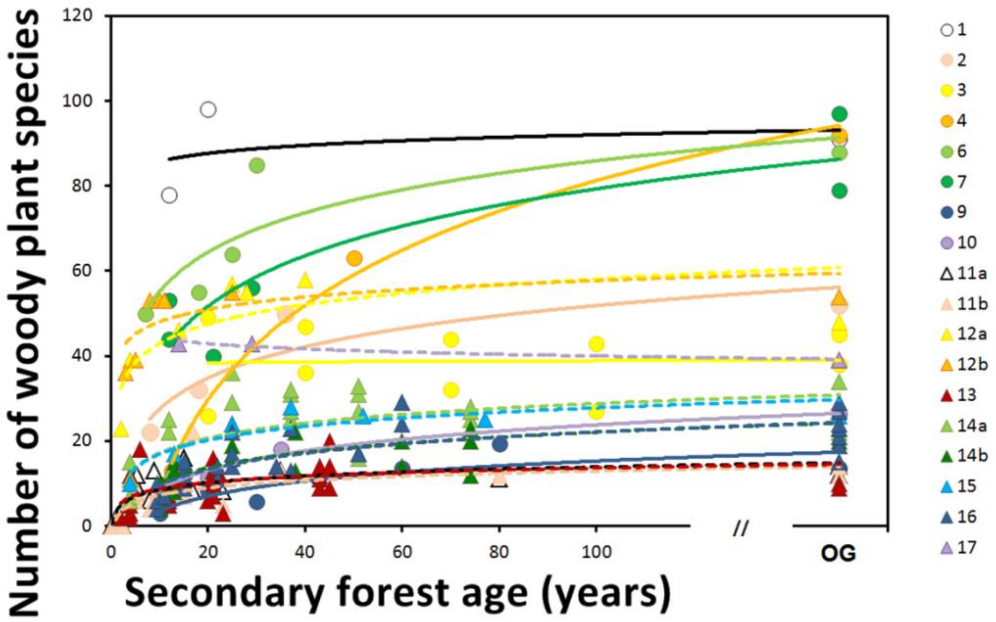

Figure 5. Number of tree species in relation to secondary forest stand age (years since land abandonment) and old-growth reference sites (OG) in chronosequences across tropical and subtropical region. Numbers in the legends refer to identification codes according to Table 1 – each number is a different study considered in the review. Solid lines refer to circles and dashed lines refer to triangles from the respective color.

Floristic convergence between old secondary forest and reference sites was reported in most studies. In most (77%) chronosequences studies, authors indicated that the woody plant communities of secondary forests were becoming more similar to reference sites with time. However, only around half of the studies had quantified convergence in floristic composition with some type of similarity index. Woody community similarity between old secondary forests and reference sites ranged from 26 to 66 %, in a variety of measures that may not be totally comparable including: Sorensen index, Chao-Jaccard similarity indicator, Horn similarity or simply by percentage of shared species. In cases where quantitative comparison was not available, floristic convergence was either interpreted as the presence of

late successional taxa, or the presence of typical primary or endemic species in older secondary forests. Despite being considered convergent, in more than half of the chronosequences (94%, n=16), woody community recovery was considered slow.

Secondary forest age was the only parameter used in 41% of the chronosequence studies . Forest age (usually described as the number of years since land abandonment) was in all cases considered a good predictor of woody species increase and community turnover from early successional to mature forest communities. The second most commonly studied factor that could influence woody community recruitment was distance from mature forests (Fig. 6). Yet, distance was a significant predictor in only one study which found it had a surprisingly negative effect on plant species accumulation. This may be due to the distances involved as some of the study sites were highly isolated at >2 km from mature forests. . In the other studies where distance from forest was not significant, the secondary forests were located in close proximity (<300m) to reference forests.

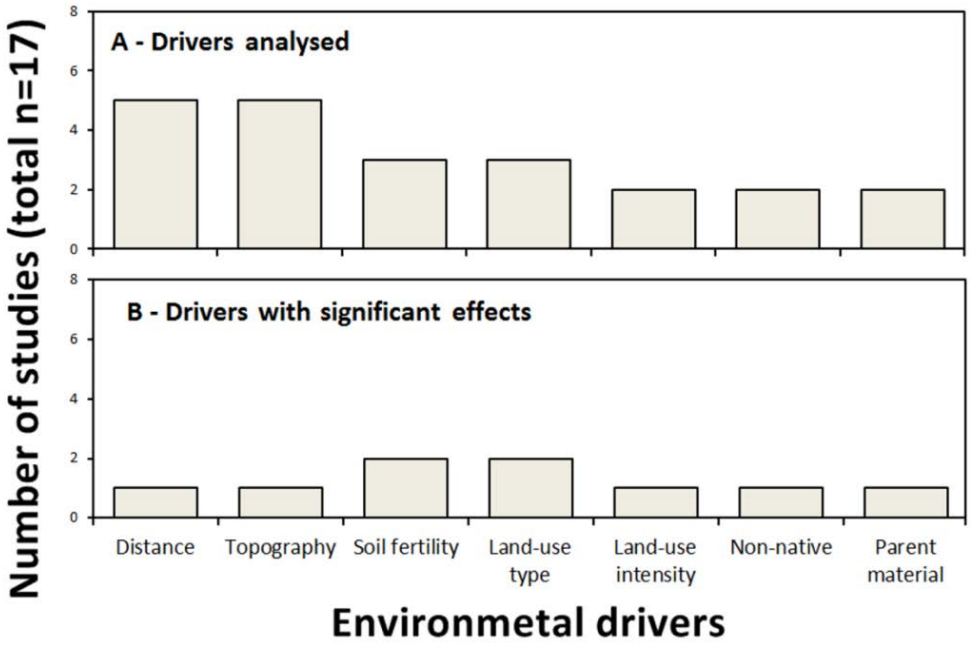

Figure 6. Frequency of studies that explored the relationship between woody plant species recovery and (**A**) environmental parameter (study may include one or more drivers) and (**B**) the environmental parameters with significant association

Topography (*e.g.* terrain slope, altitude) and soil fertility (*e.g*. soil nutrients) were investigated in five and three of the studies, respectively. Topography was important in explaining species community changes in one study, while soil fertility was significantly associated with changes in tree communities in two studies. The effects of prior land-use were analysed in three studies (17.6%), whereas land-use intensity and invasion by non-native species were analysed in two studies (11.8%). Land-use type was found to significantly affect the number of species and floristic convergence in two cases, while evidence for land-use intensity was only observed on one chronosequence. The influence of the type of substrate (*e.g.* parent material) was only evaluated in two chronosequences; with significant effects of these factors in one study each (Fig. 6).

2.4 Discussion

2.4.1 Short term studies may overestimate the rate of recovery in secondary forests

Patterns and predictability of changes in woody plant richness appear to be influenced by the length of the secondary forest chronosequence. My review indicates that asymptotic patterns are more likely to be observed in chronosequences longer than 40 years. This finding supports the conclusions of Chazdon *et al*. (2007), who found that vegetation dynamics within the first 30 years of succession cannot be accurately interpreted in Neotropical secondary forests. Yet it is likely that debates will continue on the rate of recovery in secondary forests because it is challenging to access long chronosequences whilst controlling for land-use types, soil types and distances from remnant mature forests. Hence, our research in secondary forests is constrained by the reality of the available landscape parameters.

The age of secondary forest stands comprises the most common way to investigate processes related to forest regeneration. Although the space-for-time approach has been criticized in chronosequence studies because of uncertainty about chronological links

between sites and ages or the ability to replicate successional stages, for the moment it remains the best method available to investigate long-term changes in regrowth communities (Feldpausch *et al*., 2007). Research using secondary forest chronosequence have demonstrated almost universal trends in the accumulation of biomass and species, reduction in soil erosion and improvement of overall ecosystem quality with forest age (Finegan 1996, Guariguata and Ostertag 2001, Williams-Linera 1983).

My review shows that tropical secondary forest chronosequences tend to accumulate woody species with time in quite similar patterns, regardless of the type of prior land-use, the relative number of species or the vegetation size class included. This trend agrees with the equilibrium model of forest succession, where tree species colonization is benefited by changing ecosystem properties, such as increases in shading, moisture and soil organic matter (Bazzaz 1979). Yet, the convergence of plant community composition seems to be low, even after eight decades of land abandonment.

2.4.2 Limited evidence of floristic convergence during forest succession

My comparisons of older secondary and mature forests show that there is still low resemblance in tree community composition and structure, even after 40 years of succession. The time needed for secondary forests to reach similar floristic composition to mature undisturbed forests has been estimated as low as 70 years (Kappelle *et al*. 1995), and as high as several centuries (Aide *et al*. 1996). Accordingly, Gibson *et al*. (2011) suggested that primary rainforests would, in most cases, be irreplaceable, as typical mature forest communities are not able to establish in secondary forests – at least not in the first century of succession. It is unlikely that we will find a general answer to this question of how long it takes for tropical forest to recover from clearing. First, because there are limitations in different sampling methods and data analysis within secondary and mature forests studies which hinder

comparisons (Chinea *et al*. 2002, Howorth *et al*. 2006). Second, mature rainforests globally differ enormously in floristic diversity and the demographic composition of tree communities (Condit *et a.l* 2006) which should influence succession rates and recovery time. For example, the hyper-diverse forests of central Amazon and Asia are characterised by a community of mostly late successional species whereas the low diversity communities of Australia and Africa are comprised of many more early successional species (Slik *et al*. 2015, Condit *et al.* 2006, Malhi *et al*. 2013). Biogeographical history and climatic disturbance have played an important role in the demographic characteristics of these species' pools and as a result we should not expect that convergence rates in secondary and mature forests will coincide. Regional species pools may differ up to an order of magnitude (Slik *et al.* 2015), and as a result the sampling designs should also differ in order to accurately estimate community composition. Therefore, it is challenging to predict the pathways of plant community succession and to determine when, if ever, they will reassemble to the historical state (Leps and Rejmanek 1991, Cramer *et al*. 2008).

Slow convergence in succession could be explained by multiple factors that could delay the species turnover. Besides seed and recruitment limitation, it has been shown that certain dominant species produce conditions (*e.g.* thick leaf litter layer, close canopies or abnormal soil acidity) that could help maintaining the growth of the dominant populations (native or non-native) hampering the establishment of successional species (Sarmiento 1997, Ehrenfeld *et al*. 2005). Most studies in this review reported the presence of non-native species, but testing such reciprocal process has proven challenging. To assume soil condition is limiting for the germination and establishment of recruits is not straightforward, as the increase content of soil organic matter, nitrogen or phosphorus may not directly indicate increasing in soil fertility, therefore higher growth rates (Siddique *et al*. 2010). In some cases as shown by Siddique *et al*. (2010), nitrogen and phosphorus fertilization stimulated growth of few pioneer species that rapidly dominated the site reducing species accumulation though time.

2.4.3 Environmental drivers of forest successional pathways in long chronosequences

The interest in ecological processes that drive natural forest regeneration has increased as the area of secondary forest increase globally in comparison with mature forest, even though, the landscape changes are not uniform worldwide. Based on the analysis of long chronosequences I observed that distance from mature forests, soil properties, land-use type and intensity were more commonly listed as drivers to explain forest recovery pathways. In order to trace some parallels, I have limited this discussion to chronosequences that are older than 40 years and have included environmental parameters to explain the patterns found (Long *et al*. 2012, Muniz-Castro *et al*. 2006, Chinea *et al*. 2002, Pascarella *et al*. 2000, Aide *et al*. 1996).

Distance from mature forests has been assumed to influence species accumulation rates. However, we did not find evidence of the influence of distance probably because almost all studied secondary forests were located relatively close to mature forest edges: at or within 50 m (Muniz-Castro *et al*. 2006, Aide *et al*. 1996) and within 200 m (Pascarella *et al.* 2000). Distances from mature forest of more than 500 m were uncommon and often they are not included as a driver of secondary forest recovery. Distances of up to 500 m may be important as 70% of the 11,000 ha of secondary forest in a tropical Australian landscape was within 500 m of mature forests (Sloan *et al*. 2015). The maximum distance reported in the reviewed literature was 2420 m, and this distance appeared to have a negative effect on the ability of late successional species seeds to arrive at those pastures (Chinea *et al*. 2002).

The effect of distance from mature forests on secondary forest recovery needs to be considered carefully. Secondary forest cover has been observed very high within 200m of a mature forest and declining sharply over the next 800 m in negative exponential pattern (Sloan *et al.* 2015). Hence, in order to detect how distance influences recovery rates experimental

designs need to reflect this pattern in extent and magnitude. Apart from these spatial factors, I consider soil properties and type to be a factor that is also generally overlooked in terms of direct evidence, especially because soil factors are often assumed to be influential for forest recovery. Both the type of land-use and land management (*e.g.* soil fertilization, number of cultivation cycles) are likely to be associated with soil parent material (due to different properties and relief), which makes it potentially confounding and difficult to separate these into individual effects (Chinea *et al*. 2002). In my review, different land-uses have been compared in terms of their ability to recovery after use cessation; therefore evaluations need to be careful. Some of these issues have been cited as limitations for secondary forest chronosequence studies, together with the determination of stand age and the ability to exactly replicate conditions to improve statistical power (Johnson *et al*. 2008; Walker *et al*. 2010).

According to my review, there is simply not enough evidence available about the direct effects of soil fertility on rates of species accumulation or changes in community composition. It is well established that forest clearing for different land-uses disrupts the interactions between soil and vegetation which maintain nutrient cycles and soil structure. However, evidence for the influence of soil fertility and interactions with the vegetation on the recovery of secondary forest woody plant communities is unclear. Perhaps, the chronosequence approach is not ideal for testing causal effects of soil fertility on species recovery as suggested by Zanini *et al*. (2014). The most prominent indication of an association between soil properties and woody species accumulation found during this review, proposed that reduction in total soil phosphorus with time was correlated with lower species turnover in older stands (Long *et al*. 2012). The authors also indicated that increases in organic matter and total nitrogen are associated with increases in species richness, suggesting that soil fertility may influence forest community composition; stand age, not surprisingly, was the strongest predictor (Long *et al*. 2012).

In temperate forests, Christensen and Peet (1984) showed that community composition should become more predictable with time, as the niche width of species becomes narrower. In their study, variations in soil pH decreased with age and that would be sufficient to filter species that are able to occupy that niche (Christensen and Peet 1984). In contrast, other investigations on soil properties have found that soil nutrient availability and texture do not change significantly with age, therefore they had no relationship with changes in woody vegetation (do Nascimento *et al*. 2014, Zanini *et al*. 2014). As another note, I noticed a lack of information regarding biological interactions such as those with mutualist fungi or bacteria which are likely to play a crucial for organic matter and soil nutrient cycles and plant community configuration (Robinson and Fitter 1999, Allen *et al*. 2003). For these reasons, identifying and managing forests is still a daring task for restoration and community ecologists (Bakker and Wilson 2004, Suding and Gross 2006).

2.5 Conclusion

My review of the literature demonstrates some similarities and differences in the patterns of secondary forest recovery. The rapid initial secondary forest recovery which we suspect is driven by the dispersal syndromes of pioneer plant species is associated with the predominance of wind- and small vertebrate-dispersed propagules. The later recovery of shade-tolerant, larger vertebrate-dispersed seeds we believe is slow due to the potential seed source of this functional group and the idiosyncrasies of sites as well as plant-soil feedbacks that delay plant community establishment. As Holl *et al*. (2000) state “it is unlikely that the numerous species present before disturbance will all recolonize”, hence a better understanding of dispersal mechanisms and the interactions with environmental factors of these recruitment-limited species can help target our efforts to facilitate forest recovery. And, as suggested by Meiners *et al*. (2015), forest succession still provides opportunities for expansion of our understanding regarding community ecology, however trait-based

approaches that integrate different ecosystem components may be crucial for advances in the topic.

Chapter 3

Does soil type affect woody plant community recovery during secondary forest succession?

Abstract

Understanding successional changes in secondary forests may be crucial to the assisted recovery of their biological and functional diversity. Soil condition, among other biotic and abiotic factors, is an important feature that can affect forest recovery rates. My aim in this chapter was to document secondary forest recovery patterns in two contrasting soil types (basalt- versus granite-derived soils) in the Wet Tropics of Australia. I modelled woody vegetation structure and community composition with respect to variations with soil type, the age of land abandonment controlled by distance from remnant forest. I found that species diversity and dominance showed distinct patterns of recovery between basalt and granite soils. The inclusion of distance from forest remnant in the models of forest recovery reduced the effect of soil type. In terms of community composition, I found significant differences between basalt and granite soils, with several species being significantly associated with these soil types. Contrary to my expectations, dominance by nitrogen-fixing legumes was not greater in nutrient-poor soils. I conclude that although time since abandonment is crucial for secondary forest recovery, the community composition of woody plants may be influenced by the nutritional and textural condition of different soil types. The reestablishing vegetation community and the spatial distribution of surrounding mature forest also seemed to affect the rate of rainforest recovery.

Keywords: *rainforest regeneration, parent material, chronosequence, successional pathways*.

3.1 Introduction

Secondary forest recovery may be critical for the long–term maintenance of tropical biodiversity and forest services (Chazdon 2014). However, the direction and rates of forest recovery after abandonment of agricultural lands depend on a series of biotic (*e.g*. seed availability, non-native species establishment), abiotic (*e.g.* stand age and edaphic features) and historical site factors (*e.g.* land-use type) (Brown and Lugo 1990, Holl 1999, Zimmerman *et al*. 2000, Standish *et al.* 2007). Investigating the role and magnitude of these environmental and vegetation parameters during forest succession is relevant for understanding ecological processes and managing these systems (Mesquita *et al*. 2001, Cramer *et al*. 2008, Williamson *et al*. 2012). Information on the driving mechanisms of forest recovery can be used to improve ecological models of forest change and to indicate regional priorities for restoration (Srivastava and Vellend 2005, Chazdon *et al*. 2007; Cramer *et al*. 2008).

While time since agricultural abandonment and seed limitation are well known factors affecting plant community recovery, the contrasting fertility of soil types could also influence the rates of secondary vegetation recovery (Brown and Lugo 1990, Srivastava and Vellend 2005, Cramer *et al*. 2008). In general, topsoil properties such as organic matter content and water-holding capacity tend to decrease as a result of forest clearing and intense land use, whereas the concentration of certain nutrients (*e.g*. total N, Ca and K) and soil pH can increase in the first decades of forest succession, especially when fire is used to clear the land (Buschbacher *et al.* 1988, Fernandes and Sanford 1994). Yet, certain soil types could be more resilient to drastic environmental shifts than others and therefore lead secondary forest recovery into distinctive pathways (Allen 1985, Lal 2004, Weaver *et at*. 1987).

At the large scale, edaphic variables contribute with climate variables to explain the distribution of vegetation types and structure of plant communities (Clark *et al*. 1999, Givnish

1999, Tuomisto *et al*. 2014). Recent research has shown that the inclusion of edaphic variables improved the predictability of vegetation types and also some of their functional characteristics (Beauregard and De Blois 2014, Thuiller *et al*. 2013). Locally, dispersal limitation is considered more important in determining the arrangement of plant communities, with little evidence showing differentiation in tropical tree assemblies with soil fertility at the scale of plots as small as 1-ha (John *et al*. 2007). Whether soil types with contrasting chemical and textural properties support differentiated recovery of plant communities (*e.g.* species diversity, community composition, above-ground biomass) during forest succession is still debatable (Becknell and Powers 2014).

Secondary forest recovery can be assessed through different ecological parameters. Above-ground biomass, plant community structure and floristics as well as functional diversity constitute important ecological parameters that indicate changes in different aspects of communities (Ruiz-Jaen and Aide 2005). Functional diversity, in particular, has recently received more attention, with the increased availability of data on plant functional traits and development of indices to estimate functional diversity at the community-level using multiple traits (Villéger *et al*. 2012, Laliberté and Legendre 2010). Each different measure of forest recovery corresponds to different aspects of forest regeneration of interest to ecologists but rarely reported simultaneously. The inter-relationship between these measures can also generate important insights to understanding the forest regeneration process (Martin *et al*. 2013).

I aimed to investigate patterns of natural forest recovery in a range of secondary forests of different ages in two contrasting soil types in the tropical uplands of northeast Australia. I examined nine measures of woody vegetation recovery: species diversity, species dominance, number of stems, basal area, number of rare species, relative abundance of common species, community composition, functional divergence and functional dispersion. Soil cores were analysed with respect to nutrient availability and texture for each site to

characterize the soil types. With this information, my goal was to infer whether soil types can play a role in determining patterns rainforest woody community's recovery.

I tested predictions based on the ecological models of tolerance and facilitation during forest succession proposed by Connell and Slatyer (1977). I predicted that in the early stages of succession, more fertile soils would benefit tree recruitment as well as individual growth rates, rapidly improving ecosystem complexity by accelerating ground cover, species and functional diversity (Connell and Slatyer 1977, Grime 2006, Lohbeck *et al*. 2012, Fortunel *et al*. 2014). In contrast, in poorer soils I expected to find higher species dominance by nitrogen-fixing species, which are common in secondary forests in the region especially in the early stages of succession (Yeo and Fensham 2014, Lohbeck *et al*. 2014). As site conditions became ameliorated and other forest species were able to establish, I predicted a later decrease in species dominance and increase in species diversity and numbers of rare species in the poor soils.

3.2 Methods

3.2.1 Study area

The study was carried out in the Atherton Tablelands, northeast Queensland, Australia (17˚23'S 45º36' E). The study sites range from 700 -1000 m above sea level and experience a mild tropical climate. Mean annual rainfall ranges from 1700 to 2600 mm and mean annual temperature ranges from 10 to 29˚C (BOM, 2014). Warmer and more humid weather occurs from December to March and cooler and drier days from July to October, when monthly rainfall may be reduced to 100 mm. In the early 1900s until the 1920s the rainforest in this region were cleared for establishment of the dairy industry (Frawley 1987, Gilmore 2005). Most of the study area was used as grazing pasture until financial impediments led to cessation of dairy farming practices and abandonment of land (Gilmore 2005). Currently,

secondary forests, active pastures and relatively small old-growth forest fragments cover the landscape. The distance from mature remnant forests and the secondary forest sites varies between 50 and 2090 m, but riparian vegetation often interconnects the landscape. We purposely selected sites that were not contiguous with any major primary forest to reduce the confounding effects of distance on recruitment.

3.2.2 Secondary forest age determination and vegetation survey

I selected thirty-three secondary forest sites according to historical aerial photographs, satellite imagery and information from landowners (Goosem *et al*. 2016). Stand age was considered to be years since land use ceased. We also determined years since the formation of 70 percent of canopy cover, as some sites demonstrated variable delays in attaining woody vegetation cover. Age since abandonment and forest canopy formation were significantly correlated in both soil types, but the relationship was stronger in granite (basalt: r= 0.61, P<0.02; granite: r= 0.92, P<0.0001). Stand ages were determined using successive stereo pairs of images or high-resolution scanned aerial photographs (1943 – 2011) to allow detection of vegetation transitions in terms of replacement of grasses and low weeds by woody shrubs and tree saplings. Stand age was analysed as a continuous variable that ranged from 9 to 69 years. To investigate secondary forest communities we measured diameter at breast height (dbh) and identified to species all plant stems >2.5 cm dbh along a 50 m transect (Goosem *et al*. 2016). Larger plants ($\geq$10 cm dbh) were measured within 10 m of the transect and smaller plants (>2.5 cm dbh) were measured within 3 m from the transect.

3.2.3 Soil types and soil type characterization

Soils in the study area are derived from two main parent material types that dominate in the area: volcanic lava flows (Atherton Basalt) termed “basalt soil” hereafter and, from the intrusive granitic formation (Tinaroo Granite), hereafter “granite soil”. Basalt-derived soils dominate the Tablelands (56%) followed by granite-derived soils (23%) – rhyolite, metamorphic and Quaternary alluvial derived soils are also present and cover around 21 percent of the land together (Malcolm *et al*. 1999). Of the 33 sites, 14 occurred on basalt soils and 19 on granite soils. To characterize local soil condition, I collected twenty soil sub-samples per site (one at 0-10 cm, another from 10-30 cm depth) along the 50 m transect, at a distance of 5 m from the central line to avoid the trampled zone.

Differences in soil types were assessed by analysing soil macro- and micro-nutrients (Al, Ca, Cl, Cu Fe, K, Mg, Mn, Na, total N, P available to plants, total P, S, Zn), organic C, acidity, electrical conductivity and texture (clay and sand content). I collected samples with a hand auger and kept them cool in separate plastic bags until taken to the laboratory. After drying at room temperature, samples were sieved through 2 mm mesh and bulked to comprise one soil sample per site. Processed samples were sent to a commercial laboratory for analysis which followed Commonwealth Scientific and Industrial Research Organisation (CSIRO) protocols (Rayment and Lyons, 2011). To reduce dimensionality and characterize soil types based on their nutrient availability I used Principal Component Analysis (PCA; R function “prcomp”) on the standardised data, which means that columns were divided by their standard deviation and the mean of each column was subtracted. I used Spearman’s ρ correlations to test association of PCA axes with soil pH, electrical conductivity, sand and clay content. Bonferroni’s corrections were used to adjust the significance level (α) for multiple comparisons.

The two soil types differed in nutrient content, texture and pH (Fig. S1). In general basalt soils were less sandy, had lower acidity and were higher in the concentrations of most nutrients than granite soils. PCA axes explained 62 percent of variation (PCA-1= 46.5% and

PCA-2= 15.2%). PCA-1 was positively correlated with soil pH, nutrients (concentration of total N, total P, Ca, Mg, Na, K, Zn, Cu, Mn), organic C and percentage of clay. PCA-2 was significantly negatively associated with electrical conductivity, Cl, Al, and Fe concentration. Only PCA axis 1 was marginally correlated with stand age (PCA-1 ρ= 0.07, *P-value*=0.06; PCA-2 ρ= 0.04 *P-value* =0.13).

3.2.4 Data Analysis

Species diversity and community composition

I produced species accumulation curves based on number of sites and number of stems per soil type using R function 'specaccum' with Chao 1 estimator for total extrapolated number of species (Gotelli and Colwell 2011). To examine species diversity, I used Fisher's α logarithmic index (Whittaker 1973) and Simpson's index, which is more sensitive to changes in the most common species, to provide a better estimate of species dominance (Whittaker 1973, Magurran 2004). Fisher's α was estimated with R function 'fisher.alpha' and Simpson's index was estimated with R function 'diversity' (Oksanen *et al*. 2013). I examined community composition using Nonmetric multidimensional scaling with Bray-Curtis dissimilarity on species counts (NMDS, R function 'metaMDS', Oksanen *et al*. 2013) for three community assemblies: A: the whole woody plant community, B) common species C) rare species ($\leq$5 stems from total sample). I used PermAnova to test the significance of changes in community composition between stand age categories, soil types and distance from forest remnants (R function 'adonis', Anderson 2001).

Functional diversity

To examine functional diversity across successional forests in different soil types I chose a suite of traits that reflect plant ecological strategies (Westoby *et al*. 2002, Diaz *et al*. 2004): maximum diameter at 1.3 m height; seed size, wood density (WD) and leaf mass per unit area (LMA). Maximum diameter relates to the competitive ability of plants (Coomes and Allen 2007). Seed size is associated with successional stage in forest regeneration, especially seed dispersal, germination rates and survival (Coomes and Grubb 2003). Wood density correlates with resistance to embolism (Hacke *et al*. 2001) and is part of a group of traits associated with water relations (Ackerly 2004), and successional status (Chave *et al*. 2009, Tng *et al*. 2013). LMA is associated with the ‘‘leaf economics’’ spectrum of fast-to-slow resource capture (Reich *et al*. 1999, Wright e*t al*. 2004).

Trait data for 76 tree species that occurred in at least two of the 33 plots, representing 97% of the total basal area across plots, was compiled from different literature sources (Table S1). The distribution of these species was quite balanced between soil types, with 60 species found in basalt and 67 found in granite soils. For seed size, I used seed length as a proxy trait, because seed mass data were not available for many of the species and seed length is correlated with mass (Ellison 2001). For WD and LMA, I sourced data from trait databases and from primary literature. In a number of cases where the collection of data was not possible, I assumed genus-level trait conservatism and used genus level averages. Previous studies in tropical forests, have shown that >70% of the variance in species wood density was explained by genus (Chave *et al*. 2006, 2009, Slik 2006), and so genus averages were taken to be reliable proxies where species-level data were unavailable.

As a measure of functional diversity I used functional dispersion (Laliberté and Legendre 2010) and functional divergence (Villéger *et al*. 2008), two indices which are usually not inter-correlated (Laliberté and Legendre 2010). Functional dispersion relates to the dispersion of species in trait space and is independent of species richness (Laliberté and Legendre 2010). Functional divergence indicates the distribution of individual abundances

within the functional space occupied by species (Villéger *et al*. 2008). Functional divergence is higher when the most common species have extreme trait values. Functional diversity indices were calculated using functional attributes available for our species together with functional group classes as categorical attributes (*i.e.* short pioneer, tall pioneer, sub-canopy and canopy). Functional diversity indices were generated with the R function 'dbFD' (Laliberté and Legendre 2010, Laliberté and Laliberté 2014).

I examined the linear relationships of each of our response variables (number of stems, basal area, Fisher's α diversity, Simpson's index, relative abundance of common species and number of rare species, functional dispersion and functional divergence and NMDS dimensions 1 and 2 for community composition), with secondary forest age and soil type and their interaction (R function 'lme', [Pinheiro *et al*. 2013] and 'glmmPQL' when Poisson distribution was used [Venables and Ripley 2002]). Distance from fragment remnant was added in the model as a random factor to control for differences in stand location. Spearman's ρ correlation tests (R function 'rcorr', Harrel Jr *et al*. 2014) assessed the strength of inter-correlation between response variables. Indicator species values investigated species – soil associations (Dufrêne and Legendre 1997), reporting significance of associations (*P*) from 999 permutations. This index (*IndVal*) varies from 0 to 1, with higher values (>0) indicating stronger associations. The *IndVal* index was generated with R function 'multipatt' (de Cáceres 2013). I checked the assumptions of the analysis and presence of outliers with Q-Q plots and plots of residual vs. fitted values (Zuur *et al*. 2010). All statistical analyses were performed with R version 3.0.3 (R Core Team, 2014).

3.3 Results

3.3.1 Woody plant species, soil properties and secondary forest stand distribution

In 33 secondary forest sites, 2,553 individual woody stems and 141 species were counted and measured (Table S2). On average, secondary forest chronosequences on basalt and granite soils contained similar numbers of woody plant species (basalt: mean = 18.0 ± 5.8 SD, range 8-28; granite: mean = 16.9 ± 7.9 SD, range 7-33), similar numbers of stems (basalt: mean = 79.0 ± 29.6 SD, range 31-139; granite: mean = 76.2 ±19.1 SD, range 45-112) and similar basal area (basalt: mean = 34.1 ±17.5 SD, range 7.8-66.9; granite: mean = 33.4 ±17.6 SD, range 10.2-74.4 m^2 ha^{-1}). The number of stems and basal area were positively correlated in both soil types (Basalt: ρ=0.55, *P*=0.04; Granite: ρ=0.47, *P*=0.04).

From the total species pool, 12 species were considered common as they were recorded in more than half of the sites (Fig. 7). *Guioa lasioneura* Radlk. (Sapindaceae) was the most common species with 518 individuals (representing 20.3% of all stems) across all sites. Two species (*Flindersia brayleyana*, *Polyscias elegans*) were frequent in basalt sites only, two species (*Rhodomyrtus pervagata*, *Cissus hypoglauca*) were frequent in granite soil only and the other eight species were frequent in both soil types, with only slight differences in frequency (Fig. 7). I found 94 species with < 5 individuals (rare) in this study (less than 0.2% of all stems), and when analysed together there was no difference in species number between the two soil types (basalt: 4.8, ± 3.4 SD; granite: 4.4, ± 3.9 SD). Singletons represented 26.9% of all species (38 species).

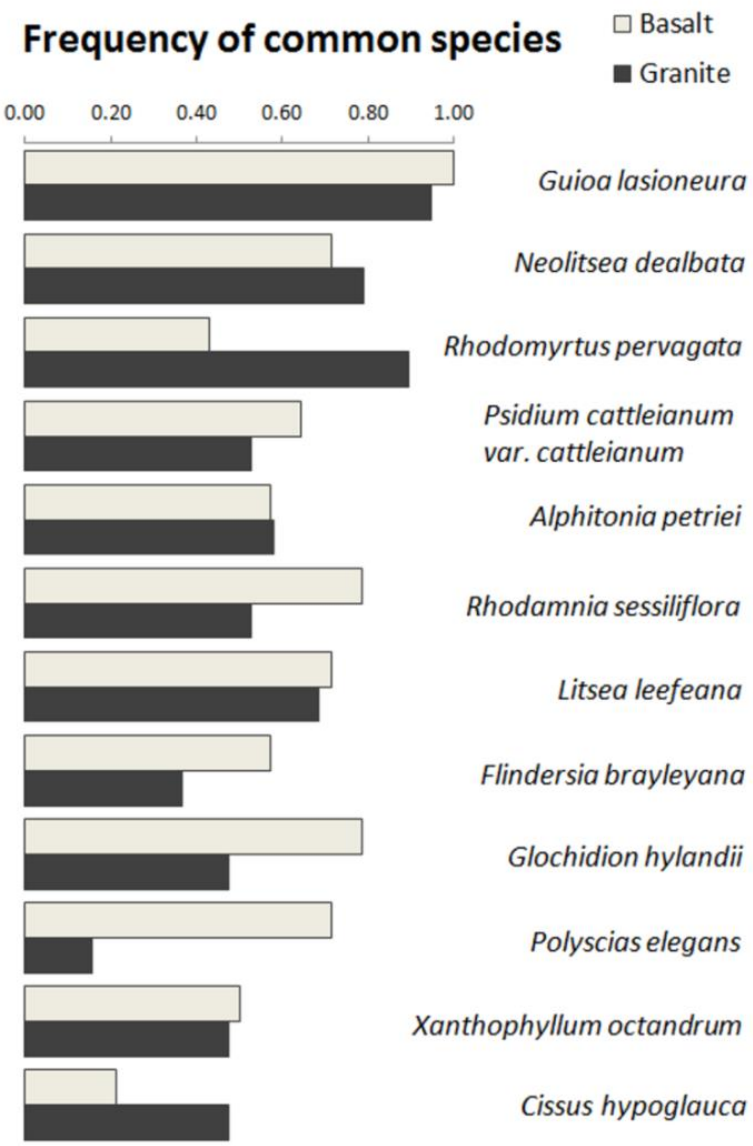

Figure 7. Frequency of the most common species from both soil types. Frequency= 1 indicates that a species occurred in all sites.

The mean distance between secondary forest sites and continuous forest did not differ significantly as a function of soil type (basalt: mean 2450.7m (860 – 4790) ± 1352.3m SD; granite: 2713.7 m (1110 – 4800) ± 1010.5m SD). However, sites on granite soils were closer on average to remnant forests than sites on basalt (granite: 455.8 m (65 - 1880) ± 427.1m SD; basalt: mean 836.4 m (230 - 2090) ± 593 SD). I did not detect any spatial autocorrelation in the data among all sites or when sites were separated by soil type (Mantel test for all sites: observation= -0.05, simulated *P*-value= 0.638; Mantel test for basalt only: observation= 0.12,

simulated *P*-value= 0.103; Mantel test for granite: observation= -0.23, simulated *P*-value= 0.935).

3.3.2 Patterns of community structure recovery with time, soil types and distance from forest remnant

Rarefaction curves of species accumulation with number of sites showed similar non-asymptotic trends in both soil types (Fig. 8A). When considering the accumulation of species with number of stems I found that soil types tended to diverge after reaching 1000 stems (Fig. 8A). The rate of species accumulation on basalt soils was slower than on granite soils. Regarding the recovery measures of secondary forests, I found that number of stems and species dominance (Simpson's index) were the only variables that differed significantly between soil types and became important in interactions with soil type (Table 2; Fig. 8 C and F), whereas basal area was the only response variable significantly influenced by forest stand age (Table 2, Fig. 8 D). Secondary forests on basalt soils appear to recover faster initially with respect to the number of stems, species diversity and species dominance but after ~30 years, forests on granite accumulate significantly more stems, and species diversity and dominance (Fig. 8F; Table 2). Basal area was the only parameter with a significant positive association with stand age, however I found that distance from remnant forest fragment was also a significant predictor of changes in basal area (Table 2, Fig. 8D, Fig S2).

Table 2. Generalised linear mixed models of species diversity (Fisher's α), species dominance (Simpson's index), numbers of stems, number of rare species, relative abundance of common species, functional divergence and functional dispersion in relation to forest age, soil types and distance from remnant forest fragment in NE Queensland, Australia. *P*-values significant at α = 0.05 are in bold. Degrees of freedom for all models = 15.

Source of variation	Coefficient (SE) and *P*-value					
	Stand Age (A)	*P*	Soil type (S)	*P*	A * S	*P*
Numbers of stems	-0.37 (0.31)	0.268	-34.92 (15.67)	**0.042**	0.96 (0.43)	**0.041**
Basal area	0.49 (0.20)	**0.025**	-20.44 (10.74)	0.076	0.64 (0.31)	0.060
Species diversity index	0.07 (0.07)	0.275	-6.99 (3.52)	0.066	0.20 (0.10)	0.069
Dominance index	0.001 (0.001)	0.451	-0.23 (0.08)	**0.011**	0.006 (0.002)	**0.012**
Common species	-0.61 (0.29)	0.051	-24.33 (14.59)	0.116	0.75 (0.41)	0.088
Rare species	0.01 (0.01)	0.453	-1.03 (0.63)	0.119	0.03 (0.02)	0.092
Functional divergence	0.47E-03 (1.47E-03)	0.753	-0.28 E-02 (7.79E-02)	0.728	1.54E-04 (2.25E-04)	0.946
Functional dispersion	5.98-04 (6.65E-04)	0.383	-5.43E-02 (3.67E-02)	0.149	1.33E-03 (1.04E-03)	0.219

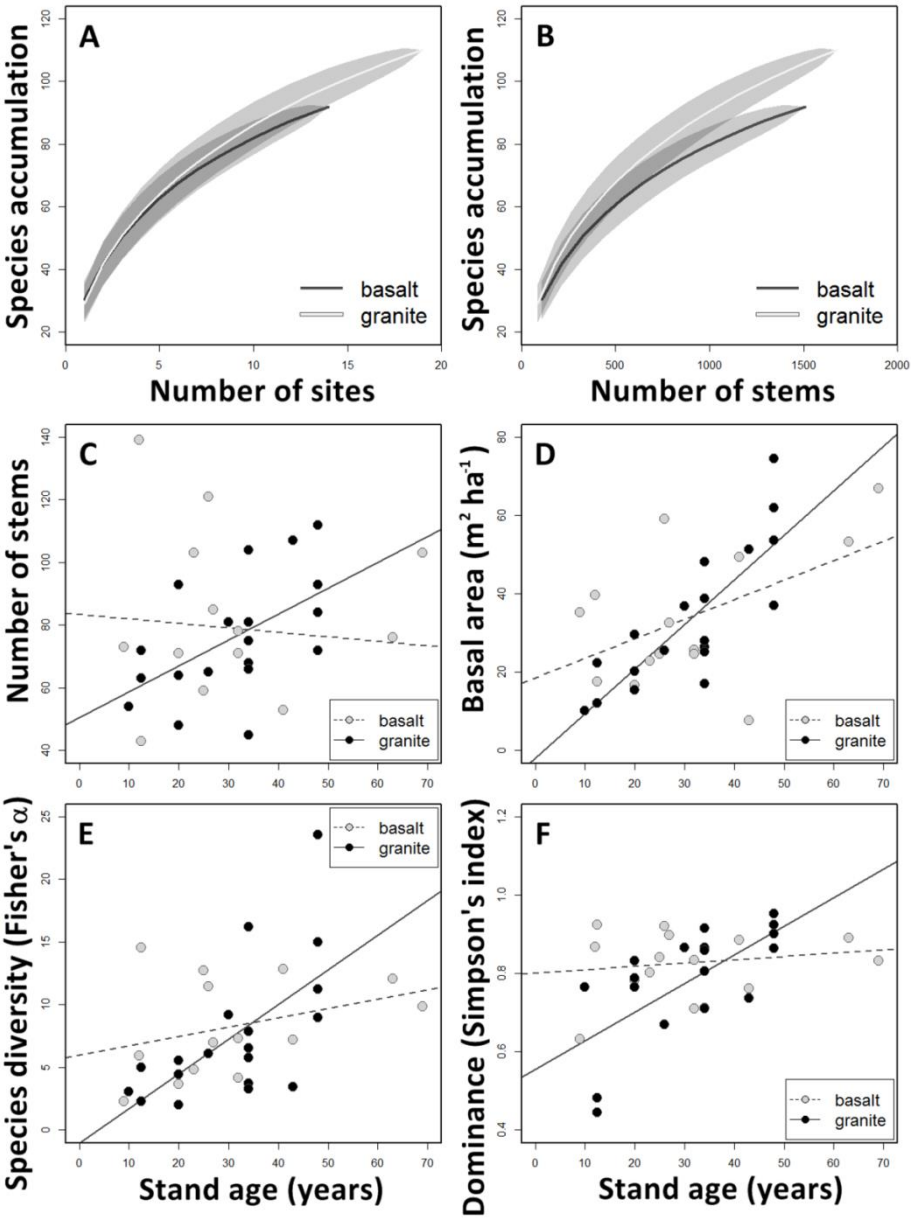

Figure 8. (**A**) Site-based and (**B**) individuals-based species accumulation curves for secondary forest on two soil types (shaded area is 95% confidence interval). (**C**) Number of woody stems, (**D**) Basal area (m^2 ha^{-1}) (**E**) Species diversity (Fisher's α) and (**F**) Species dominance (Simpson's index) across secondary forest age (years since pasture abandonment) on two soil types in northeast Queensland, Australia.

The age of secondary forest had no significant effect on proportion of rare or common species or function diversity indices in this study (Table 2, Fig. 9 and 10). Stand age did not significantly influence the relative abundance of common species, although I observed a minor

declining trend on basalt soils compared to the relatively flat relationship detected on granite (Fig. 9A; Table 2). There is an increasing trend of more rare species in older secondary forests on both soil types (Fig. 9B) but this relationship is not significant (Table 2), largely due to the low classification of rarity in this analysis (species with ≤ 5 stems in total). Similarly, there was an increasing trend for functional dispersion for both soil types with stand age that was not significant (Fig. 10A, Table 2), and a surprisingly flat relationship between functional diversity and stand age (Fig. 10B, Table 2). Regarding functional dispersion, which measures the distribution of species in trait space, there was a trend similar to species diversity. These two indices (species and functional dispersion) were significantly correlated in both soil types (basalt: r= 0.75, P= 0.002; granite r= 0.48, P= 0.039). Functional divergence did not show any tendency for change with time or soil type (Fig. 10B; Table 2) or association with species diversity (basalt: r= 0.09, P= 0.75; granite r= 0.09, P= 0.69).

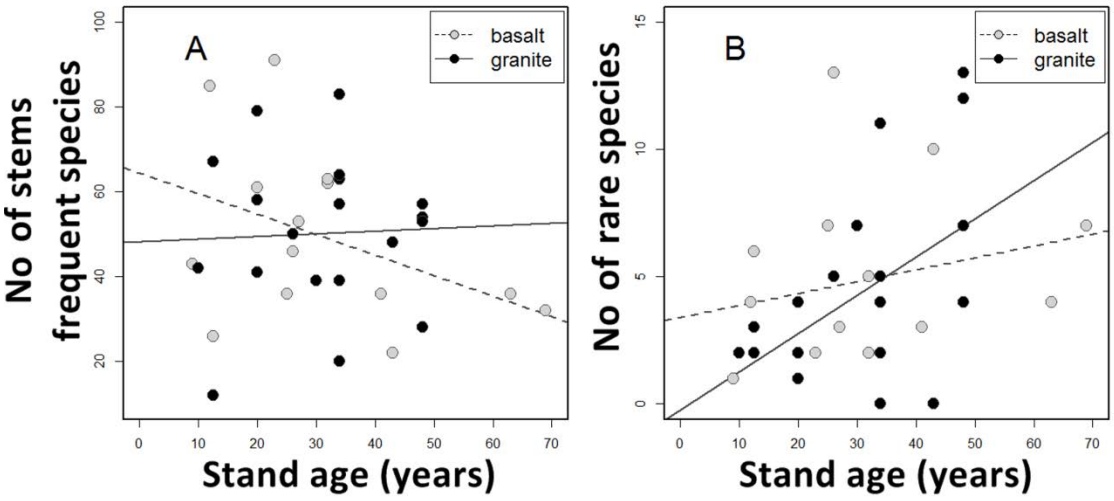

Figure 9. Number of (**A**) stems of the twelve most frequent species and (**B**) rare species (species with less than 5 individuals in total) in relation to secondary forest stand age on two soil types in NE Queensland, Australia**.**

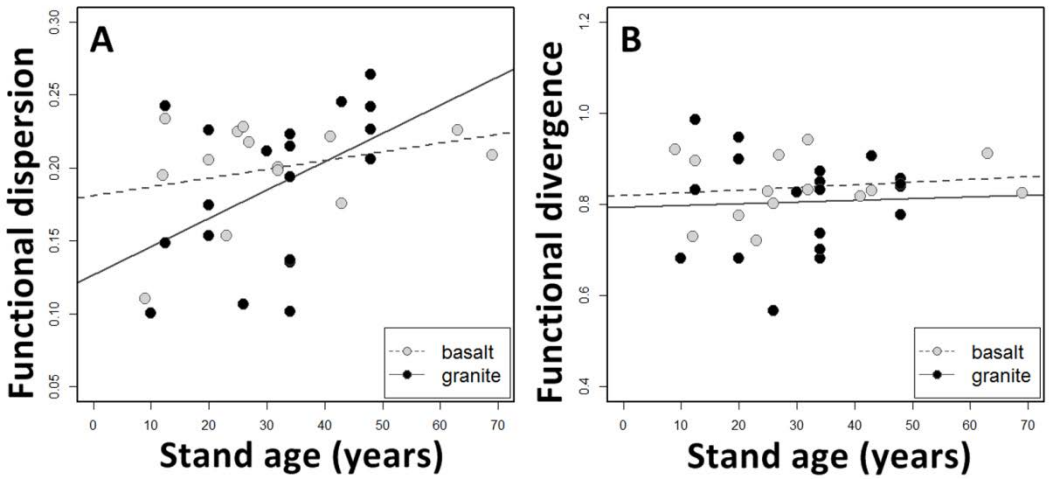

Figure 10. Relationships between functional diversity components in relation to secondary forest age (years since land abandonment) on two soil types in NE Queensland, Australia.

3.3.3 Patterns of community composition change with time, soil types and distance from forest remnant

There were differences in the woody plant community between the two soil types. Three community associations were analysed with Permanova and ordination (NMDS) to detect compositional changes and their relationships with stand age, soil type and distance from forest remnants (Table 3, Fig. 11). All three communities (A: complete community; B: common species only; and C: rare species only) showed consistent changes with stand age (Table 3), with the first ordination axis (NMDS1) from all three ordinations significantly correlated with stand age (A: complete community: r= 0.54, P= 0.001; B: common species: r= 0.32, P= 0.068; C: rare species: r= 0.44, P= 0.014), but not the second axes axis (NMDS-2). Soil type was significantly associated with community composition in the two ordinations (the whole community and common species, Fig. 11A and B; Table 3) but there was no indication of a relationship with rare species (Fig. 11C; Table 3). Distance from forest fragment was only negatively correlated with the second ordination axis (NMDS-2) for the whole plant community (r= -0.39, P=0.023; Fig. 11A). In basalt soils, *Mischocarpus macrocarpus*

(Sapindaceae) [*IndVal*= 0.66, *P*= 0.006], *Polyscias elegans* (Araliaceae) [*IndVal*= 0.71, *P*=0.018] and *Schefflera actinophylla* (Araliaceae) *[IndVal*= 0.51, *P*= 0.048]) had significant differences in distribution among soil types according to indicator species analysis. On granite soils, *Rhodomyrtus pervagata* (Myrtaceae) (*IndVal*= 0.85, *P*= 0.004) was the only significant indicator species.

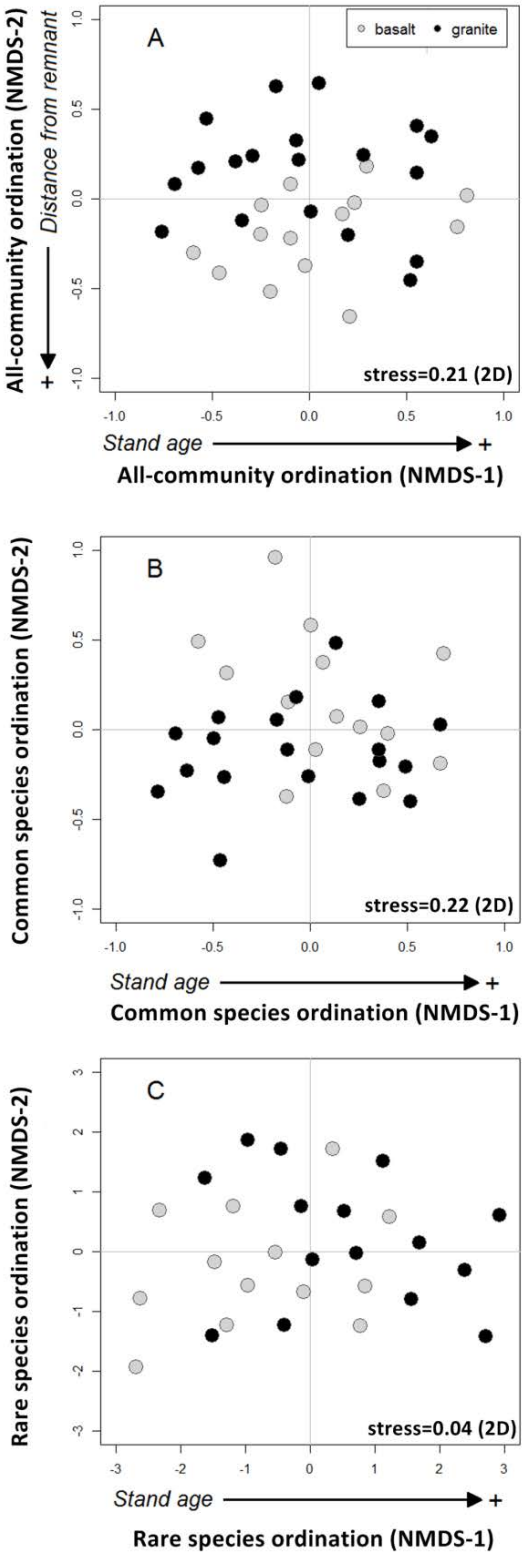

Figure 11. Community composition analyses based on nonmetric multidimensional scaling ordinations (2D) for (**A**) entire woody plant community; (**B**) common species and (**C**) Rare species, in secondary forests in NE Queensland, Australia. Arrows next to ordination axes indicate the direction of increase in distance from forest remnant or stand age when they were significantly correlated with the axis.

Table 3. Permutational ANOVA comparisons of woody community composition (count-based) in secondary forest sites in NE Queensland, Australia as a function of stand age (years), soil types, distance from forest remnant and the interactions between these factors. Three subsets of the data were considered separately: the complete community, which includes all 141 woody species; a sub-group of common species, which includes only species with more than 50 individuals in total; and a sub-group of rare species, which includes only species that had less than 5 individuals. *P*-values in bold are significant at $\alpha = 0.05$.

Sources of variation	df	SS	*F*	*P*-value
All-community				
Stand Age (A)	2	0.92	1.92	**0.007**
Soil type (S)	1	0.40	1.65	**0.044**
Distance (D)	1	0.33	1.39	0.127
A * S	2	0.71	1.49	**0.048**
Residuals	26	6.22		
Frequent species				
Stand Age (A)	2	0.56	2.02	**0.017**
Soil type (S)	1	0.61	4.38	**0.001**
Distance (D)	1	0.17	1.28	0.253
A * S	2	0.28	0.99	0.442
Residuals	26	3.62		
Rare species				
Stand Age (A)	2	1.49	1.70	**0.001**
Soil type (S)	1	0.57	1.31	0.102
Distance (D)	1	0.42	0.97	0.506
A * S	2	1.01	1.16	0.194
Residuals	23	10.06		

The two soil types shared similar abundances of the most common early successional species including *Guioa lasioneura* (Sapindaceae), *Neolitsea dealbata* (Lauraceae) and *Alphitonia petriei* (Rhamnaceae). *Acacia celsa* (Mimosaceae) was relatively abundant in both soil types with no difference in dominance between soil types. *Acacia cincinnata*

(Mimosaceae) was recorded on one granite site, but it was not the most abundant species at that site. *Psidium cattleianum* (Myrtaceae), an exotic invader from South America, represented 8.5 percent of all stems on granite soil compared with 3.8 percent on basalt soils. Despite this two-fold difference in relative abundance, this species did not seem to be associated with either soil type in this region according to our species indicator analysis.

On basalt soils, I found the average Bray-Curtis similarity index between older secondary forests (>30 years) and mature forests was almost twice as high as the average similarity between these two forest groups on granite soils (basalt: similarity= 0.11; ±0.07 SD; granite: similarity= 0.06; ±0.04 SD). Community similarity between younger (<30 years) and older secondary forests was much higher for both soil types (basalt: similarity= 0.27; ±0.13 SD; granite: similarity= 0.29; ±0.16 SD).

3.4 Discussion

3.4.1 Influence of soil type on vegetation recovery during forest succession

In the secondary forests of tropical Australia, I compared nine measures of community and structural recovery and found only partial concordance among two soil types. As anticipated, basal area increased with stand age in both soil types. Basal area is closely related with above-ground biomass, which has been shown to increase rapidly after land abandonment and with little influence of soil fertility in tropical Australia (Goosem *et al.* 2016) and in Neotropical forests (Poorter *et al*. 2016). Nonetheless, I found a lack of correlation between stem number and basal area in basalt soils, suggesting that self-thinning on this soil type may occur at faster rates compared with granite soils.

Two mechanisms, individually or in combination, may be controlling the self-thinning differences between soil types. The slow self-thinning in granite could be a combination of high recruitment rates and slow growth rates when they reach ≤2.5 cm dbh. Also, it is

important to consider the high invasibility of *Psidium cattleianum*, which produces dense thickets that remain even in the old secondary forest understory (Fortini *et al*. 2010, Tng et al. 2015). Aligned with this idea, variations in soil fertility could affect the ecosystem resistance to disturbance and help explaining differences in stem density (Connell 1978, Gleason *et al*. 2008). For instance, Gleason *et al*. (2010) found that on infertile soils, plants are less susceptible to damage to leaves, branches and stems due to modifications in their tissues to conserve nutrients. Where nutrients are less available, plants would tend to produce tissues with more C compounds which are structurally more resistant to wind breakage (Gleason *et al*. 2008, Ordonez *et al*. 2009), and more secondary compounds to reduce herbivory (Coley *et al*. 1985). It was found that after a cyclone, forests on less fertile soils were less affected (Gleason *et al*. 2010). Tropical cyclones are a common occurrence in our region with two extremely destructive storms passing over the study sites in the past eleven years (BOM, 2016). If secondary forests on granite (poorer soils) possessed greater resistance to damage, this would lead to a gradual recovery of secondary forest structure and diversity, whereas on basalt, events of strong winds would cause more destruction to the plant community and require a longer period to recover.

In combination with the differences in soil fertility, the fact that secondary forests on granite are in average closer to forest remnants could also increase seed arrival and recruitment in these sites (Standish *et al*. 2007). Denser communities would persist for longer periods, increasing the probability of having higher diversity of species as well (John *et al*. 2007). The lack of self-thinning in granite compared to basalt does not necessarily indicate lack of species accrual, however, forests in this less fertile soil may take longer to resemble the mature forest structure compared to basalt. The lack of historical data on logging for my mature forest hampers my ability to characterize how the mature forest in each soil type should look like. Nonetheless, forest recovery is occurring at different patterns depending on the soil type.

Additionally, I believe the importance of spatial isolation increases as succession unfolds. Distance from propagule sources may become more limiting with time, as pioneer species can usually disperse for longer distances (Swaine and Whitmore 1988, Dalling and Hubbell 2002). The difficulty in finding established secondary forests at longer distances may be indicative of such barriers for forest regeneration (Sloan *et al*. 2015).

3.4.2 Relationships between soil type and species dominance

The prediction that different soil types affect the dominance patterns and consequently the pathways of succession was partially supported. However, the relatively higher dominance in younger stands on basalt soils was contrary to predictions. Similarly, I did not expect the increasing dominance on granite soils during succession. Additionally, on granite soil I observed a simultaneous increase in species diversity and dominance. The positive relationship between species diversity and dominance could be due to a facilitative effect of dominant species on the establishment of new species during succession (Connell and Slatyer 1977, Callaway *et al*. 1995, Callaway and Walker 1997). Early and late successional species appeared to be coexisting, as evidenced by an increase in basal area and stem number at granite sites. This indicates that forest regeneration was occurring in most secondary forest sites on poor soils (although there were exceptions where secondary forest stands presented lower than expected signs of recovery (Goosem *et al*. 2016).

Unlike reports from other successional forests in the broader north Queensland region (Yeo and Fensham 2014), *Acacia* spp., which are well-known as nitrogen-fixers, were not dominant with respect to stem number at our sites, with the exception of one very young stand (9 years old) on basalt soil. Despite low frequency of N-fixers, availability of nitrogen for the vegetation cannot be inferred without further experimentation. Findings from successional forests in Central Amazonia indicated limitation of N, however N-fixers were also rare

(Davidson *et al*. 2004). In our study sites, the main native dominants in these secondary forests, *Guioa lasioneura* (Sapindaceae) and *Neolitsea dealbata* (Lauraceae) are both small-seeded (8 and 7 mm length, respectively) and animal-dispersed species that may play important roles in ameliorating biotic (*e.g.* microbial activity) and/or abiotic (*e.g.* shading and soil moisture) conditions during succession (Goosem and Tucker 2013).

3.4.3 Slow convergence of the secondary forest community to mature phase composition

Another important finding of this study relates to variations in community composition between soil types. Community convergence towards mature phase forests is an important parameter in the evaluation of recovery pathways in secondary forests (Williamson *et al*. 2012). In that regard, my data suggests faster rates of convergence in the nutrient-rich environment provided by basalt soils, even though the community similarity is still very low. Overall low community similarity between secondary and mature forest has been found in other studies (Aide *et al*. 2000, Pascarella *et al*. 2000, Zanini *et al*. 2014), suggesting that intervention (*e.g.* planting or control of invasive species) to accelerate secondary forest biodiversity recovery is needed (Chazdon 2014).

Invasion by exotic species in regenerating forests is also a concern. Low community similarities between secondary and mature forests have been assumed to be caused by competition between native colonizers and exotic species (Aide *et al*. 2000, Chazdon 2008). The occurrence of exotic species at my sites such as *Lantana camara*, *Cinnamomum camphora* and especially high densities of *Psidium cattleianum* (exotic spp; Tng *et al.* 2015) cannot be ignored. The presence of *P. cattleianum* as one of the most abundant species at my study sites, indicates the novelty of these secondary forests and the negative implications this may have for the long-term recovery of these forests (Hobbs *et al.* 2009, Tng *et al.* 2015). *Psidium cattleianum* is a shade-tolerant weed which is already present in 27 of our 33 secondary

forests (Tng *et al.* 2015). Whether the invasion of these exotic species will leave permanent legacies or impede secondary forest recovery still remains to be investigated (Tng *et al.* 2015).

3.4.4 Functional diversity

I did not find strong evidence to support the prediction that functional diversity increases during secondary forest succession. I anticipated an increase in functional diversity with stand age in both soil types, despite their differences in fertility and clay/sand content (Fortunel *et al*. 2014). Nonetheless, I found that functional dispersion (one of the functional diversity indices) tends to follow a similar pattern to species diversity. This relationship between functional and species diversity has been detected previously in southeast Mexico (Lohbeck *et al*. 2012) although with a far stronger relationships (R^2= 0.99). Also similarly to my findings, the authors did not find a significant effect of stand age (Lohbeck *et al*. 2012). However, there are limitations in my study where I compiled trait data for species from different sources which may have used different methods to estimate trait values. This also means I was unable to account for intra-specific variation (Siefert *et al*. 2015) in traits.

3.5 Conclusion

My results demonstrate that the parameters used to measure forest recovery influence the conclusion about forest stand age and soil type. To conclude this chapter, I would like to highlight two interesting findings. Firstly, while basal area is the only parameter that increases significantly with age in both soil types, changes in other parameters such as number of stems and species dominance seem to be influenced by soil type. An increasing number of stems in the natural forest succession on granite is unusual, indicating that these forests are far from reaching a mature phase where number of individual are reduced while basal area of fewer late-successional species increase. Secondly, even though forests on granite maintain

an increasing trend in number of stems, species diversity also increase, which is contradictory to what we would expect from a case of slow forest recovery. Despite differences in rates of number of stems change, both soil types can accumulate species at very similar rates. Such findings make me wonder about the effects of the isolation of forest patches. Perhaps, the distance from seed sources is being more important in structuring the secondary forest in granite soil compared to basalt sites, which are more fertile, however more distant from the forest remnants. Further experiments to isolate the effects of soil fertility and distance from seed sources would contribute to elucidation of such forest recovery patterns found in this study.

3.5 Supporting material

Table S1. Complete woody plant species list with functional trait values presented for the species included in the functional diversity indices calculations. Functional trait values come from a variety of published literature and personal communications. Life history categories are: PS= short pioneer, PT= tall pioneer, CS= sub-canopy and CU= upper canopy. Functional traits are: Dmax= maximum diameter (cm), SL= seed length (mm), WD= wood density (g cm^{-3}) and LMA= Leaf mass per area (g m^{-2}). Complete references for cited literature sources are given in the footnote.

Woody plant species	Life History	Functional traits				Source
		Dmax	SL	WD	LMA	
Acacia celsa	PT	91	5.5	0.49	145	Falster and Westoby 2005
Acacia cincinnata						
Acronychia acidula	CS	43	4.5	0.52	85	Falster and Westoby 2005
Acronychia acronychioides						
Acronychia vestita	CS	23.4	5.5	0.52	108	Tng unpublished
Aglaia australiensis	CS	15.5	42	0.76	83	Grubb *et al.* 2008 , WAC
Aglaia meridionalis						
Alphitonia petriei	PT	42.6	5	0.43	149	Falster and Westoby 2005, Ilic *et al* 2000
Alphitonia whitei	CS	48.8	6	0.58	163.81	Tng *et al*. 2013
Alstonia muelleriana	PT	5.5	6	0.67	95.54	Tng *et al*. 2013
Archidendron ramiflorum	CS	14	14	0.53	133	Tng unpublished, WAC
Archirhodomyrtus beckleri						
Archontophoenix alexandrae						
Ardisia brevipedata	CS	2.8	6	0.69	73	Apgaua unpublished
Argyrodendron trifoliolatum						
Arytera divaricata						
Austrosteenisia stipularis						
Balanops australiana						
Beilschmiedia collina	CU	64.2	24	0.58	140	Tng unpublished, WAC
Beilschmiedia tooram	CU	40.2	50	0.75	108	Tng unpublished, WAC
Bleasdalea bleasdalei						
Brackenridgea australiana						

Woody plant species	Life History	Functional traits				Source
		Dmax	SL	WD	LMA	
Calamus australis						
Calamus moti						
Caldcluvia australiensis	CS	57.5	1	0.47	80	Tng unpublished, Ilic *et al* 2000
Cardwellia sublimis	CU	39.1	70	0.56	110.69	Tng *et al*. 2013
Carnarvonia araliifolia var. araliifolia						
Casearia costulata						
Castanospora alphandii	CU	40.9	25	0.63	97.93	Tng *et al*. 2013
Ceratopetalum succirubrum						
Cinnamomum camphora	PT	23.4	9	0.47	177.74	WAC
Cinnamomum laubatii	CS	11.5	13	0.41	84	Tng unpublished, WAC
Cissus hypoglauca						
Cissus vinosa						
Claoxylon tenerifolium						
Cnesmocarpon dasyantha						
Commersonia bartramia						
Corynocarpus cribbianus						
Cryptocarya lividula	CU	33	14	0.61	65	Gleason *et al.* 2011, WAC
Cryptocarya mackinnoniana	CU	47.9	20	0.65	204	Tng unpublished, WAC
Cryptocarya melanocarpa	CU	25.1	6	0.61	57	Tng unpublished, WAC
Cryptocarya murrayi	CU	24.4	5	0.67	109	Tng unpublished, Falster and Westoby 2005
Cryptocarya oblata						
Cupaniopsis flagelliformis var. flagelliformis	CS	14.1	8	0.71	94	Tng unpublished
Cyathea cooperi						
Cyathea rebeccae						
Cyclophyllum multiflorum						
Daphnandra repandula						
Darlingia darlingiana						
Davidsonia pruriens	CS	11.5	36	0.79	77	Tng unpublished, WAC
Doryphora aromatica	CU	70.2	15	0.55	76.03	Tng *et al*. 2013
Dysoxylum rufum	CU	17.7	8	0.551	37	Tng unpublished
Elaeocarpus grandis	PT	18.5	20.4	0.49	122	Falster and Westoby 2005
Elaeocarpus largiflorens s bsp. largiflorens	CU	8.9	17	0.40	130.46	Tng unpublished, Ilic *et al*. 2000
Elaeocarpus sp. (Mt	CU	31.2	14	0.52	81	Tng unpublished,

Woody plant species	Life History	Functional traits				Source
		Dmax	SL	WD	LMA	
Bellenden Ker L.J.Brass 1836)						WAC
Embelia grayi						
Endiandra acuminata						
Endiandra bessaphila						
Endiandra dielsiana						
Endiandra leptodendron	CS	13.9	18	0.61	151	Falster and Westoby 2005
Endiandra monothyra subsp. monothyra	CU	66.9	34	0.68	83	Grubb *et al* 2008, WAC
Endiandra sankeyana	CU	38.2	45	0.60	78.826	Tng unpublished, Ilic *et al.* 2000
Endiandra wolfei	CS	4 6.8	2 1	0. 86	102	Tng unpublished, WAC
Eupomatia laurina	CS	11	6	0.50	69.45	Tng *et al.* 2013
Fagraea fagraeacea						
Ficus congesta var. congesta						
Ficus copiosa						
Ficus leptoclada	CS	12.6	1	0.48	76.94	Tng *et al*. 2013
Ficus pleurocarpa	CU	82	1.5	0.39	199	Tng unpublished
Flindersia bourjotiana						
Flindersia brayleyana	PT	91	65	0.52	171.32	Tng *et al.* 2013
Flindersia pimenteliana	CU	65.8	55	0.50	93.81	Tng *et al*. 2013
Franciscodendron laurifolium	CU	56.2	15	0.38	63	Grubb *et al*. 2008, Ilic et al. 2000
Gardenia ovularis	CS	35.3	2	0.67	101	Tng unpublished, Ilic *et al*. 2000
Geissois biagiana	CU	90.3	2.4	0.46	103.3	Tng *et al*. 2013
Glochidion harveyanum var. harveyanum	PT	29.1	4.2	0.63	78	Tng unpublished
Glochidion hylandii	CS	42.5	5	0.57	106	Falster and Westoby 2005
Goniothalamus australis	CS	14.2	20	0.46	48	Grubb *et al.* 2008, WAC
Guioa lasioneura	CS	42.5	8	0.72	128.83	Tng *et al*. 2013
Haplostichanthus submontanus subsp. sessiliflorus						
Hedycarya loxocarya	CS	11.2	7	0.51	68.75	Tng *et al*. 2013
Helicia blakei						
Helicia lamingtoniana						
Helicia nortoniana	CS	16.6	11	0.63	80	Tng unpublished
Homalanthus novoguineensis	PT	26.3	3	0.32	82	Falster and Westoby 2005
Hylandia dockrillii	CU	84.6	15	0.51	118	Tng unpublished

Woody plant species	Life History	Functional traits				Source
		Dmax	SL	WD	LMA	
Lantana camara	PS	3.2	1	0.37	50.84	Carrion-Tacuri *et al*. 2011
Lethedon setosa						
Ligustrum sinense						
Litsea connorsii	PT	28.3	14	0.50	118.35	Tng *et al*. 2013
Litsea leefeana	PT	93.5	19	0.49	95.3	Tng *et al*. 2013
Lomatia fraxinifolia	CS	29.2	12	0.76	62	Tng unpublished, Ilic *et al*. 2000
Macaranga involucrata var. mallotoides						
Macaranga tanarius						
Maclura cochinchinensis						
Maesa dependens						
Mallotus mollissimus	PS	12.3	3	0.37	63	Falster and Westoby 2005
Marsdenia rostrata						
Melastoma malabathricum subsp. malabathricum	PS	3.9	1	0.51	90	Apgaua unpublished
Melicope elleryana						
Melicope jonesii	CU	75	4	0.54	82	Tng unpublished
Melicope xanthoxyloides	CS	13.6	3	0.43	37	Tng unpublished, WAC
Michelia champaca	PT	15.8	10	0.54	74.4	Tng unpublished, WAC
Mischarytera lautereriana						
Mischocarpus macrocarpus	CS	42.6	10	0.81	124	Tng unpublished, WAC
Myristica globosa subsp. muelleri	CS	12.4	22	0.43	106	Falster and Westoby 2005
Neolitsea dealbata	PS	19.8	7	0.47	102.2	Tng *et al*. 2013
Palmeria scandens						
Pilidiostigma tropicum	CS	21.1	8	0.63	47.3	Tng unpublished, WAC
Polyscias australiana	PT	11.1	7	0.41	64.38	Tng *et al*. 2013
Polyscias elegans	PT	32.4	2	0.40	53.13	Tng unpublished, Ilic *et al*. 2000
Psidium cattleianum var. cattleianum	PS		3	1.12	125.47	Baruch and Goldstein 1999
Pullea stutzeri	CS	49.5	10	0.69	106	Tng unpublished, WAC
Rhodamnia sessiliflora	CS	21.3	3	0.76	102	Apgaua, Ilic *et al.* 2000
Rhodomyrtus canescens						
Rhodomyrtus pervagata	CS	28	2	0.78	97	Tng unpublished, WAC
Ripogonum album						

Woody plant species	Life History	Functional traits				Source
		Dmax	SL	WD	LMA	
Sarcopteryx martyana						
Sarcotoechia lanceolata	CS	7.2	11	0.66	95	Tng unpublished, WAC
Schefflera actinophylla	PT	24.4	6	0.42	143	Apgaua unpublished
Sloanea australis subsp. parviflora						
Sloanea langii						
Sloanea macbrydei	CU	46.1	13	0.48	84	Tng unpublished, WAC
Symplocos gittinsii	CS	33.6	8	0.57	127.06	Tng *et al*. 2013
Symplocos glabra						
Synima cordierorum	CU	16.9	11	0.79	109	Apgaua unpublished
Syzygium cormiflorum						
Syzygium endophloium	CU	16	8	0.73	101	Tng unpublished, Ilic *et al*. 2000
Syzygium gustavioides						
Syzygium johnsonii						
Syzygium papyraceum						
Tasmannia membranea						
Tetracera nordtiana						
Tetrastigma nitens						
Toechima erythrocarpum	CU	23.7	15	0.67	64	Apgaua unpublished
Toechima monticola						
Vanroyena castanosperma	CS	54	40	0.76	41	Tng unpublished, Ilic *et al*. 2000
Wikstroemia indica	PS	3.7	6	0.58	39.75	Tng *et al*. 2013
Wilkiea angustifolia						
Xanthophyllum octandrum	CS	25.9	12	0.64	122	Weerasinghe et al. 2014, Ilic *et al*. 2000
Zanthoxylum veneficum						

Sources cited:

WAC- World Agroforestry Centre database (http://www.worldagroforestry.org/our_products/databases)

Baruch, Z., Goldstein, G., 1999. Leaf construction cost, nutrient concentration, and net CO2 assimilation of native and invasive species in Hawaii. Oecologia 121, 183–192.

Carrión-Tacuri, J., Rubio-Casal, A.E., de Cires, A., Figueroa, M.E., Castillo, J.M., 2011. Lantana camara L.: A weed with great light-acclimation capacity. Photosynthetica 49, 321–329.

Falster, D.S., Westoby, M., 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. J. Ecol. 93, 521–535.

Gleason, S.M., Read, J., Ares, A., 2011. Biomass allocation and phosphorus economics of rain-forest seedlings: effects of fertilization and radiation on soil specialists and soil generalists. J. Trop. Ecol. 27, 147–161.

Grubb, P.J., Jackson, R. V., Barberis, I.M., Bee, J.N., Coomes, D.A., Dominy, N.J., De La Fuente, M.A.S., Lucas, P.W., Metcalfe, D.J., Svenning, J.C., Turner, I.M., Vargas, O., 2008. Monocot leaves are eaten less than dicot leaves in tropical lowland rain forests: Correlations with toughness and leaf presentation. Ann. Bot. 101, 1379–1389.

Ilic, J., Boland, D., McDonald, M., Downes, G., Blakemore, P., 2000. Woody density: Phase 1 - State of knowledge.

Tng, D.Y.P., Jordan, G.J., Bowman, D.M.J.S., 2013. Plant traits demonstrate that temperate and tropical giant eucalypt forests are ecologically convergent with rainforest not savanna. PLoS One 8, 1–13.

Weerasinghe, L.K., Creek, D., Crous, K.Y., Xiang, S., Liddell, M.J., Turnbull, M.H., Atkin, O.K., 2014. Canopy position affects the relationships between leaf respiration and associated traits in a tropical rainforest in Far North Queensland. Tree Physiol. 34, 564–584.

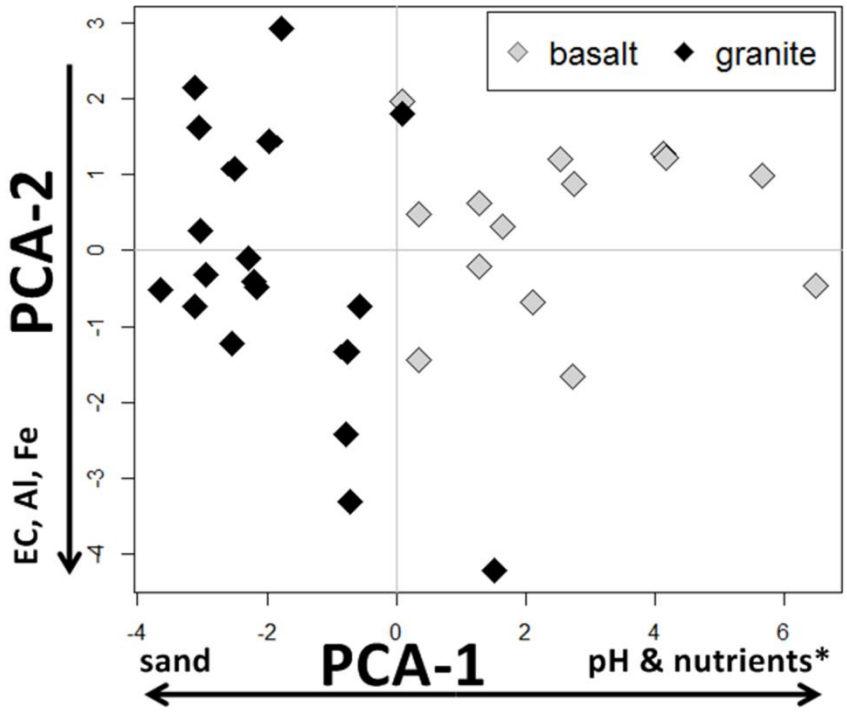

Figure S1. Two main axes from Principal Components Analysis (PCA) for soil macro- and micro-nutrients in different soil types derived from basaltic and granitic parent material in NE Queensland, Australia. PCA-1 (explaining 46.5% of variation) and PCA-2 (explaining 15.2%) were significantly correlated with the following soil parameters (α=0.003 with Bonferroni's correction): *nutrients (concentration of total N, total P, Ca, Mg, Na, K, Zn, Cu, Mn), soil pH, sand content, electrical conductivity (EC), concentrations of Al, Fe and Cl. The arrows indicate the direction of increase in each parameter.

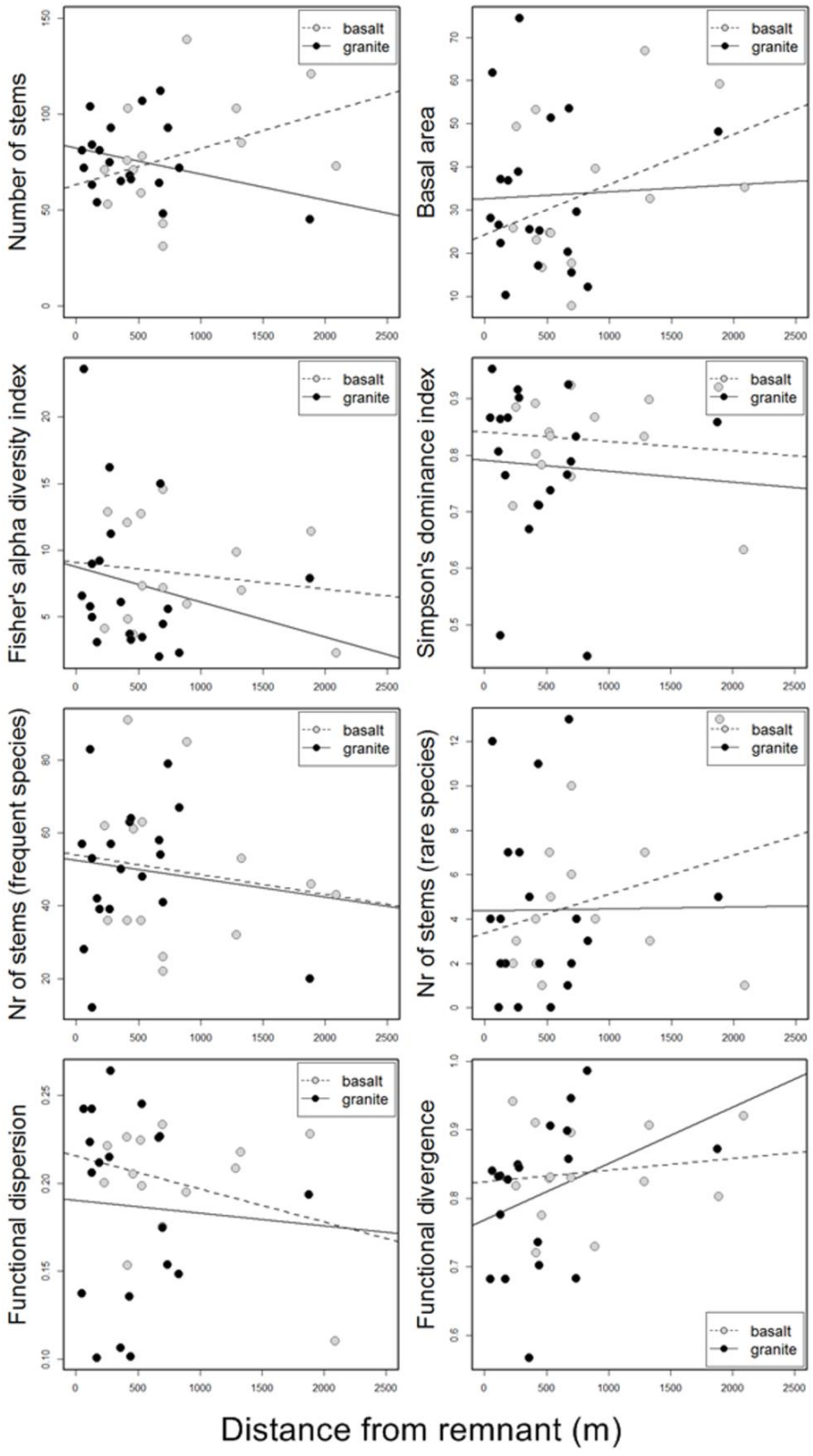

Figure S2. Simple linear models for each of the response variables for vegetation recovery as function of distance from forest fragment remnant for the two soil types.

Chapter 4

The effects of soil types on arbuscular mycorrhizal communities during tropical forest succession

Abstract

Secondary forest areas are increasing rapidly across the tropics. Abandoned pastures and agricultural fields have the potential to recover to historical states; however, soil degradation; exotic species invasion and lack of seed sources can delay this process. Soil microorganisms play a crucial role in soil and forest regeneration, as they participate in the soil carbon and nutrient cycles. Arbuscular mycorrhizal soil fungi (AMF) form mutualistic associations with plant roots, providing water and nutrients in exchange for plant-derived sugars. Little is known about the patterns of AMF diversity during forest succession and regeneration but much has been proposed. Hence, I examined AMF community structure and composition changes in successional habitats in tropical Australia. To describe AMF communities, I identified virtual taxa with DNA analysis of soil samples from mature forests and secondary forests of different ages. Vegetation community and soil parameters, leaf-litter cover, and proximity to the mature forest were investigated in models to explore AMF community distribution and similarities. I found a total of 100 virtual taxa, with the great majority in the family Glomeraceae (number of species= 58). This is one quarter of the total taxa known globally. I found that changes in AMF richness and community composition after land abandonment depend on soil type (basalt- versus granite-derived soils). Soil pH and total phosphorus were the environmental predictors that best explained variation in AMF richness and community composition, although the latter may also be influenced by soil nitrogen and tree basal area. Variation in AMF community

composition may indicate the role of environmental filters, particularly soil acidity and P content, on secondary forest succession.

Keywords: *rainforest succession, plant-fungi interaction, parent material, abandoned pasture*

4.1 Introduction

Secondary forests are rapidly dominating tropical landscapes. The abandonment of non-productive lands eventually leads to forest regeneration. However, soil degradation, invasion by non-native species and lack of seed sources and seed dispersers can delay or alter the recovery process (Cramer *et al*. 2008, Norden *et al*. 2001, Goosem *et al*. 2016). It is well-accepted that soil physical and nutritional alterations caused by forest clearing and agricultural use can affect soil biotic and abiotic condition and the regeneration of abandoned lands (Wardle 2006, Kardol *et al*. 2006; van der Heijden *et al*. 2008). Soil microorganisms such as fungi play important roles in soil structure and maintenance of biogeochemical cycles (Brundrett 2004, Fischer *et al*. 1994).

The relevance of interactions between fungi and plants is evidenced by estimates that *ca*. 80% of terrestrial plants in natural and man-made systems have mycorrhizal partnerships (Brundett 2004, Treseder and Cross 2006, Dighton, 2009). For plants, the benefits come from fungal hyphae that increase nutrient acquisition through an expanded root surface area, which protects roots from drought and also improves root resistance to pathogenic infections (Jeffries *et al*. 2003, Brundett 2004, Herre *et al*. 2005, Heijden *et al*. 2006, Lambers *et al*. 2008). In return, plants provide carbohydrates required for fungal growth. As a consequence, not only plant productivity but also the maintenance and configuration of plant communities are assumed to be associated with mycorrhizal fungal community diversity and composition (van der Heijden *et al*. 1998).

Diversity of AMF communities is expected to provide a range of functional strategies to cope with the dynamic environmental conditions during forest regeneration (*e.g.*

heterogeneous soil nutrient and acidity distribution). The vegetation is likely to benefit from a diverse microbial community especially because the soil and light condition as well as the plant community composition fluctuate more rapidly compared with mature forests. The way in which fungal communities change during forest succession is poorly understood (Van Veen and Kuikman 1990, van der Heijden *et al*. 2008). Supposedly, plant-root interactions are vital to plant nutrition especially in infertile soils where there is low diffusion of phosphates, ammonium, potassium and nitrates (Chapin II 1980, Janos 1980). An increased diversity of fungal species within communities would be expected to assist forest regeneration as this would allow more resilience to stress and/or perturbation (Helgason *et al*. 2007).

In naturally fertile soils, however, association with mycorrhizal fungi may not always be beneficial for plants, especially if light is limiting, which is usually true for seedlings in tropical rainforests (Janos 1980, Gehring and Connell 2006). Studies found that seedlings of pioneer and late successional plant species differed in terms of AMF dependency, due to differences in seed size (Zangaro *et al*., 2007; Gehring and Connell 2006). The amount of resources provided by large seeds enabled seedlings to grow faster without obligatory association with AMF (Zangaro *et al*. 2007), but this relationship may change as individuals grow or soil conditions change (Gehring and Connell 2006). Diversity of AMF was found to be important in at least two ways: (i) variation in hyphal length and morphology, which relates to strategies to reach and obtain resources; and (ii) variation in spore size and abundance which relates to the ability to disperse and colonize new roots (*i.e.* generalists vs. specialists) (Avio *et al*. 2006, Maherali and Klironomos 2007, Jeffries *et al*. 2003, Helgason *et al*. 2007).

To investigate changes in the AMF community during forest succession I compared young and old secondary forests with mature forests growing on two contrasting soil types in the Australian Wet Tropics. I asked two main questions: (i) Do AMF richness and composition differ among secondary and mature forest categories in the two soil types? (ii) Do soil and vegetation factors help predicting the changes in AMF communities equally in the two soil

types? Firstly, I predicted that there would be an increase in AMF richness from young to secondary and mature forest because, as forest succession proceeds, the increase in plant diversity would support richer and different fungal communities. Secondly, since plant communities on more fertile soils would depend less on AMF, I expected greater species number on the less fertile soils (Janos 1980). Third, I anticipated that soil fertility and vegetation factors are good predictors of AMF richness and compositional changes during rainforest succession (van der Heijden *et al*. 1998, Burrows and Pfleger 2002, Allen *et al*. 2003).

4.2 Methods

4.2.1 Study area

The study area was located in the southern region of the Atherton Tablelands, north-eastern Queensland, Australia (17˚23'S 45˚36' E, see area description in Chapter 3). Soils in the study area are either derived from the volcanic lava flows which formed Atherton Basalt, hereafter termed "basalt soil" or from Tully Granite intrusions, hereafter "granite soil". Basalt-derived soils dominate the Atherton Tablelands (56% land cover) followed by granite-derived soils (23%), with rhyolite, metamorphic and Quaternary alluvial-derived soils also present (21%) (Malcolm *et al*. 1999). The research sites were stratified by soil type (basalt (n=9) and granite (n=9) and forest age (young: ≤30 years since forest abandonment (n=6); old: >31 years (n=6); and six mature forest sites (n=6)). Secondary forests ranged in age from 9 to 69 years. Mature forests have never been cleared, although they all have experienced selective logging in the past. Secondary forest sites were not adjacent to mature rainforests but ranged in proximity of 1200 to 4790 m from continuous forests and 50 to 2100 m from remnant forest fragments. These distances were not stratified by soil type during study site selection, hence sites on granite soils were significantly closer to continuous mature forests (basalt: 1840 –

4790 m; granite: 1200 – 3090 m; *F*-value= 7.5, *P*=0.02) but not to remnants (basalt: 255 – 2090 m; granite: 50 – 740 m; *F*-value= 2.01, *P*=0.186).

4.2.2 Secondary forest age determination and vegetation survey

Secondary forest age was established by analysis of time-series aerial photography, satellite imagery and information from landowners. Stand ages were determined using stereo pairs of images and high-resolution scanned photographs to detect changes in vegetation transition. Successive images were examined to estimate as accurately as possible the year(s) when grasses and low weeds were replaced by woody shrubs and scattered tree saplings. Here I employ stand age as years since land abandonment.

4.2.3 Environmental predictors: soil and vegetation properties

To characterize soil and vegetation properties at each site, I installed a 50 m long linear transect where vegetation and soil samples were analysed. Soil type and edaphic condition were characterized from ten topsoil (0-10 cm depth) samples. To avoid any trampled zone, I sampled soils at approximately 5 m from the central transect line. I used a hand auger and kept sub-samples in separate plastic bags at cool temperatures until taken to the laboratory. After drying at room temperature, sub-samples were sieved through 2mm mesh and bulked to comprise one soil sample per site. Processed samples were sent to a commercial laboratory for analysis following the Commonwealth Scientific and Industrial Research Organization CSIRO protocols (Rayment and Lyons, 2011). For this study, I investigated soil pH (1:5 water), clay content (%), and total content of macronutrients P, N and K.

Woody vegetation characteristics were assessed along the 50 m transects. All stems were identified and measured (diameter at breast height [dbh]) along the transect, with large

individuals (> 10 cm dbh) measured in plots 50 x 10 m and smaller individuals (>2.5 cm and < 10 cm) in plots of 50 x 3 m. Basal area were scaled to per hectare. Leaf-litter cover was also measured to investigate the accumulation of organic matter on the forest floor. Vegetation under different soil conditions may differ in species composition and the amount and composition of leaves shed, which would in turn influence the resource availability and quality for mycorrhizal fungi (Sayer 2006, Posada *et al*. 2012). To quantify leaf-litter cover, I collected the loose organic material on the forest floor from 10 quadrats of 30 cm x 30 cm along each transect. I stored leaves in paper bags until arriving at the laboratory where samples were cleaned from soil attached, larger twigs (>2 cm) and other residues before drying them in an oven at 40˚C for 48 h then weighing (in g). Soil samples for the arbuscular mycorrhizal fungi were collected immediately after litter removal inside the same quadrats.

4.2.4 Arbuscular mycorrhizal fungi survey

Arbuscular mycorrhizal fungal (Glomeromycota) diversity was investigated through the analysis of DNA sequences from soil samples. At 10 m intervals along the 50 m transects, I used a 5 cm diameter stainless steel ring (98.1 cm^3) to sample the 10 cm topsoil layer, where fine-roots are expected to be more abundant (Treseder and Cross 2006); each sub-sample comprised two soil cores (2-3 cm apart) which were bulked to create one sample. Before taking soil cores, leaf-litter was removed. I used a hammer to insert the ring into the soil, aiming for the organic and upper mineral layer. Sub-samples were kept in plastic bags and a cool box until being processed later on the same day. Ethanol (70%) was used to clean all material between samples and a new pair of disposable gloves was used for each sample. A total of 90 soil samples were collected from 18 sites over a six day period from 2nd September 2014.

Sample processing involved cleaning away coarse (>2 mm) stones and roots and then letting samples air-dry in a shady place at a low temperature (<30˚ C). After 24 hours, samples were gently crushed inside the sealed bag and the finer fraction was collected into a new plastic bag with two tablespoons of silica gel wrapped in a clean paper towel envelope. About 20 g of silica-dried sub-samples were posted to the analytical laboratory for DNA extraction and sequencing, where each was analysed separately.

4.2.5 Molecular methods

DNA from soil samples was extracted using a PowerSoil© DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, CA, USA) according to Davison *et al*. (2012). The laboratory BiotaP LLC (Tallinn, Estonia) carried out amplicon library preparation, where multiple-step polymerase chain reaction (PCR) was used to attach GS Titanium Shotgun adaptor sequences for Roche 454 sequencing. Region-specific primers were used to target the 18S rDNA V4 region of arbuscular mycorrhizal fungi. Samples were then sent for sequencing to Microsynth AG (Balgach, Switzerland). The intensity of the amplicon bands on agarose gels were assessed under the UV transilluminator. Two of the 90 samples, failed to yield a clearly detectable amplicon in PCR I and were excluded from the sequencing pool. PCR was carried out in two sequential reactions. The first reaction was a targeted PCR with region specific primers, multiplex identifying barcodes and partial adapters for sequencing. The second PCR reaction was used to complete sequencing adapters. In between sequential reactions, each amplicon was diluted 10-fold. Three µl of stock DNA sample or 10-fold dilution of DNA sample was used in the first PCR and 3 µl of 10-fold dilution of amplicon was used in the second PCR reaction. Amplicons of PCR II were purified using an Agencourt AMPureXP Kit (Beckman Coulter Inc.). The total reaction volume of PCRs was 30 µl, contained primers with 0.2 µM in the final concentrations and Smart-Taq Hot Red 2x PCR Mix (0.1 U/µL Smart Taq Hot Red Thermostable

DNA Polymerase, 4 mM $MgCl_2$, 0.4 mM dATP, 0.4 mM dCTP, 0.4 mM dGTP, 0.4 mM dTTP; Naxo OÜ, Estonia). Samples were eluted in Buffer EB (10 mM Tris-Cl, pH 8.5; QIAGEN Inc.). The DNA concentration of purified amplicons was measured using an Appliskan fluorescence-based microplate reader (Thermo Scientific) and PicoGreen® dsDNA Quantitation Reagent (Quant-iT dsDNA Broad Range Assay Kit, Invitrogen). After measurement of amplicon concentrations, they were equimolarly pooled and repurified with the Agencourt AMPureXP Kit (Beckman Coulter Inc.). Concentration of DNA in the repurified pools was measured in three replicates on a QubitTM fluorometer.

Bioinformatics analysis followed Davison *et al*. (2012) where sequence reads were included in the analysis if they contained the correct forward primer sequence. In this study, 150 885 sequences matched sequences in GenBank. To proceed with taxonomic identification, sequence reads were assigned to virtual taxa (VT) via BLAST against the MaarjAM database (Glomeromycota SSU rRNA gene sequences; Öpik *et al*., 2010). Remaining reads that did not find a match at first BLAST were subjected to a further BLAST search against the International Nucleotide Sequence Database (INSD) non-redundant nucleotide database. In total, 47 347 reads matched 115 VT Glomeromycota in the (INSD). Potential novel VTs were also detected: four *Archaeospora*, two *Paraglomus*, one *Acaulospora* and one *Glomus*. Standard bioinformatics procedures were carried out using Python and Java scripts developed at the Department of Botany, University of Tartu, Estonia (Davison *et al*., 2012).

4.2.6 Data analysis

I tested variation in AMF richness among forest successional categories, environmental predictors and soil types with linear models. Model assumptions were tested with the Global Validation of Linear Models Assumptions (R function 'gvlma'). I used Box-Cox power transformations on the number of AMF taxa to meet the assumptions of linear models (λ= 1.3,

R function 'BoxCoxTrans'). Pearson's Chi-squared tests (X^2) were used to compare the percentage of family richness among forest successional stages and soil types (R functions 'chi.test' and 'chisq.post.hoc'). I used Constrained Analysis of Principal Coordinates (CAP) to analyse changes in AMF community composition according to environmental predictors (R function 'capscale'). AMF community composition (presence-absence) was tested with Permutational ANOVA (PERMANOVA, R function 'adonis' with Bray-Curtis dissimilarities, Anderson 2001). I used Non-Metric Multidimensional Scaling (NMDS) to examine the community composition of both AMF and woody plants in two-dimensional space (R function 'metaNMDS'). Indicator species analysis was performed with *IndVal* function for R (R Development Team [2014]). Pearson's correlation coefficient (*r*) was used to test relationships between predictors.

4.3 Results

4.3.1 AMF taxa distribution

I detected a total of 100 arbuscular mycorrhizal (AMF) virtual taxa (VT) in all secondary and mature forests, from 47 206 DNA sequences. Glomeraceae comprised the dominant family with 58 VTs (Glomus spp.), followed by Acaulosporaceae (8, *Acaulospora* spp.), Archaeosporaceae (5, *Archaeospora* spp.), Gigasporaceae (4, *Scutellospora* spp., 1 *Gigaspora* sp.), Diversisporaceae (3, *Diversispora* spp.), Claroideoglomeraceae (3, *Claroideoglomus* sp.), Paraglomaceae (3, *Paraglomus* spp.) and Ambisporaceae (1, *Ambispora* spp.) (Table S2 in supporting material). Fourteen taxa did not find a match on the MaarjAM database and are listed as operational taxonomic units, but for data analysis and discussion purposes are mentioned as VT or simply "taxa" (Table S2). I found fifteen unique occurrences (single read in single sample) which have been excluded from statistical analysis. Basalt and granite soils had similar numbers of singletons (basalt n=9, granite n=6).

4.3.2 Effects of soil type on number of AMF taxa

Soil types had contrasting soil fertility. Basalt soils were significantly higher in P, N, and clay content in all forest successional stages. However, soil pH showed different patterns (Fig. S3). Basalt soils were less acidic in secondary forests than in mature forests, whereas granite soils showa gradual increase in soil pH from young secondary to mature forests (Fig. S3). Moreover, these soil predictors were inter-correlated. For example, P and N were positively correlated in both soil types (basalt: r=0.89, P=0.001; granite: r=0.86, P=0.003). However, in basalt soils several correlations were unique, including the negative correlations between P and clay (r= -0.89, P= 0.001) and N and pH (r= -0.91, P= 0.001) (Table S3). The relationship of total P with soil pH also varied depending on soil type. In basalt, total P tended to decrease with pH (r= -0.80, P=0.009), while in granite soils the positive trend was not significant (r= 0.57, P= 0.112).

Soil types also differed in terms of patterns of change in AMF taxa richness between successional stages (Table 4; Fig. 12A). While in granite soils AMF species richness tended to be more stable, in basalt there was more variation across successional stages. Yet, I did not find significant differences in richness between soil and forest types nor an interaction between them (Table 4; Fig. 12A). The most remarkable difference between soil types was found in mature forest, where basalt soils tended to have lower numbers of AMF taxa compared with granite, but variation around the mean values was relatively high. With respect to species accumulation, the two soil types presented similar patterns of species rarefaction with number of reads and number of sites (Fig. 12 B-C). The trend line for basalt soil was slightly higher compared with granite, but confidence intervals overlap sufficiently to reject the assumption of differences between soil types. There was a positive significant correlation between AMF richness and number of reads (r=0.75, P=0.021).

Table 4. Linear model analysis comparing mean numbers of arbuscular mycorrhizal fungi (AMF) virtual taxa (VT) between soil types (basalt vs granite) and forest categories - younger secondary forest (<30 years since pasture abandonment), older secondary forests (>31 years) and mature forest (uncleared) in North Queensland, Australia. Power transformation (Box Cox) was applied to numbers of taxa.

Source of variation	Estimate (±SD)	t-value	P-value
Forest category (F)	-2.5 (3.1)	-0.81	0.4333
Soil type (S)	-9.3 (9.5)	-0.98	0.3445
F × S	5.6 (4.4)	1.28	0.2217
Residual Error	7.6 (*df*= 14)		

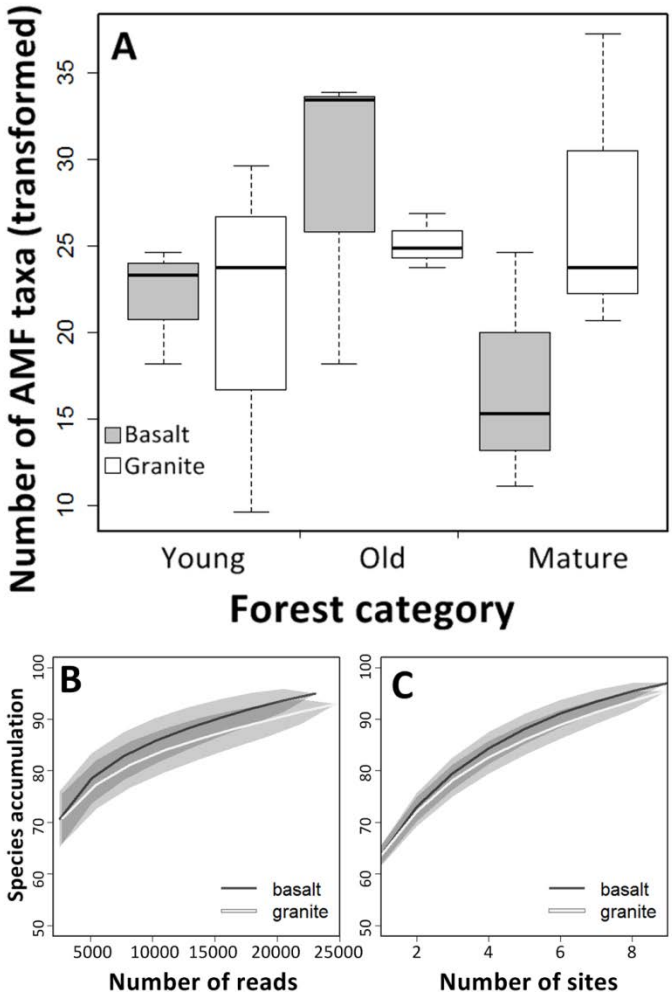

Figure 12. Mean numbers of virtual taxa of arbuscular mycorrhizal (AM) fungi in forest categories: young secondary forest (<30 years since pasture abandonment), old secondary forest (>31 years) and mature forest (never cleared). Species (virtual taxa) rarefaction curves according to B: number of DNA sequence reads and C: number of forest sites in two soil types (basalt and granite) in North Queensland, Australia.

Family richness also changed with forest and soil type (Table 5). Five out of six families varied significantly between soil types and forest categories, whereas Acaulosporaceae only differed between soil types. Higher percentages of taxa occurred in basalt soils in Archaeosporaceae, Claroideoglomeraceae, Diversisporacea and Paraglomeraceae (Table 5), contrasting with Gigasporaceae, a family with more taxa occurring in granite soils. In 53% of the cases, differences in family richness were significant between secondary forests (young and old) and mature forest. Only in Diversisporaceae and Gigasporaceae did there seem to be

differences in family richness between young and old secondary forest. The richest family Glomeraceae did not differ significantly between soil or forest types. Similarly, percentages of novel taxa did not differ among soil or forest types (Table 5). Ambisporaceae had only one taxon, in old secondary forest in granite, therefore it could not be included in the analysis.

Table 5. Comparison of each family of arbuscular mycorrhizal fungi across secondary and mature forests in two soil types. Values correspond to frequency of taxa in each case (percentage), total number of taxa in each family and Pearson's Chi quare tests. Bonferroni's correction for multiple comparisons was applied. Significance at *alpha*= 0.006 (in bold). B= basalt, G= granite, Y= young secondary forest, O= old secondary forest, M= mature rainforest, na= not applicable.

Family	Basalt			Granite			Total *N*	Chi square test (*df*=2)		Significant pair comparisons
	Young	Old	Mature	Young	Old	Mature		X^2	*P*-value	
Acaulosporaceae	50.0	58.3	37.5	25.0	29.2	50.0	8	13.2	**0.0013**	B-G
Archaeosporaceae	20.0	46.7	20.0	0	13.3	46.7	5	45.9	**<0.0001**	B-G; Y-M; O-M
Claroideoglomeraceae	33.3	77.8	44.4	0	11.1	33.3	3	33.5	**<0.0001**	B-G; Y-M; O-M
Diversisporaceae	22.2	44.4	44.4	22.2	0	55.6	3	41.1	**<0.0001**	B-G; Y-O; O-M
Gigasporaceae	60.0	40.0	33.3	26.7	66.7	66.7	5	38.4	**<0.0001**	B-G; Y-O; Y-M
Glomeraceae	37.9	35.6	24.7	30.5	36.8	43.1	58	5.1	0.0774	na
Paraglomeraceae	55.6	33.3	11.1	0	0	11.1	3	49.4	**<0.0001**	B-G; Y-M; O-M
Novel taxa	14.3	16.7	14.3	11.9	19.0	33.3	14	4.8	0.0891	na

4.3.3 AMF community composition

The composition of the fungal community changed with forest category and soil type (Table 6). I found significant differences in the community composition with respect to forest age, soil type and a significant interaction between these factors (Table 6). Basalt and granite shared more than half of the taxa (71 out of 100), with four species of *Glomus* being the dominant taxa in both soil types and recorded in all 18 sites. Indicator species analysis suggested that two taxa were significantly associated with basalt (*Paraglomus* sp1 [*IndVal*=0.82; P=0.008] and *Claroideoglomus* sp2. [*IndVal*=0.7582; *P*=0.026]), whereas two other species were indicative of granite soils (*Glomus* sp9 [*IndVal*=0.83; *P*=0.031] and *Glomus* sp11. [*IndVal*=0.75; *P*=0.023]). The distribution of species in ordination space showed that the greatest variation in AMF families occurred along the first axis, which was positively correlated with forest successional stage (*r*=0.77; *P* <0.0001; Fig. 13A). Constrained ordination analysis with AMF communities in the two soil types and environmental predictors showed that both soil and vegetation properties may be influencing AMF species distribution. Above- and below-ground predictors explained 77% (first ordination axis) and 51% (second ordination axis; Fig. 13B) of variation in each axis.

Table 6. Effects of forest category (young secondary forest <30 years since pasture abandonment, old secondary forests >31 years, mature uncleared forest) and soil types (basalt and granite) on arbuscular mycorrhizal fungi community composition (Permutational ANOVA) in North Queensland, Australia.

Source of variation	df	SS	*F*-value	P-value
Forest category (A)	2	0.70	2.79	**0.001**
Soil type (S)	1	0.31	2.47	**0.005**
F * S	2	0.48	1.92	**0.023**
Residuals	12	1.49		
Total	17	2.97		

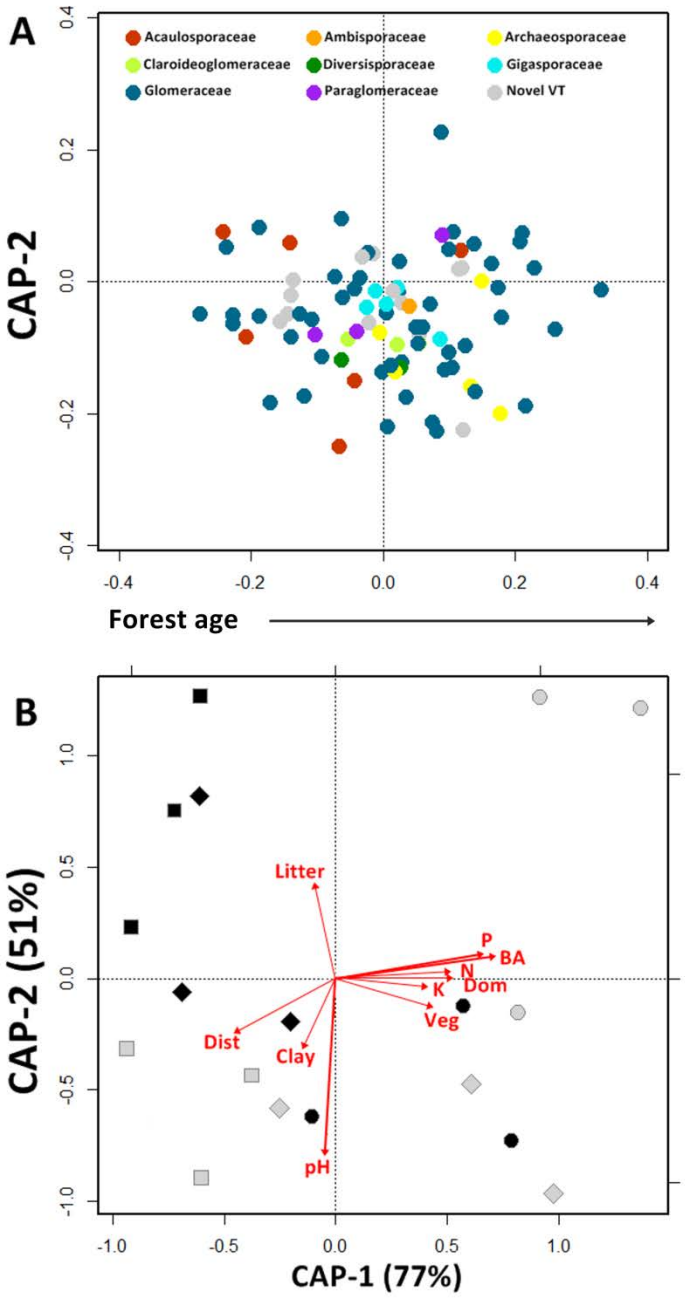

Figure 13. Distribution of the community of arbuscular mycorrhizal (AM) fungi (presence-absence) from secondary and mature forest site in the two main constrained axes from CAP (Constrained Analysis of Principal Coordinates). (**A**) AMF taxa are colored according to taxonomic family. (**B**) Distribution of study sites in AMF species space. Arrows indicate the direction of change in distance from forest fragment (Dist), clay content, soil pH, soil nutrients (total N, P and K), leaf-litter mass, number of woody species (Veg), woody species dominance (Dom) and basal area (BA) of woody stems >2.5 cm dbh in soil types in North Queensland, Australia. Sites on basalt soil are in gray and granite in black. Different shapes represent successional stages: squares = young secondary forest (<30 years), diamonds= old secondary forest (>31 years) and circles = mature forest.

4.3.4 Soil and vegetation predictor of number of AMF taxa

Stepwise model selection indicated that soil pH, basal area and tP were important in predicting AMF community variation (*P*=0.01; *P*=0.01; *P*=0.02, respectively). Individually, only soil pH was a significant predictor of numbers of AMF taxa in both soil types (Adjusted R^2= 0.45, *P*= 0.01, Fig. 14A), even though other soil predictors (*i.e.* P and N) had significant effects on numbers of AMF taxa in multivariate models. The strength of the relationship differed, being stronger in basalt (Adjusted R^2= 0.57, *P*= 0.01) than granite (Adjusted R^2= 0.36, *P*= 0.05). When I analysed the interactions between predictors and soil types other patterns were revealed. I found significant interactions of number of AMF taxa with total P, total N and clay content (Fig. 14 C, D and E). However, the strength of such relationships is generally weak. Only in basalt soil, the relationship was negative (Adjusted R^2= 0.35, *P*=0.05, Fig. 14D), with number of taxa of AMF significantly decreasing with increasing N concentration. Numbers of AMF taxa did not show any significant changes with tree basal area, woody species dominance and richness, soil K or leaf-litter cover (Fig. 14 B, F, G, H and I).

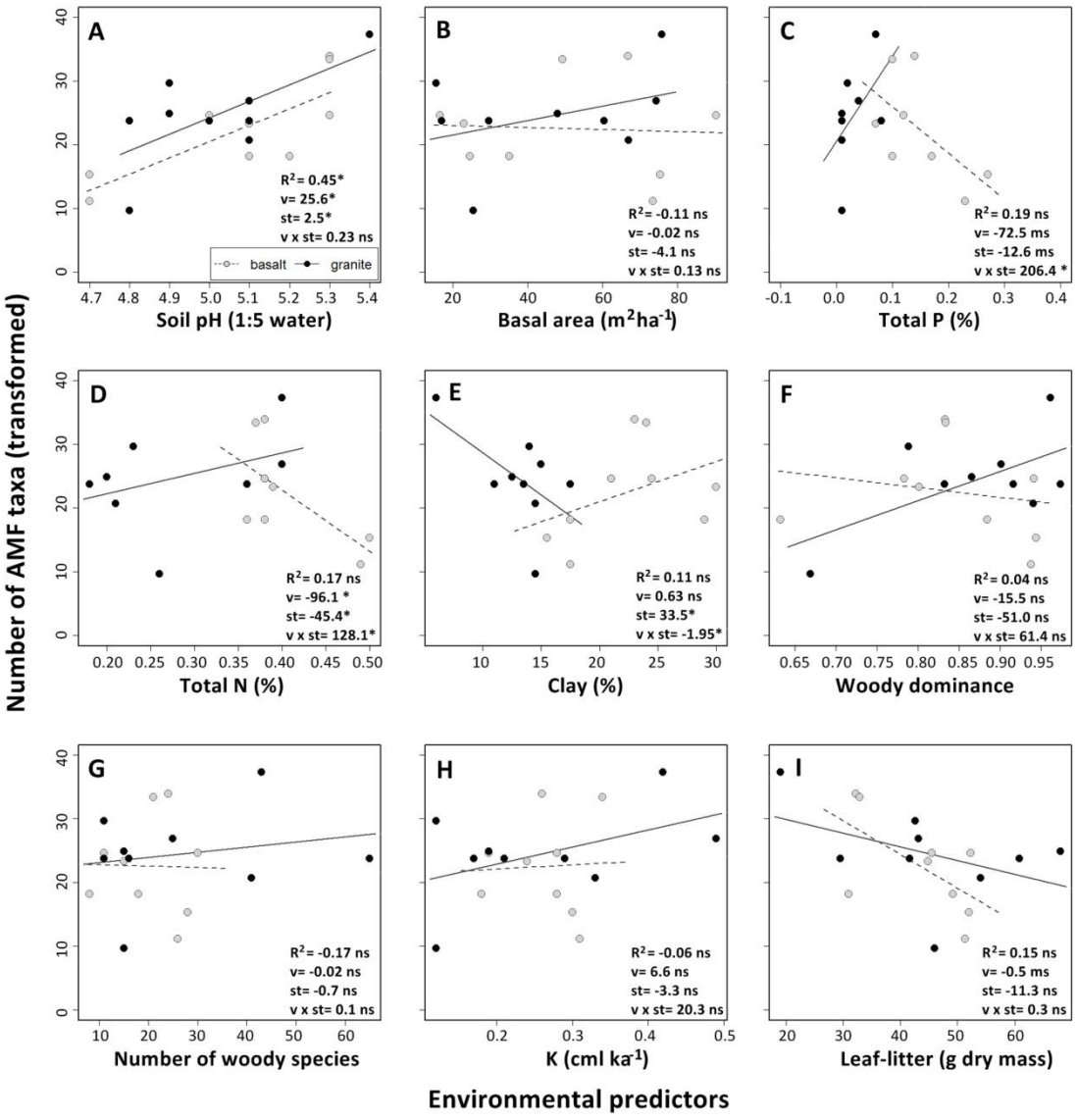

Figure 14. Patterns of arbuscular mycorrhizal fungi (AMF) virtual taxa (VT) richness change according to environmental predictors in two soil types in North Queensland, Australia. R^2 represents the fitness of the full model; '*v*' indicates the regression estimate and significance of the environmental predictor of the linear model in question; '*st*' indicates the estimate and significance of soil type; '*v x st*' indicates the estimates and significance of the interaction between environmental predictor and soil type. * P<0.05, ms= marginally significant (P<0.07), ns=not significant at α=0.05.

I was also interested in the associations between AMF and woody plant communities of secondary and mature forest. To explore these associations I used separate ordination analysis and compared the proximity of sites based on AMF and woody plant composition (Fig 15). This is an attempt to detect whether the distribution of sites in the two-dimensional

ordination space based in AMF and plants overlap in the two soil types. If the pairs of AMF and woody plant communities are consistently close together (shorter distance between pairs) I would assume that communities that are more similar in terms of plant community are also more similar in their fungi community. Shorter distances between AMF-plant community pairs, presented by the size of the line connecting them, would indicate that plant communities are good predictors of AMF communities. The question here was whether these relationships between AMF and woody plant communities are similar in soil types with contrasting properties.

The analysis revealed that AMF and woody plant communities occurred in closer proximity on basalt than granite, as indicated by the shorter lines that connect the same site as pairs (Fig 15). Moreover, on basalt soil, the distribution of pairs of AMF and woody plant communities showed a clearer structure in relation to the order of successional stage compared with granite. For instance, young secondary forest sites tended to occur more toward the negative end of NMDS1, whereas mature forest sites occurred clustered at the positive end of the same gradient (Fig 15). In granite, the woody plant communities of mature forests are more distant from secondary forests compared with basalt and differences between young and old successional stages are not clearly defined in the ordination space (Fig 15). The shorter connections between pairs of AMF and woody plant communities in basalt may indicate that woody plant community composition is a good predictor of AMF composition, while in granite other factor may be affecting the structuring of AMF communities.

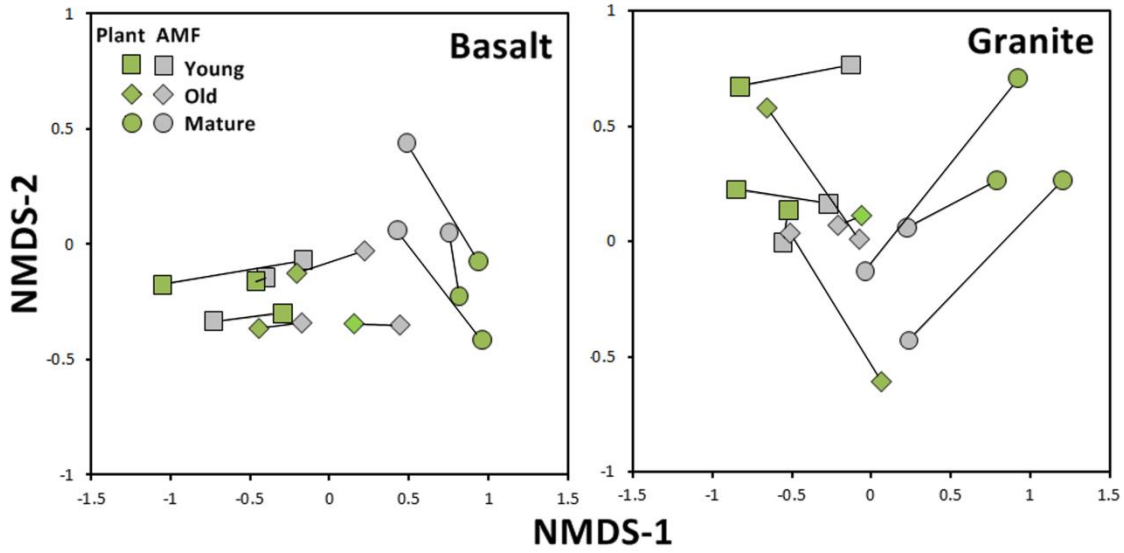

Figure 15. Non-metric multidimensional scaling (NMDS, *k*=2) ordination plot showing similarity (distances between points) in basalt and granite soils. Symbols that are closer together have greater similarity in community composition. Lines between symbols connect the paired arbuscular mycorrhizal fungi (AMF) and woody plant communities at each site (young secondary forests were <30 years since pasture abandonment, old secondary forests were >31 years and mature forests were never cleared).

4.4 Discussion

Along a chronosequence of secondary forest in tropical Australia, I explored the effects of soil type and forest recovery on the composition of arbuscular mycorrhizal communities. Arbuscular mycorrhizal fungi are known to be ubiquitous and widespread, yet it was unexpected that this relatively small study would record approximately one-fourth of all known taxa globally (Davison *et al*. 2015). Apart from recording known and unknown AMF taxa in these forests, my predictions were partially met as I found a higher number of AMF taxa in mature forests on the less fertile soil. Despite differences in AMF community composition between forest successional categories and soil types, the number of taxa of AMF seemed to be more variable in secondary forests. Moreover, soil pH was positively associated with AMF richness and a predictor of AMF community changes in basalt and granite. Total P was also a good predictor of AMF richness, but with differences in the direction of the effect depending

on the soil type. With this information, I attempted to expand the knowledge on the AMF ecology and secondary forest succession.

4.4.1 AMF diversity during rainforest succession in two soil types

To my knowledge, this is the first time that interactions between AMF richness with soil types have been tested in tropical rainforest succession. These results partially support the prediction that less fertile soils would contain higher AMF richness (Janos 1980). However, I found that differences in arbuscular mycorrhizal communities between soil types were more pronounced when forests reached their mature phase. Mature forests on nutrient-poor granites supported higher taxa richness compared with mature forests on the nutrient-rich basalts. In my results, AMF richness in mature forest growing on nutrient-rich soils appeared to be lower than in older secondary forests on the same soil type. Similarly, observations from the Western Amazon also showed that mature forests on richer soils tended to contain lower AMF diversity than secondary forests (Stürmer and Siqueira 2011). Moreover, in my study, I found differences in AMF communities between soil types, even though endemism and host specificity are not common within arbuscular mycorrhizal fungi (Brundrett 2004, Davison *et al*. 2015) with the majority of taxa being found across most ecosystems.

Arbuscular mycorrhizal fungi are known to be ubiquitous and widespread, yet it was unexpected that this relatively small study would record approximately one-fourth of all known taxa globally (Davidson *et al*. 2015). I recorded 100 taxa including 14 novel taxa and a relatively high number of taxa from the more basal groups, such as Archaeosporaceae and Paraglomeraceae (Davison *et al*. 2015). Interestingly, even though plant community structure tends to present similar patterns of changes, plant composition of these successional forests may differ between soil types and be closely associated with AMF communities. For instance, the presence of a relatively high proportion of basal fungal groups could be explained by the

evidence that Australian tropical rainforests hold an ancient flora, with 16 near-basal angiosperm plant families found in the Wet Tropics of Australia (Metcalfe and Ford 2009). The long isolation of the continent may have affected not only the flora but also the mutualistic fungi that evolved alongside the plants. Associations between phylogenetic traits of these plant and mycorrhizal fungi communities remain to be investigated.

4.4.2 AMF community and soil fertility gradients

Similar to findings from my study, soil pH has been shown to affect availability of nutrients, but also to directly affect AMF activity (Porter *et al*. 1987, Clark 1997). For instance, a greenhouse experiment demonstrated that the expansion of mycelium of two AMF species through the soil was greater at a higher soil pH of 7 than a more acid pH of 5 (van Aarle *et al*. 2002). Lower soil pH inhibited mycelium growth and spore production in the two AMF species tested (van Aarle *et al*. 2002), which may explain the positive relationships between pH and AMF richness for both soil types observed in my study. Nonetheless, it is considered likely that certain AMF species would be more tolerant to acid soils than others, and consequently, more effective in obtaining nutrients (Clark 1997).

Interestingly, there is some evidence for the link between mycorrhiza and tree communities being negatively affected by acid soils. A field study by Coughlan *et al*. (2000) found that a reduction in AMF diversity and spore production in sugar maple (*Acer saccharum*) forests was linked to soil acidification caused by natural and anthropogenic stresses. The authors found a connection between declines in fungal spore production and growth to the decline in sugar maple populations (Coughlan *et al*. 2000). In my study, the similar response of AMF richness to pH in both types indicates the potential of soil acidity in predicting AMF diversity. Globally, the consequence of soil acidification for the AMF and plant populations and therefore tropical rainforest regeneration is still unknown (Clark 1997, van Aarle *et al*.

2000). Further experiments on the interactions between plant and fungal communities at different successional stages would provide new insights on the mechanisms that control or contribute to the pathways of forest regeneration.

In my study, soil P and N appear to vary independently from soil pH. Phosphorus and nitrogen are commonly limiting in secondary and mature tropical forests (Vitousek *et al*. 2010, Davidson *et al*. 2004). P and N content seem to be stronger predictors of changes in community composition, than predictors of AMF richness as expected *a priori*. Diversity of AMF results in a variety of strategies to uptake P and N, and therefore AMF diversity is vital for the maintenance of plant productivity, especially in poorer soils (Bolan 1991, George *et al*. 1995, Smith *et al*. 2011). Perhaps, not the numbers of taxa, but their functional characteristics are more important in this context. Nonetheless, the relationship between P and N content and AMF communities is slightly more complex than relationships with soil pH, because the response soil types can generate opposite patterns of change across forest successional stages.

Contrary to my expectation, I found that, in granite soil, an increase in the percentage of soil N was concurrent with an increase in the number of AMF taxa. I anticipated that AMF richness would decrease with soil fertility due to lower demand by trees for assistance with nutrient uptake. When plants no longer benefit through mycorrhizal associations increasing the uptake of nutrients, root colonization by fungi can become detrimental to the plants as they supply photosynthetic C but receive nothing in return (Jeffries *et al*. 2003, van Geel *et al*. 2015). In the case of substrates with very low concentrations of N such as granite soils, the increase in AMF richness with soil fertility could be indicative of a minimum soil condition required to support AMF diversity. If AMF richness distribution is analysed along the N gradient I found that at an intermediate fertility AMF richness is higher. Similar findings were also observed in apple orchards, where moderated P fertilization preserved higher AMF diversity (van Geel *et al*. 2015). I believe that experimental manipulations and more

information on other forest mycorrhizal groups (i.e ectomycorrhizal species) would help in clarifying the patterns seen here.

4.4.3 AMF and vegetation recovery

The legacy of past land-use is claimed to have a long-term effect on soil properties and vegetation recovery (Dwyer *et al*. 2010). The soils studied here have historically been used as pastures in my study area. However, it is possible that fertilizers or lime could have been applied but unfortunately I could not obtain that information from each site to consider in the analysis. Nonetheless, I found that soil P and N increase with forest succession and remain consistently different along successional stages. These successional changes in soil condition were shown to be related to AMF community structure, with richness and composition varying along the soil gradients. Even though there was a transition in plant communities, vegetation parameters appeared to be less influential on the structuring of AMF communities than soil properties. Interestingly, some authors argue that it is the diversity of mycorrhizal fungi which control plant diversity and not the opposite (van der Heijden *et al*. 1998, Kernaghan 2005). In a review of the literature, Kernaghan points out the reciprocal nature of the mycorrhizal fungi and plant relationship which makes it difficult to separate cause and effect.

It is expected that diversification of mutualists would increase plant performance (through higher productivity and resistance to pathogens) and promote plant diversification (Bever 2002, Maherali and Klironomos 2007; van de Heijden *et al*. 1998). My data do not provide support for the prediction that AMF diversity and woody species richness and basal area are positively associated. However, comparing plant community characteristics with the current AMF diversity may not be appropriate as there should be a lag between growth and outcome. Hence, predictions of AMF richness based on woody species community structure (or vice versa) should be taken with care. Facultative associations, mycorrhizae type, stand age

and seed limitation, for example, could be more important in determining plant community variation in successional forests (Allen *et al*. 1995, Abbott and Robson 1991, Brundrett 2004, Allen *et al*. 2003).

Interestingly, the strength of association between AMF and woody plant communities depends on the soil type. I found that in more fertile soil (basalt), plant communities that are more similar tend to also have more similar AMF communities. In contrast, in poorer soils, plant communities that are more similar do not necessarily present similar AMF composition. These patterns could be evidence that basalt soil is a more homogeneous system and may also to be more resistant to disturbance. Association between fungi and plants may be even more predictable in basalt soils. Conversely, granite soils would be more dynamic or even more susceptible to disturbance, which would generate more variation in substrate condition and subsequently in fungal and plant communities (Connell 1978, Jeffries *et al*. 2003). Successional trajectories in granite soils appear to be more unpredictable in the long term (Cramer *et al*. 2008). The ecological mechanisms behind these differentiations between soil types and other factors that might be contributing to these patterns need to be elucidated in future research.

In terms of plant composition, secondary forests on basalt and granite present some distinctions that could be influencing the composition of AMF community. As shown in Chapter 3 (this thesis) sites on basalt and granite are both dominated by *Guioa lasioneura* (Sapindaceae). *Rhodomyrtus pervagata* (Myrtaceae) dominated in secondary forests only in granite, while on basalt, *Rhodamnia sessiliflora* (Myrtaceae) was relatively more dominant in young secondary forest. In mature forests, Lauraceae such as *Litsea leefeana* and *Beilschmiedia tooram* dominated in basalt and granite respectively. Whether these communities' arrangements are directly and strongly associated with the AMF community, need further analysis.

Soils have long been thought of as one of the last science frontiers, with respect to their biological communities and interactions in ecosystem functions. New technologies such

as those used here have provided us with opportunities to study these communities in the form of species identification but this approach is limited to a species list only and lacks important information on community structure with respect to species abundance, interactions and its implications for a broader function. Hence, while I have gathered information on the presence and absence of AMF taxa, with respect to AMF communities I am limited in the ability to extrapolate these findings to wider community interactions and functions.

4.5 Conclusion

The variation in AMF communities associated with soil properties in my study may indicate the role of environmental filters, particularly soil acidity and P and N content, on secondary forest succession. The secondary forests in both soil types contained a relatively high AMF richness indicating that AMF inoculants are available and should not be a limitation to seedling establishment and adult tree growth in the early stages of succession (Picone 2000, Zangaro *et al*. 2013). However, the AMF community composition of old secondary forests was still very distinct from that of mature forest. These results suggest that there is still an ecological gap between these two forest categories. The finding that mature forests hold not only more "species" in granite but also a greater number of families, including basal phylogenetic groups (Davison *et al*. 2015), suggests that secondary forests have not fully recovered.

4.6 Supporting material

Table S2. Arbuscular mycorrhizal fungi virtual taxa (VT) recorded in secondary (young and old) and mature forests in two soil types in North Queensland, Australia. ID= morphotypes based on MaarjAM database assignments: Acau= *Acaulospora*, Ambi= *Ambisporaceae*, Archae= *Archaeospora*, Cloroi= *Cloroideospora*, Divers= *Diversispora*, Glom= *Glomus*, Paraglom= *Paraglomeraceae*, Scut= *Scutellospora*, OTU= operational taxonomic unit that did find match in the database. **R**= total DNA sequence reads, *n*= number of sites taxon was present.

VT	ID	Basalt						Granite						Total reads
		Y		O		M		Y		O		M		
		R	*n*	R	*n*	R	*n*	R	*n*	R	*n*	R	*n*	
VT 372	Glom1	1090	3	1974	3	1004	3	142	3	859	3	1544	3	6628
VT 213	Glom3	62	3	1508	3	1772	3	215	3	812	3	1574	3	5958
VT 191	Glom2	1036	3	430	3	805	3	1282	3	1029	3	787	3	5384
VT 80	Glom4	1473	3	331	3	10	3	321	3	1011	3	474	3	3635
VT 24	Acau2	75	3	456	3	157	3	73	2	363	2	381	3	1518
MO-G77	ni1	659	3	3	2	3	1	771	3	54	3	10	2	1513
VT 166	Glom5	184	3	162	3	49	2	811	2	42	3	246	3	1508
VT 410	Glom13	0	0	639	2	385	3	0	0	0	0	382	2	1410
VT 360	Glom7	357	3	26	3	0	0	190	2	536	2	80	1	1200
VT 124	Glom12	3	1	413	2	148	3	6	2	380	2	202	3	1162
VT 361	Glom9	191	3	6	1	0	0	653	3	284	3	18	3	1165
VT 364	Glom14	1	1	196	0	148	2	0	0	0	0	636	2	984
VT 70	Glom11	0	0	0	0	0	0	433	2	355	2	109	1	902
VT 231	Acau1	93	2	20	3	0	0	316	3	306	3	89	1	836
VT 327	Glom8	294	3	0	1	0	0	224	2	298	3	1	1	827
VT 52	Scutello1	163	3	10	3	34	2	215	2	139	3	180	3	755
VT 253	Glom15	23	1	6	1	3	2	433	2	180	3	28	2	682
VT 227	Acau4	336	2	195	3	28	2	13	2	18	1	7	2	607
VT 181	Glom10	283	3	13	2	2	1	190	2	21	3	16	3	538
VT 318	Scutello2	208	3	21	2	24	1	134	1	75	3	49	3	523
VT 108	Glom21	0	0	158	1	0	0	1	1	152	1	162	2	478
VT 96	Glom18	316	3	58	3	2	1	15	2	27	2	13	3	444
VT 322	Glom6	53	2	1	1	0	0	291	2	66	3	12	3	434
VT 399	Glom19	14	1	0	1	1	1	117	3	92	3	194	1	427
VT 126	Glom17	2	2	9	0	0	0	317	1	45	3	9	1	389
VT 92	Glom23	12	2	102	3	64	2	0	0	57	3	126	3	372
VT 57	Cloroi1	74	1	155	3	19	2	0	0	23	1	55	3	334
VT 122	Glom28	0	0	155	1	0	0	0	0	0	0	151	1	308
VT 64	Glom30	0	0	150	0	0	0	0	0	0	0	150	1	301
MO-G63	ni3	0	0	0	0	0	0	207	1	84	2	0	0	294
MO-Ar6	ni4	0	0	68	0	0	0	0	0	109	1	105	3	286
VT 222	Glom22	24	1	158	2	0	0	0	0	29	1	48	2	265
VT 295	Glom26	0	0	59	0	0	0	1	1	117	1	59	1	239
MO-G74	ni2	0	0	0	0	4	2	40	1	180	1	0	0	226
VT 60	Diversi1	0	0	110	2	6	2	1	1	0	0	82	2	204

VT	ID	Basalt						Granite						Total reads
		Y		O		M		Y		O		M		
		R	*n*	R	*n*	R	*n*	R	*n*	R	*n*	R	*n*	
VT 69	Glom25	0	0	187	2	0	0	0	0	0	0	8	2	199
VT 239	Paraglom1	9	2	175	3	3	1	0	0	0	0	0	0	192
VT 380	Diversi2	0	0	89	1	4	2	2	1	0	0	83	1	181
VT 312	Glom24	61	3	7	1	15	1	4	1	77	2	8	2	181
VT 73	Glom27	0	0	7	0	156	2	0	0	0	0	4	1	168
VT 4	Archae1	11	1	18	3	19	1	0	0	46	2	69	3	172
VT 315	Glom32	0	0	97	2	27	2	0	0	0	0	35	1	162
VT 49	Scutello3	18	2	2	0	65	2	0	0	27	2	16	2	134
VT 85	Glom33	105	2	0	0	0	0	6	1	0	0	0	0	114
MO-P6	ni7	0	0	90	1	0	0	0	0	0	0	10	1	102
VT 256	Glom34	1	1	0	0	0	0	97	1	0	0	0	0	100
VT 28	Acau3	87	3	1	1	1	1	7	2	0	0	0	0	102
VT 89	Glom16	0	0	0	1	0	0	93	3	1	1	0	0	99
VT 125	Glom29	5	1	41	2	0	0	0	0	28	1	15	1	94
VT 26	Acau6	0	0	12	1	1	1	0	0	61	1	12	1	89
VT 178	Glom31	37	3	0	1	0	0	45	2	2	1	2	1	94
VT 186	Glom35	8	2	0	0	1	1	28	1	0	0	38	3	81
VT 112	Glom36	0	0	1	1	2	1	0	0	71	1	1	1	78
VT 111	Glom37	11	1	1	1	0	0	0	0	48	1	15	3	81
VT 342	Glom38	0	0	64	1	1	1	2	1	4	1	1	1	76
VT 328	Acau7	71	2	0	1	0	0	0	0	0	0	0	0	74
VT 39	Gigas1	44	1	0	0	0	0	0	0	22	1	0	0	68
VT 338	Archae2	0	0	32	0	0	0	0	0	0	0	32	1	65
MO-P7	ni6	0	0	60	2	0	0	0	0	0	0	1	1	64
VT 403	Glom41	0	0	23	0	2	1	0	0	12	1	23	1	62
VT 103	Glom20	0	0	0	0	2	1	0	0	53	1	0	0	56
MO-Ar8	ni8	0	0	1	0	0	0	0	0	0	0	50	2	53
VT 113	Glom39	3	1	21	3	1	1	0	0	2	1	20	1	53
VT 268	Glom40	42	1	0	1	0	0	0	0	0	0	0	0	44
LH-Gl01	ni11	0	0	18	1	18	1	0	0	0	0	1	1	39
MO-Ar7	ni9	0	0	0	0	0	0	0	0	0	0	37	1	38
VT 56	Cloroi2	0	0	26	3	10	2	0	0	0	0	0	0	39
VT 255	Scutello4	0	0	2	1	0	0	22	1	2	1	5	2	36
VT 153	Glom43	1	1	19	1	0	0	1	1	1	1	8	1	35
VT 9	Archae3	2	1	24	1	0	0	0	0	0	0	0	0	28
MO-Ac11	ni10	2	1	0	0	0	0	24	1	0	0	0	0	28
VT 53	Glom42	24	2	0	0	0	0	1	1	0	0	0	0	28
VT 15	Acau5	1	1	10	2	0	0	0	0	0	0	13	2	29
MO-G78	ni5	24	2	0	0	0	0	0	0	0	0	0	0	26
VT 30	Acau8	0	0	5	0	10	2	0	0	0	0	8	3	26
VT 155	Glom44	0	0	22	1	0	0	1	1	0	0	0	0	25
VT 245	Archae4	0	0	20	1	1	1	0	0	0	0	0	0	22
VT 310	Glom45	0	0	2	0	0	0	0	0	0	0	18	1	21
VT 5	Archae5	3	1	8	2	3	1	0	0	0	0	5	3	25
VT 61	Diversi3	6	2	7	1	0	0	0	0	0	0	5	2	23
VT 398	Glom46	0	0	0	0	0	0	17	1	0	0	1	1	20
VT 193	Cloroi3	11	2	6	1	0	0	0	0	0	0	0	0	20
VT 281	Paraglom2	3	1	0	0	0	0	0	0	0	0	13	1	18
VT 93	Glom48	9	2	3	0	0	0	0	0	0	0	3	1	18

VT	ID	Basalt						Granite						Total reads
		Y		O		M		Y		O		M		
		R	*n*	R	*n*	R	*n*	R	*n*	R	*n*	R	*n*	
VT 219	Glom47	12	1	1	1	0	0	0	0	0	0	1	1	17
MO-Ac13	ni13	0	0	1	0	1	1	0	0	1	1	11	2	17
MO-Ar9	ni14	0	0	9	1	3	1	0	0	0	0	0	0	13
VT 214	Glom49	10	1	0	0	0	0	0	0	0	0	0	0	11
VT 238	Paraglom3	10	2	0	0	0	0	0	0	0	0	0	0	12
MO-G64	ni15	0	0	4	0	0	0	0	0	0	0	4	1	9
VT 270	Glom51	0	0	0	0	6	1	0	0	0	0	0	0	6
VT 415	Glom55	0	0	3	0	0	0	0	0	0	0	3	1	7
VT 283	Ambi1	0	0	0	0	0	0	0	0	4	1	0	0	5
VT 105	Glom53	0	0	0	0	0	0	0	0	4	1	0	0	5
VT 167	Glom52	2	2	0	1	0	0	1	1	0	0	0	0	7
VT 54	Diversi4	0	0	1	0	0	0	0	0	0	0	1	1	3
VT 263	Diversi6	0	0	1	0	0	0	0	0	0	0	1	1	3
VT 248	Glom54	1	1	0	0	0	0	0	0	1	1	0	0	4
VT 280	Glom58	0	0	0	0	2	2	0	0	0	0	0	0	2
VT 196	Glom59	0	0	0	0	0	0	2	1	0	0	0	0	3
Total	100	7660	56	8713	60	5022	45	7765	44	8210	50	8560	71	46442

Table S3. Paired correlations between environmental predictors used to explain variations in AMF richness and community composition in two soil types (basalt and granite) in North Queensland, Australia. Pearson correlation coefficients are shown in the shaded area in each correlation matrix and P-values for each comparison are shown in the upper half (non-shaded area) of each matrix. Variables are: clay content, soil pH, soil nutrients (total N, P and K), leaf-litter mass, number of woody species (Veg), basal area of woody stems >2.5 dbh (BA) and woody species dominance (Dom).

All sites	Clay	pH	N	P	K	Litter	Veg	BA	Dom
Clay		0.286	0.135	0.229	0.485	0.66	0.262	0.495	**0.041**
pH	0.27		0.743	0.561	0.189	**0.007**	0.831	0.904	0.769
N	0.37	0.08		**0.000**	**0.028**	0.177	0.319	**0.036**	0.401
P	0.3	-0.15	0.85		0.322	0.821	0.661	0.115	0.331
K	-0.18	0.32	0.52	0.25		0.172	**0.017**	**0.001**	**0.004**
Litter	-0.11	-0.61	-0.33	-0.06	-0.34		0.137	0.464	0.966
Veg	-0.28	0.05	0.25	0.11	0.55	-0.36		**0.004**	**0.002**
BA	-0.17	-0.03	0.5	0.38	0.71	-0.18	0.65		**0.006**
Simp	-0.49	-0.07	0.21	0.24	0.64	0.01	0.68	0.62	
Basalt									
Clay		0.054	**0.045**	**0.001**	0.074	0.114	**0.033**	0.137	**0.006**
pH	0.66		**0.001**	**0.009**	0.257	0.076	0.098	0.124	0.057
N	-0.68	-0.91		**0.001**	0.233	0.091	0.125	0.183	0.073
P	-0.89	-0.8	0.89		0.232	0.124	0.111	0.176	0.062
K	-0.62	-0.42	0.44	0.44		0.792	**0.014**	0.115	**0.017**
Litter	-0.56	-0.62	0.6	0.55	0.1		0.535	0.992	0.09
Veg	-0.71	-0.59	0.55	0.57	0.78	0.24		**0.001**	**0.001**
BA	-0.54	-0.55	0.49	0.49	0.56	0	0.89		0.065
Dom	-0.82	-0.65	0.62	0.64	0.76	0.6	0.89	0.64	
Granite									
Clay		0.065	0.815	0.823	0.606	0.398	0.692	0.781	0.604
pH	-0.64		0.104	0.112	**0.014**	**0.045**	0.202	0.058	**0.026**
N	-0.09	0.58		**0.003**	**0.018**	**0.023**	0.083	**0.030**	0.34
P	-0.09	0.57	0.86		0.100	**0.008**	**0.008**	0.080	0.105
K	-0.2	0.78	0.76	0.58		0.227	0.130	**0.001**	**0.039**
Litter	0.32	-0.68	-0.74	-0.81	-0.45		0.123	0.410	0.332
Veg	0.15	0.47	0.61	0.81	0.54	-0.55		**0.032**	**0.049**
BA	-0.11	0.65	0.72	0.61	0.89	-0.31	0.71		0.056
Dom	-0.2	0.73	0.36	0.57	0.69	-0.37	0.67	0.65	

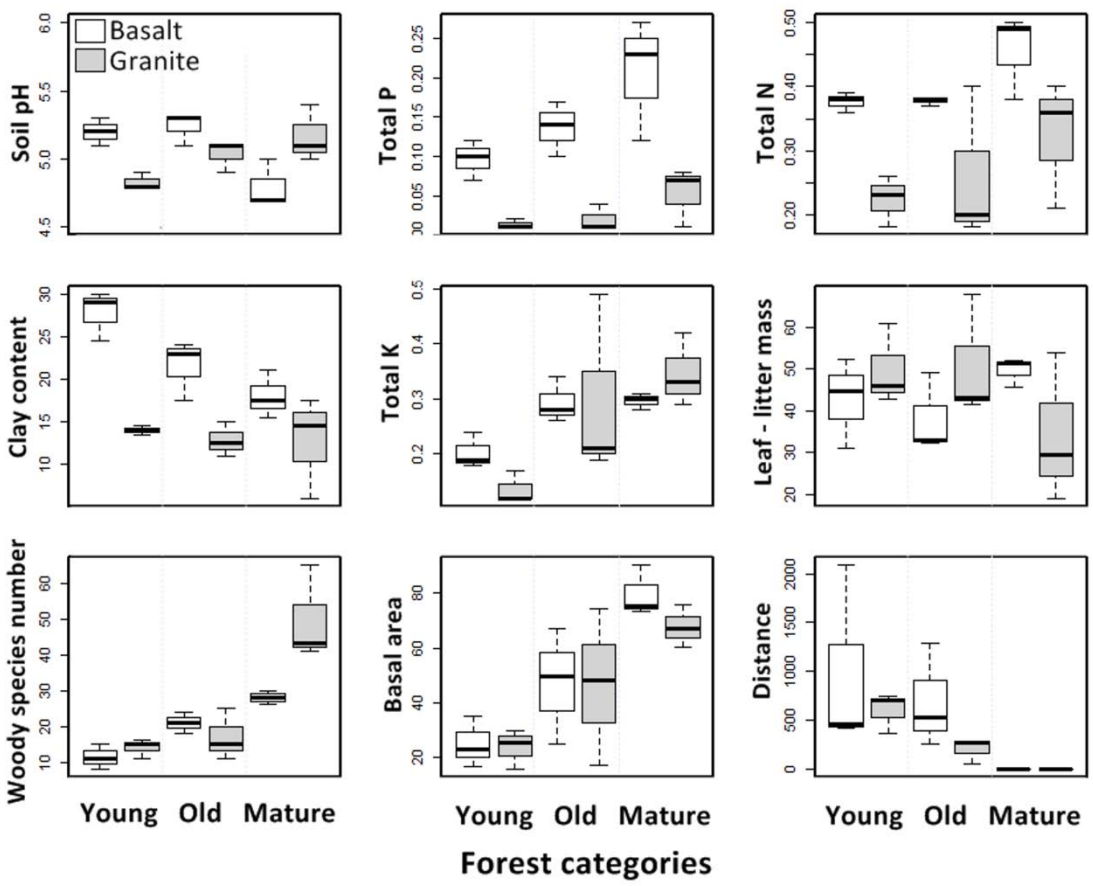

Figure S3. Variation in environmental predictors across secondary and mature forest categories in two soil types (B= basalt, G= granite) in North Queensland, Australia

Chapter 5

Soil types influence predictions of soil carbon stock recovery in tropical secondary forests

Abstract

Tropical forests are major sinks of terrestrial carbon (C) both above- and below-ground. As a consequence their destruction and degradation is considered the second largest anthropogenic source of carbon dioxide to the atmosphere. Also contributing to the changing dynamics of the global carbon cycle is the widespread and significant expansion of secondary forest. Secondary forests that colonise abandoned agricultural lands can potentially recover above-ground C stocks to historical levels in a few decades. However, the dynamics of below-ground C stored as soil C stocks are unaccounted for in several tropical regions. Similarly, although parent materials are known to differ in chemical and physical properties, little is known about the relationships of soil C stocks with environmental predictors and whether they interact with soil types during natural forest regeneration. I investigated whether soil organic carbon (SOC) stocks change with secondary forest age in two contrasting soil types (derived from either basalt or granite). Soil and vegetation parameters were analysed to determine the best predictors of SOC stock changes in secondary forests. SOC stocks from 24 secondary forests (up to 69 years since pasture abandonment) were compared with those from active pastures and mature forests. I found that clay-rich soils (originating from basalt parent material) stored higher amounts of SOC, although these stocks remain unchanged as secondary forests matured. In contrast, SOC stocks in granite soils tend to be lower in young

secondary forests and increase rapidly to levels comparable to mature forests. Moreover, my analysis indicated that soil pH and woody plant diversity are strong candidates as predictors of SOC stock variations, yet it appears this is within context of soil type. My results support the contention that models predicting SOC stocks during forest succession should not rely only on secondary forest age. Instead, predictions of SOC stocks can be improved with the inclusion of basic information on vegetation cover and soil type (especially soil texture). In this study, two lines of evidence support these conclusions that soil types should be considered in modeling below-ground SOC stocks during forest succession: the rate of change in SOC stocks and the rate of change in $\delta^{13}C$ values of the organic matter.

Keywords: *Soil organic carbon (SOC); regrowth forests; abandoned pastures; Wet Tropics; Australia*

5.1 Introduction

Forests are a major carbon (C) sink (Dixon *et al.* 1994, Lal 2005, Pan *et al.* 2011). Tropical mature forests contain *ca.* 471 ± 93 Pg C (above and below-ground biomass, dead wood, litter and soil) which represents 55 percent of the estimated C stock for all forest ecosystems (*i.e.* boreal, temperate and tropical forests; Pan *et al.* 2011). The first metre of tropical forest soil is of great importance in carbon stocks, contributing more than half of the total forest C (excluding roots) in Neotropical forests (Kauffman *et al.* 2009).

When tropical forests are cleared, substantial amounts of C are lost to the atmosphere (Fearnside and Barbosa 1998, Pan *et al.* 2011). One of the main drivers of deforestation is agricultural expansion (Geist and Lambin 2002). However, once soil productivity declines due to agricultural use, cleared lands are often abandoned and secondary forests subsequently colonise (Barbier 1997, Munroe *et al.* 2013). This cycle of deforestation and abandonment is

contributing to the predominance of secondary forests over primary forest in the tropics today (ITTO 2002, Chazdon 2014). Therefore, secondary forests (considered here as the regrowth vegetation after land abandonment) have a crucial role in the global C budget (Lugo and Brown 1992, Knops and Tilman 2000, Letcher and Chazdon 2009).

Despite a growing understanding of the factors that affect vegetation recovery and net productivity during forest succession there are uncertainties regarding the accumulation of soil organic C (SOC) (Buschbacher *et al*. 1988, Marín-Spiotta and Sharma 2013). While above-ground biomass may recover rapidly after land abandonment (*i.e.* within a few decades); community structure and composition may continue to be dissimilar from the original forest even after many decades (Aide *et al* 2000, Letcher and Chazdon 2009, Goosem *et al*. 2016). Biomass accrual is expected to be a main determinant of SOC accumulation, however increase in SOC stocks after land abandonment appears to be variable and influenced by an array of factors (Guo and Gifford 2002, Lal 2005). For instance, alterations in the balance of soil nutrients and the characteristics of regenerating vegetation (*e.g*. species diversity and species composition) could be important determinants of SOC change over time (Davidson and Janssens 2006).

Soil types vary in their fertility and can influence the distribution of plants and vegetation characteristics (Herrera and Finegan 1997, Fyllas *et al.* 2009). Inherent properties of parent materials provide a range of physical and mineralogical features that affect the process of soil formation and vegetation recovery (FAO 2005). However, with forest clearing and agricultural use, topsoils tend to become more compacted (*i.e.* less porous), which negatively affects oxygenation, water holding capacity, root penetration and soil biological communities (Kaiser and Guggenberger 2003, Davidson and Janssens 2006, von Lützow *et al.* 2007). Not surprisingly, therefore, soil types can respond differently in terms of soil C loss and accumulation after land-use transitions (Laganière *et al*. 2010, López-Ulloa *et al.* 2005, McLauchlan 2006). Despite a growing interest, the influence of environmental parameters on

SOC stock accumulation and their interaction with soil types during natural rainforest succession remains poorly documented in the tropics (Post and Kwon 2000, Pan *et al.* 2011).

The study region is comprised of a mosaic of active and abandoned pastures at various stages of natural succession (from *ca.* 9 to 69 years since pasture abandonment) and mature rainforest on different soil types. In this context, I was able to investigate SOC changes across a vegetation gradient on two contrasting parent materials. I addressed two main questions. First, I asked whether soil types influence SOC stocks and dynamics (soil C isotopic composition) in active pastures, young (< 30 years) and old (>30 yrs) secondary forests of different ages and mature forests. Secondly, I asked whether secondary forest age, soil properties, vegetation structure or woody plant community best predict SOC stock variation and whether these predictors are similar in both soil types.

SOC stock estimations should assist in placing tropical Australian secondary forests in a regional and global context, whereas the comparison of C isotopic composition should contribute to a better understanding of SOC dynamics during succession from pastures to older secondary forests (Trumbore *et al*. 1995, Schedlbauer and Kavanagh 2008).Tracking changes in C isotopic signatures through secondary forest succession was possible because C_4 plant species (most commercial tropical species of pasture grass) comprise the dominant cover of active pastures in these warmer tropics. As forest succession proceeds, C_3 species are expected to outcompete pasture cover and dominate the site, gradually shifting the $\delta^{13}C$ signature back to forest levels (Peterson and Fry 1987, Staddon 2004, Schedlbauer and Kavanagh 2008).

5.2 Methods

5.2.1 Study area

The study was carried out on the southern Atherton Tablelands in the Wet Tropics bioregion of Australia (17º25'32" S 45º36'13" E, Figure 16). The study area is a 700 – 850 m plateau which experiences a mild tropical climate. Mean annual rainfall ranges from 1,100 to 2,240 mm and temperature ranges from a mean minimum of 10°C in winter months to a mean maximum of 29˚C in summer months (BOM 2014). Warmer and more humid weather occurs from December to March with a cooler and drier period from July to October, during which monthly rainfall falls below 100 mm. In the early 1900's, rainforest clearing began for the dairy industry, converting rainforest into pastures dominated by C_4 fodder grass species (Kerridge *et al.* 1972; Maggs and Hewett 1993; Malcolm *et al*. 1999). Tropical C_4 grass species include *Paspalum* spp, *Imperata cylindrica* (L.) Raeusch. var. *major* (Ness) C. E. Hubb and *Axonopus affinis* Chase. There is no report of temperate or legume pasture species around my study sites, although they have been recorded in southern regions (Malcolm *et al*. 1999). Pastures were abandoned due to changing financial incentives that led to a widespread decline in dairy farming. The pasture phase at my study sites lasted from 40 to 100 years, which is considered sufficient time for changes in C isotopic signature in topsoil levels (Trumbore *et al.* 1995).

Soils in the study area are deep and highly weathered with relatively low concentrations of macro- and micro-nutrients (Kerridge *et al.* 1972, Malcolm *et al*. 1999). Basalt-derived soils dominate the Tablelands (56%), followed by granite-derived soils (23%), rhyolite (12%), metamorphic (7%) and Quaternary alluvial soil (2%). I selected sites on soils derived from the two dominant geological parent materials: granite (Tully Granite) and basalt (Atherton Basalt). Basaltic soils are classified as red and brown Ferrosols and normally contain higher proportions of clays and retain more organic matter, nutrients and water, whereas granitic soils are classified as red Dermosols, which comprise a sandier texture with lower organic matter content and high water infiltration rates (Kerridge *et al.* 1972, Malcolm *et al.* 1999).

5.2.2 Study sites

I surveyed 36 plots in total: twenty-four secondary forest stands (SF), six active pastures dominated by C_4 grasses (AP) and six mature forests as reference (R) (Fig. 16). Study sites were chosen after examination of historical aerial photographs and satellite imagery, complemented by information from landowners. Active pastures were defined as man-made grasslands that are currently being grazed by cattle. Secondary forest was considered to be the vegetation regrowing spontaneously after pasture abandonment. Mature forest sites were old-growth rainforest sites that have not been cleared in the last 150 years, however, they might have been selectively-logged in the past century; as evidenced by logging tracks discernible on the ground and from aerial photography. I assume that these activities produced non-significant loss of SOC (Houghton 1995). Active pastures and secondary forests were chosen so as not to be contiguous with the major rainforest tracts within the Wet Tropics World Heritage Area.

Secondary forest age was determined as the number of years since pasture abandonment. The age of secondary forest sites was determined as the mid-point year between two successive aerial photographs or satellite images where it was evident in the first that pasture had been abandoned and replaced by another vegetation type (*e.g.* low weeds, scramblers, shrubs and scattered tree saplings). I used secondary forest age as a continuous variable in the regression models to predict variations in SOC stock and dynamics and also investigated forest age as a categorical variable (SF1 ≤ 30 years, SF2 ≥31 years) to provide estimates of SOC stocks in two different stages of forest recovery and compare them with active pastures and mature forests.

At each site, I installed a 50 m x 10 m transect, along which I collected soil samples from the surface (0-10 cm) and subsurface (10-30 cm) at 5 m intervals. Soil sample analyses and vegetation measurements all came from this main transect. Samples from each transect

and soil layer were pooled for SOC stocks, physical and chemical analyses. Soil parameters were averaged across layers, whereas bulk density and soil C concentration were kept separate for SOC stock estimations. For the woody vegetation, diameter at breast height (dbh) was measured to estimate basal area (m^2 ha^{-1}). All woody stems $\geq$2.5 cm dbh (within 50 m x 3 m) and ≥10 cm dbh (within 50 m x 10 m) along each transect were identified to species level. Terrain slope (˚) was measured along and perpendicularly to each transect; values were averaged per site.

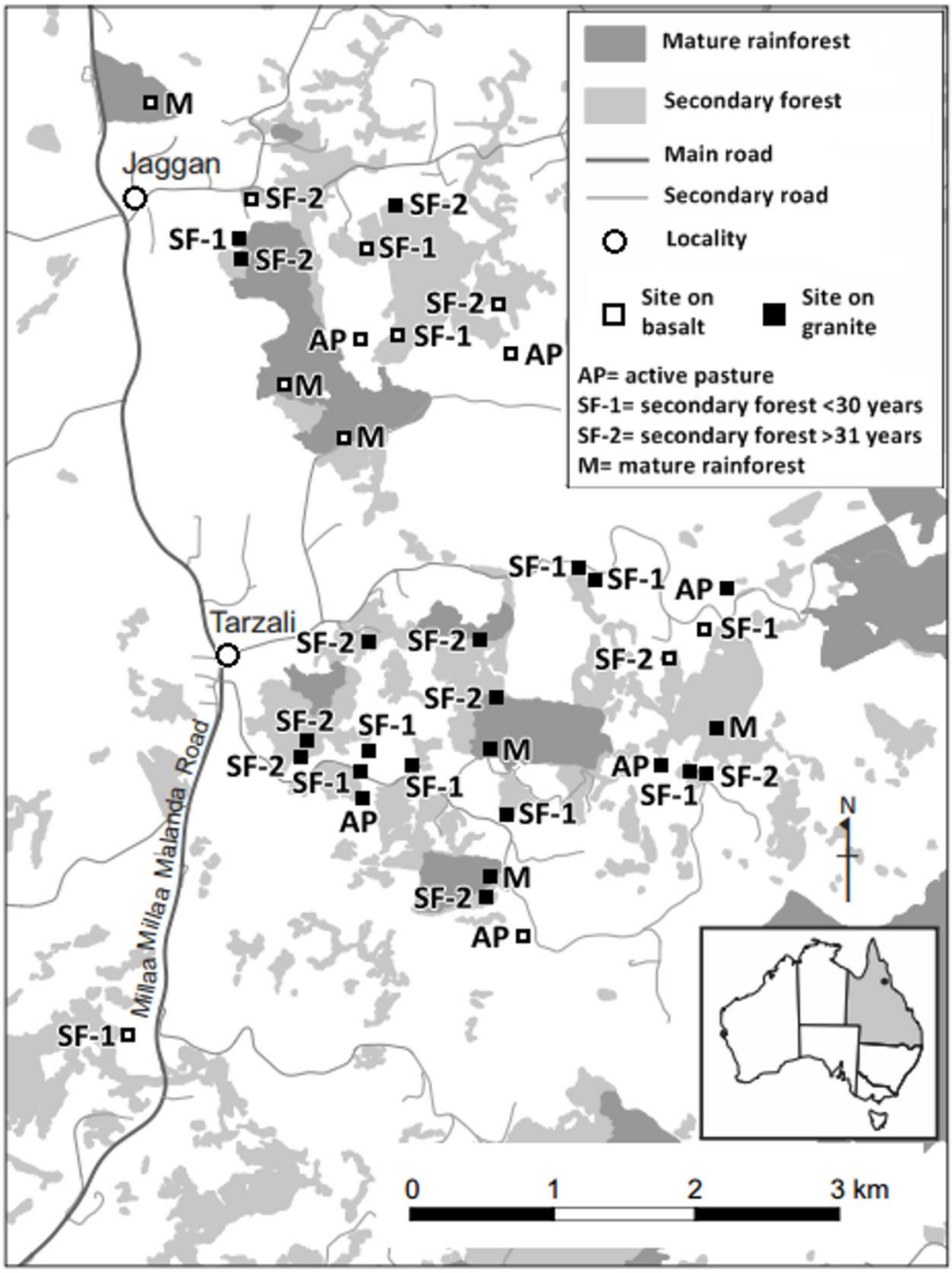

Figure 16. Map indicating study site location, site type (active pastures, secondary forests and reference mature forest), soil derivation of each site (basaltic or granitic parent material) and the area of secondary forest and remnant mature rainforest.

5.2.3 Soil physical and chemical characterization

Soil types were classified according to field observations and topsoil samples from each site. Soil samples for analysis of clay content, pH (1:5 water), along with macronutrients (percent of total N, P and plant available Colwell-P) and exchangeable cations ($[Ca^{+}]$, $[Mg^{+}]$, $[K^{2+}]$, $[Na^{2+}]$, $[Al^{3+}]$ in $cmol_c\ kg^{-1}$) were kept cool until dried at room temperature and sieved through 2 mm mesh. Coarse fragments (> 2 mm) were also weighed to estimate their proportion in relation to the whole sample. Processed samples were sent to a commercial laboratory (Nutrient Advantage - Incitec Pivot ®, Victoria, Australia) for analysis using the standard protocols of Rayment and Lyons (2001). For bulk density measurements ($g\ cm^{-3}$), I obtained soil samples from the 0-10 and 10-30 cm layers using a 5 cm x 5 cm (width x diameter) stainless steel ring from a soil pit dug in the center of each transect. Soil samples were dried at 105ºC (48 hr) and the dry soil weight divided by the volume of the ring.

Soil types differed in clay content, total N (tN), available P(aP), total P (tP), Mg, Na and soil C:N ratio (Table S4, Fig. S4). Basalt soil had significantly higher clay content than granite soils in all vegetation types, but mean values did not change across vegetation types. Clay content varied together with aP, tP, and tN and was unrelated to soil pH and soil C:N. Cations (Na, Ca, K and Mg) tended to vary similarly but were not significantly correlated with other soil parameters (Fig. S5). Bulk density of the topsoil layer differed only marginally among vegetation types (ANOVA type II for 0-10 cm: vegetation type $F_{[3,28]} = 2.72$ $P = 0.063$) and did not differ among soil types (ANOVA type II for 0-10 cm: $F_{[1,28]} = 1.35$, $P = 0.255$). However, bulk density in the sub-surface layer was significantly higher in granite than basalt soil (ANOVA type II 10-30 cm: $F_{[1,28]} = 37.94$, $P = 0.000$), with a small non-significant decrease from active pastures, through secondary forests to mature rainforest (ANOVA type II 10-30 cm: $F_{[3,28]} = 0.82$, $P = 0.496$).

5.2.4 Soil organic carbon (SOC) stocks and stable isotope composition

Soil carbon stocks were assessed from the fine particle soil fraction (≤2 mm) for the two soil depths. I estimated SOC stocks at fixed mass per site according to Ellert *et al*. (2008). The estimation of SOC stock based on the fixed mass is recommended when bulk density across treatments is not uniform (Ellert *et al*. 2008, Tesfaye *et al*. 2016, Schrumpf *et al*. 2011). I calculated the SOC stocks (SOC_{FM} in Mg C ha^{-1}) according to Eq 1:

$$SOC_{FM} = SOC_{FD} - M_{ex} * C_c / 1000 \quad (1)$$

where, SOC_{FD} (SOC stock for fixed depth) is estimated as the SOC concentration (C_c mg C g^{-1} dry soil) from each soil layer corrected for percentage of coarse fragments >2mm (C_c) multiplied by D_s (bulk density estimated for each site in g cm^{-3}) and L_c (length of the core sampled in meters). M_{ex} is the excess of mass of soil (M_{soil} in Mg ha^{-1}) found by subtracting the reference soil mass (M_{ref}) from the mass of soil for each soil segment. M_{soil} is the mass of soil at fixed depth calculated by D_s multiplied by L_c times 100. M_{ref} is the lowest M_{soil} at a given depth from all samples.

To investigate SOC dynamics, the upper soil samples (0-10 cm) were analysed for stable C isotopic signature ($\delta^{13}C$ values) using a Costech Elemental Analyzer fitted with a zero-blank auto-sampler coupled via a ConFloIV to a Thermo Finnigan Delta VPLUS using Continuous-Flow Isotope Ratio Mass Spectrometry (EA-IRMS) at the Advanced Analytical Centre, James Cook University, Cairns, Australia. Stable isotope results are reported as per mil (‰) deviations from the VPDB reference standard scale for $\delta^{13}C$ values. Precision (SD) on internal standards was better than ±0.1‰ for carbon.

5.2.5 Data analysis

To examine and compare variation in SOC stocks, $\delta^{13}C$ composition, bulk density, clay content, soil pH and macro-nutrients across active pasture, young and old secondary forests

and mature forest I performed ANOVA type II (for unbalanced numbers of replicates among treatments) using these four vegetation types, the two soil types (basalt and granite) and the interaction between vegetation and soil categories (R function 'Anova', Fox and Weisberg 2011, Langsrud 2003). Normality and homoscedasticity of residuals were checked with Q-Q plots and distribution of frequencies (Zuur *et al*. 2010).

To investigate soil-related predictors of SOC stocks I examined clay content and soil pH as they varied independently in my samples. As vegetation-related predictors of SOC stocks I estimated basal area, woody plant diversity (Fisher's α logarithmic index with species counts) and the two reduced community composition dimensions obtained with non-metric multidimensional scaling using Bray-Curtis dissimilarity and species counts (NMDS, R function 'metaMDS', Oksanen *et al*. 2013). I characterized the community dimensions with paired correlations between NMDS axes and the most common species (>10 stems in total). To test the inter-correlation between secondary forest age, soil and vegetation predictors I used Spearman rank correlation coefficients with standardised data (R function 'rcorr'*)*.

Simple and multiple generalised regression models were used to predict changes in SOC stocks in secondary forests (R function 'glm' with gamma distribution to normalize the dispersal of model residuals without transforming the response variable). First, simple models investigated the patterns of SOC stocks and $\delta^{13}C$ composition within secondary forests using age as a continuous variable and soil type as a factor. Second, I tested ten alternative models with different combinations of predictors. Models that combined soil and vegetation variables were tested *a priori* with and without forest age and with and without soil type. Soil type was included in all models as it improved model fitness in all cases, whereas inclusion of forest age was not consistent. I used R function 'mod.sel' to rank regression models based on their AICc (corrected Akaike information criterion). Only the models with best fit (ΔAICc <4) were considered further in results and discussion. I selected the variables from the best-supported models and plotted the partial regressions of SOC stock against predictors. By removing the

effects (residuals) of other competitive predictors I expect to observe the individual effect of the predictors in question without the influence of others. Pairs of predictors were analysed to simplify analysis and interpretation. Statistical analyses were performed with R version 3.0.3 (R Core Team 2014).

5.3 Results

5.3.1 Are SOC stocks and dynamics different in the two soil types?

Soil carbon stocks varied with soil type, but not among the vegetation types of active pasture, secondary forests and mature rainforest (Table 7). Across all vegetation types, SOC stock in the top 30 cm of soil was significantly higher in basalt soils (average of 78.8 Mg C ha^{-1} (± 9.5 SD) than granite (54.9 Mg C ha^{-1} ± 13.4 SD) (Table 7). The minimum overall SOC value was 33.5 Mg C ha^{-1} (26 year secondary forest on granite) and the maximum value was 96 Mg C ha^{-1} (20 year secondary forest on basalt).

When I analysed changes within secondary forest only, I found that SOC stock accumulated at faster rates in granite than basalt soils, with the latter tending to maintain similar values over time, and with values generally much higher than the granite soils in early successional stages (Table 7, Fig. 17A). In granite soil, SOC stocks decreased an average 22 percent in the first 30 years after pasture abandonment. However, in granite soils SOC stocks increased by more than 98 percent compared in older (>30 years) secondary forests compared with active pastures (Fig. 17A). There were no significant differences in SOC stocks between active pasture and mature forest in either soil type (Table 7, Fig. 17A).

Table 7. Mean (±1 standard deviation) for soil organic carbon (SOC) stock values estimated for soil from 0-30 cm depth and δ ^{13}C (0-10 cm depth) from four vegetation types (VT): active pastures (AP), two categories of secondary forest (SF1 <30 years, SF2 ≥ 31 years) and mature forest (MF) in two soil types (basalt and granite) from the Atherton Tablelands (Northeast Queensland, Australia). ANOVA type II was used to compare vegetation and soil types. Generalised linear models were used to compare secondary forests sites only, with stand age as continuous variable. *P*-values ≤ 0.05 are in bold.

		Mean values (± SD) for vegetation types (VT)				*Comparison among all vegetation types* *Anova F* (*P*-value)			*Comparison among secondary forests only* *GLM Estimates* (*P*-value)		
		AP	**SF1**	**SF2**	**MF**	VT	Soil type (S)	VT x S	Age (A)	Soil type (S)	A x S
SOC stock	**Basalt**	76.4 (± 6.5)	80.7 (± 14.6)	79.5 (± 10.1)	78.1 (± 7.5)	0.95	30.43	0.86	4.41	1.29	-2.04
	Granite	60.5 (± 10.7)	47.1 (± 9.9)	59.6 (± 15.8)	56.6 (± 11.1)	(0.427)	(**0.000**)	(0.474)	(0.936)	(**0.002**)	(**0.053**)
δ 13C	**Basalt**	-16.9 (± 2.0)	-23.4 (± 1.2)	-24.9 (± 2.2)	-25.4 (± 0.4)	18.14	7.27	0.61	-0.01	0.195	-0.02
	Granite	-18.2 (± 1.8)	-24.8 (± 2.4)	-27.0 (± 1.1)	-26.3 (± 0.4)	(**0.000**)	(**0.012**)	(0.615)	(**0.047**)	(0.485)	(**0.022**)
		+									

In contrast to SOC stocks, $\delta^{13}C$ was significantly affected by vegetation type (Table 7; Fig 17B). The C isotopic signature characteristic of C_4 grasses was typical of active pastures (minimum values around -16 ‰) whereas forest sites tended to have values within the expected range for C_3 plants (maximum values around -24 ‰). Similarly to the SOC stocks, basalt and granite soils contained significantly different $\delta^{13}C$ values in the topsoil, but changes along the gradient from active pastures to mature rainforest were not significantly different between the two soil types (Table 7, Fig. 17B). Again, when only secondary forests were analysed, I found steeper rates of change in the $\delta^{13}C$ in granite soil than in basalt (Table 7; Fig. 17B).

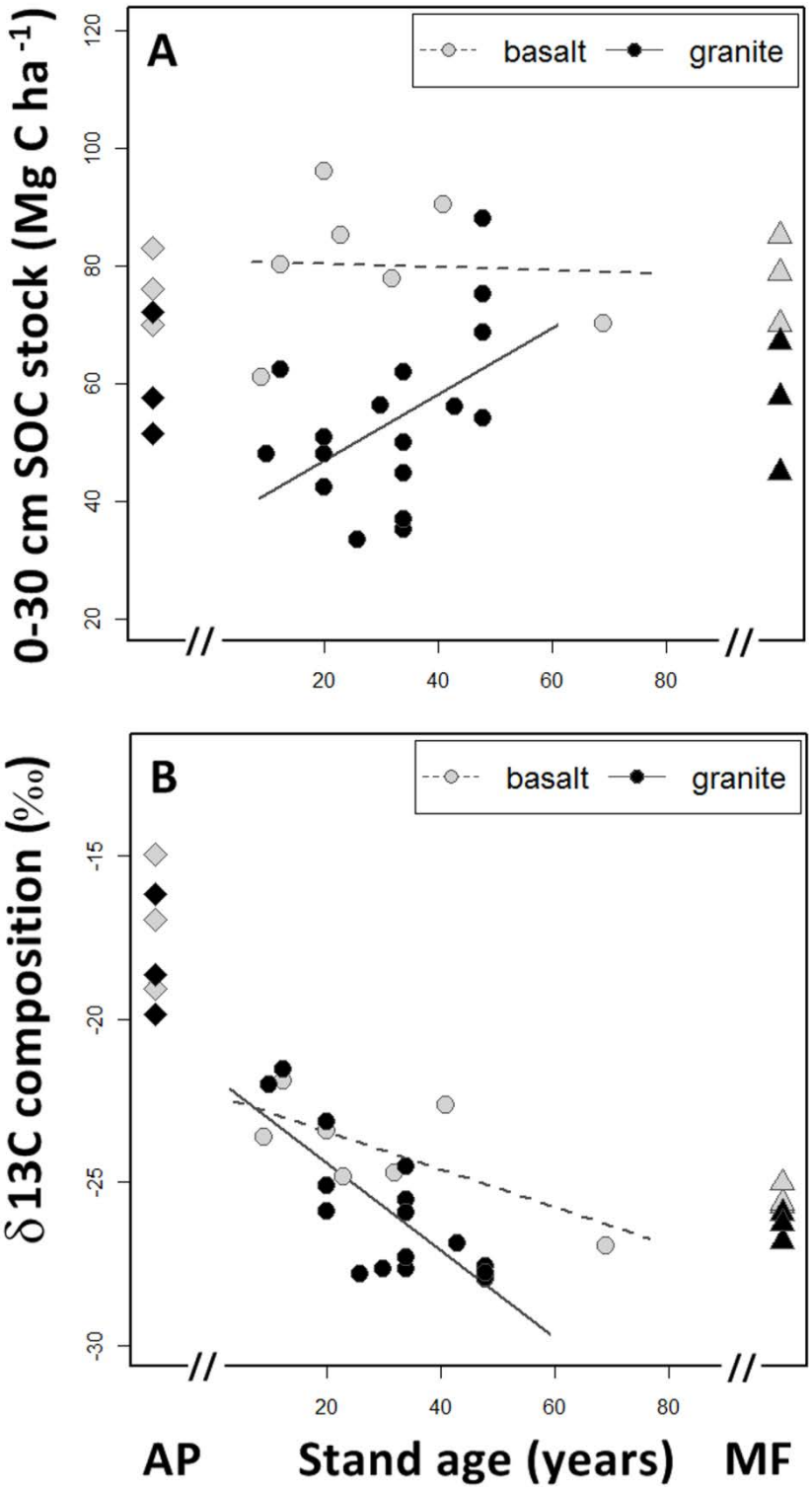

Figure 17. **A**: Soil organic carbon (SOC) stocks at 0-30 cm depth and **B:** δ ^{13}C at 0-10 cm depth from active pastures (AP, diamond symbols), secondary forest (circles) and mature forest (MF, triangles) in basalt (gray symbols) and granite (black symbols) soil types. Active pasture and mature forests were not included in the regression model.

5.3.2 Are forest structure and community composition different in the two soil types?

Basal area and species diversity increased significantly from young secondary to mature forests (basal area: ANOVA type II: $F_{[2,26]} = 29.9$ $P < 0.0001$, diversity: $F_{[2,26]} = 20.5$, $P < 0.0001$), but there were no significant differences between soil types (basal area: ANOVA type II: $F_{[1,26]} = 0.51$ $P = 0.4831$, diversity: $F_{[1,26]} = 2.49$, $P = 0.1264$). The active pasture category was excluded from this analysis because transects were arranged to avoid remnant shrubs and trees. The woody plant community changed with forest succession, with the two soil types supporting different compositions (Table S5). Through correlations of common species with the ordination axes (of study sites in soil parameter space), I found that *Rhodomyrtus pervagata* was more dominant in granite soils, whereas *Rhodamnia sessiliflora* and *Flindersia brayleyana* seemed to 'prefer' basalt soils (Figure S5, Table S5). Nonetheless, woody plant communities in these secondary forests were characterized by early to mid-successional species with mid to late successional species appearing in lower abundances (Table S5). *Guioa lasioneura* was the most dominant species in both soil types, followed by *Neolitsea dealbata, Alphitonia petriei* and *Psidium cattleianum var. cattleianum* (exotic species).

5.3.3 What are the best predictors of SOC stock change in secondary forests?

The three best-supported multiple regression models to predict SOC stock variation in secondary forests were selected, based on the ΔAICc (< 4) (Table 8). Woody species diversity was present in all three models selected, whereas soil pH occurred in two models. Stand age and basal area were also included in the second and third models, respectively, however I note that these variables were significantly correlated with species diversity. Soil type was also included in all models, because, as in the previous analysis, they improved the overall fitness of

models. Clay content and community composition appeared to be of less importance as predictors of SOC stock changes in secondary forest succession.

The most important finding from the analysis of partial effects of the predictors was that without the influence of species diversity, stand age did not explain the variation in SOC stocks in either soil type (Fig. 18B). The opposite was not necessarily true as without the effect of stand age, plant diversity still showed a positive relationship with SOC stock (Fig. 18E). For basalt soils, a positive association between SOC stock and species diversity was found when the effect of basal area was removed, whereas in granite the relationship was not as strong (Fig. 18H). Secondly, I did not find significant changes in the response of SOC stock to soil pH when residuals from forest age and diversity were removed (Fig. 18C-D). Third, an unanticipated negative relationship of SOC and basal area was detected in basalt soils when the effect of species diversity was removed (Fig. 18G).

Table 8 Comparison of four alternative multiple linear models to explain variations in soil organic carbon (SOC) stocks from 0-30 cm depth in secondary forests on the Atherton Tablelands (Northeast Queensland, Australia). The first three models are presented sequentially from lowest to highest corrected Akaike Information Criteria (AICc) values. Only models with ΔAICc (difference between one estimated AICc and the lowest AICc) lower than 4 are shown. The final model (Mod1) shows the full model with all soil and vegetation predictors included.

	Predictors of soil carbon stocks in secondary forests									*Multivariate model results*			
Models	*Interc.*	Age	BA	Clay	Comp1	Comp2	Diversity	pH	Soil type	df	logLik	AICc	ΔAICc	weight
Mod 2	1.86	-	-	-	-	-	0.01	0.43	+	5	-91.4	196.1	0.0	0.61
Mod 7	1.33	-5.6e-3	-	-	-	-	0.02	0.54	+	6	-90.5	198.0	1.87	0.24
Mod 4	4.13	-	-1.8e-4	-	-	-	0.01		+	5	-93.3	200.0	3.85	0.09
Mod 1	1.34	-3.23e-3	4.4-e4	1.5e-3	-0.11	-0.18	0.03	0.49	+	10	-90.0	217.7	20.9	0.0

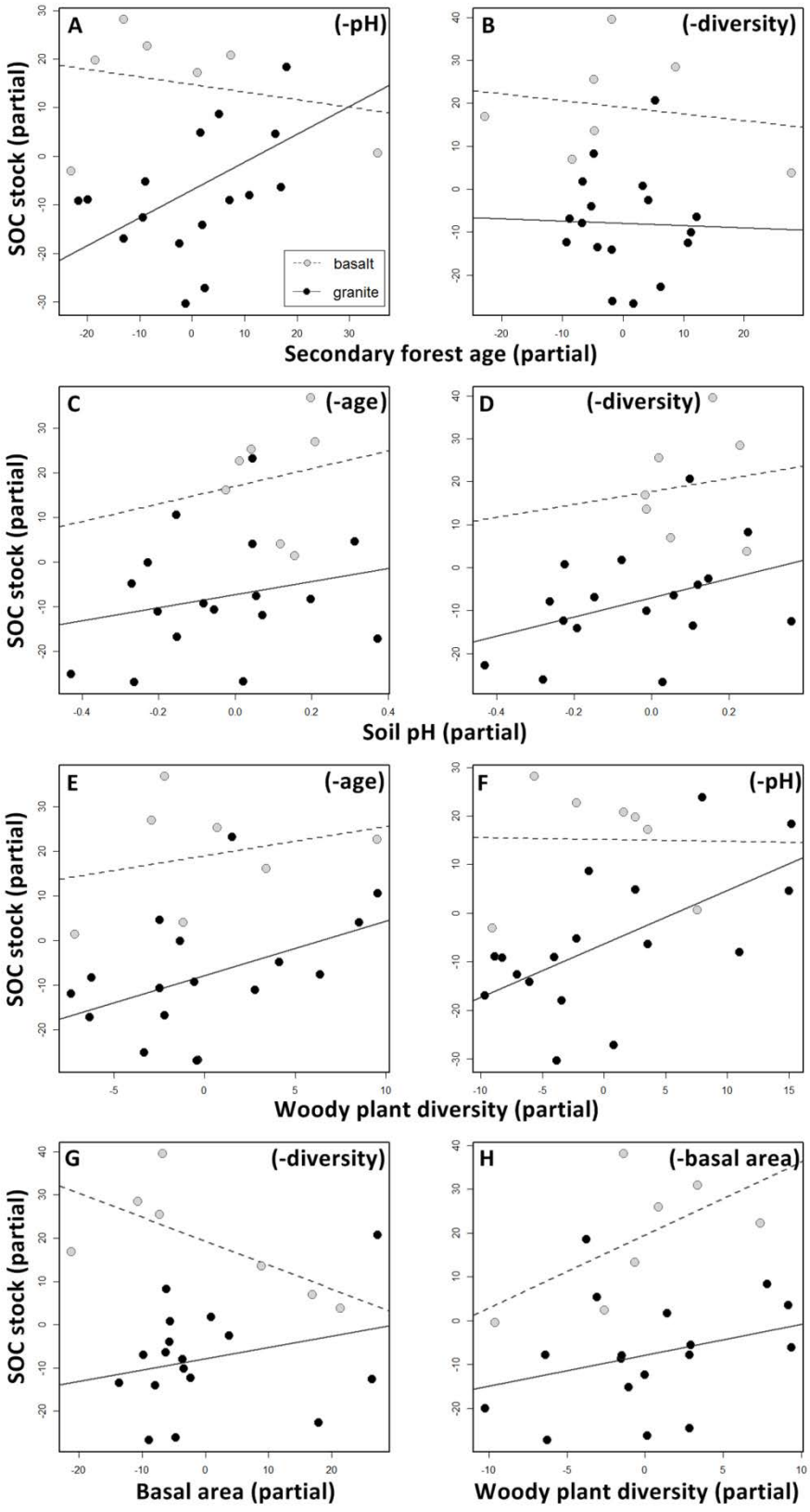

Figure 18. Partial regression of best supported variables that affect SOC stock variation in secondary forests. Variables were selected based on corrected Akaike's Criterion Information (AICc and ΔAICc) from multiple regression models.

5.4 Discussion

5.4.1 Variation of SOC stocks and dynamics depends on soil type

In recovering secondary forests of tropical Australia, I found that the accumulation and dynamics of soil organic carbon stock was influenced by soil type. My findings support the conclusions of the meta-analysis by Laganiére *et al*. (2010), that found soils with higher clay content (basalt soils) tended to accumulate higher SOC stocks compared to soils with lower clay content (granite soils). Topsoil C stocks in at my basalt soils were on average 32.5 percent larger than in granite soils from regenerating forests. The observed dependence of SOC stocks and dynamics on soil type has important implications for the estimation of SOC stocks across ecosystems as well as for large-scale predictions of recovery after land abandonment (Guo and Gifford 2002, Chapin III *et al*. 2009, Laganiére *et al*. 2010, Pan *et al.* 2011).

Even though basalt soils maintain higher SOC stocks, they appeared to be more resistant to changes after pasture abandonment. The finding that SOC accumulations in clay-rich soil are unaltered by land-use change is probably due to the presence of larger recalcitrant SOC pools (López-Ulloa *et al*. 2005, Schedlbauer and Kavanagh 2008). Recalcitrant SOC pools are associated with the capacity of the soil to form stable mineral aggregates or with the complexity of organic carbon compounds produced by vegetation (Guggenberger and Zech 1999). Similar to my findings, López-Ulloa *et al*. (2005) found different soil C dynamics in two soil groups. They suggested the higher stabilization of C in clay-rich soils and the production of more decomposable plant residue both contributed positively to higher C inputs that maintained larger SOC stocks in clay/loamy soils before and after pasture abandonment.

In contrast, granite soils in this study appear to have much more dynamic SOC stocks. An initial decrease in SOC stocks in the first decade after pasture abandonment was followed by a continuous increase as succession unfolds. This result is not surprising as similar patterns of SOC loss due to land-use transitions have been reported previously (Guo and Gifford 2002).

Transition from vegetation dominated by C_4 grasses to forest (C_3 dominated) was assumed to interfere in SOC stock storage, as the leaves and roots in woody vegetation tend to live longer than grasses and therefore contribute less to C input to soil during early forest regeneration (Guo and Gifford 2002). I assume that slower organic matter turnover due to lower soil nutrient fertility in granite soil could be inducing C loss from the mineral pool in granite soils at more elevated rates than basalt (Chen *et al*. 2016). However, increases in woody vegetation cover and accumulation of organic matter in older sites would compensate for poorer soil condition and contribute to a gradual recovery of SOC stocks.

5.4.2 Effects of soil pH versus plant community structure on SOC stocks

SOC storage is closely linked to soil properties and vegetation inputs. The isolation of such effects can perhaps be unrealistic as plant and soil change simultaneously in a process of positive feedback (Ehrenfeld *et al*. 2005). My attempt to separate individual effects of environmental predictors suggests that SOC stocks in the two soil types may be better predicted by different variables. I found that soil pH and woody plant diversity may be good candidates to explain SOC stock accumulation, with certain differences in their effects. Soil acidity is likely to have an indirect effect on soil carbon (Berthrong *et al*. 2009), because it interferes with the availability of elements which plants require for their metabolism (*e.g.* N, P, K, Mg and micro-nutrients; Chapin III, 1980). For example, in more acidic soil P can become unavailable for plants, leading to lower plant productivity, which in turn affects the amount and quality of plant input to soil (*i.e.* litter) (Hughes *et al*.1999, Post and Kwon 2000). Soil pH can also affect soil microorganisms, which in turn accelerate or delay organic matter decomposition (Nicol *et al*. 2008).

Despite being present in the best supported multivariate models in my study, the effect of species diversity is confounded by secondary forest age and basal area. Dawud *et al*.

(2016) also found that species diversity can explain variations in SOC stocks and soil C:N ratios, indicating that plant diversity may be playing a more important role in SOC accumulation than previously expected. Although my results help support this notion, the lack of correlation of SOC stock and plant diversity in basalt soil is contradictory. In further exploring the individual effects of each explanatory variable, I note that plant diversity is interacting with forest age. Either forest age or plant diversity would be good predictors of SOC stock in secondary forest if vegetation followed the same trajectories of succession in all soil types, but this is not always the case (Cramer *et al*. 2008, Guariguata and Ostertag 2001).

Above-ground biomass is expected to occur in close association with below-ground C (Houghton 2005). Interestingly, I found a negative trend between SOC stock and basal area in basalt soil. Variation in resource allocation might explain these relationships. Whereas in sandier, less fertile soils, plants must invest more in fine roots to uptake nutrients and water, in clay-rich soils the allocation to roots is reduced (Chapin III 1980, Mokany *et al*. 2006). This difference in below-ground occupation could lead to differences in SOC stock accumulation, however these hypotheses and the analysis of root: shoot ratios require further investigation. In basalt soil, basal area and species diversity are not significantly correlated (r=0.54; P= 0.2152), whereas in granite these parameters are significantly associated (r=0.79; P= 0.0001).

5.4.3 Woody plant community composition

As expected, there is a great overlap in species occurrence between soil types mainly caused by generalist early successional native species and the non-native invasive *Psidium cattleyanum*. These species were not influenced by differences in soil condition and occur indiscriminately on both soil types (Tng *et al* 2015). On the other hand, some species occur exclusively (or with significantly different abundances) in one soil type or another (*e.g. Rhodomyrtus pervagata* on granite, Table S6). My data suggest that these small shifts in

community assemblages do not explain the variation in SOC stocks, however whether certain species exert stronger direct effects on SOC accumulation needs to be investigated. For instance, it was found that *Alphitonia petriei* leaves decompose at slower rates than mixed rainforest species (Parsons and Congdon 2008). A heterogeneous distribution of *A. petriei* among sites in this work (1 to 33 individual stems) could explain part of the variability in SOC stock accumulation, as the turnover of organic matter may differ depending on the soil condition (Hattenschwiler *et al*. 2005, Parsons and Congdon 2008).

5.4.4 Final considerations and limitations

Intuitively, secondary forest age is the most likely factor affecting changes in SOC stock during secondary forest succession. Despite forest age being a good predictor of vegetation recovery (*e.g*. biomass, species and functional composition) in secondary forest (Johnson *et al*. 2001, 2001, Zarin *et al*. 2001, Feldpausch *et al*. 2004, Yeo and Fensham 2014, Goosem *et al.* 2016),there are instances where this pattern is not universal (Chazdon *et al*. 2007). From a review on tropical SOC stocks in both secondary forests and tree plantations it was suggested that forest age alone is not a key predictor of SOC stocks (Marín-Spiotta and Sharma 2013). My results partially concur with this assumption, but the tendencies of my SOC stocks to change with time may be influenced by interactions with above- and below-ground parameters that were not examined in my study. Indeed, my sites occur within different private farms and therefore it is plausible that they may have experienced slightly different treatments (*e.g*. access to sites by cattle, remnant trees, and fire) that have caused the high variability observed within some age classes (Post and Kwon 2000, Guo and Gifford 2002, Dwyer *et al*. 2010). Upon reflection, greater site replication on the basalt soils would assist in clarifying some patterns but these sites are less common (than secondary forest on granite) in the region, making it a challenge to expand this study in that direction. Methodological issues might still impose some

limitations for my SOC stock quantification and predictions. By disregarding the presence of charcoal, I might be underestimating the total SOC stocks (Bauhus *et al*. 2002, Vyšná *et al*. 2014). I managed to separate larger charcoal fragments (>2mm); but the amount was negligible and is not included in my calculation. Yet, as I was unable to separate fine charcoal fragments (< 2 mm) from mineral soil without affecting the whole sample, they were analysed as part of the fine fraction. Lastly, uncertainties in site age quantification have been reported as limitations for robust predictions in the chronosequence approach (Feldpausch *et al*. 2007, Walker *et al*. 2010). In this study, a wide range of aerial photographs were accessible (from 1943 to 2011 at an average 7 year interval) allowing observations of clear changes in vegetation and greater confidence in the determination of site ages with a minimal error.

5.5 Conclusion

Secondary forests are expanding and have become a dominant feature of tropical landscapes, with approximately 60% of the total tropical forest area classified as secondary or degraded (ITTO 2002). These regrowth forests are therefore highly relevant for estimations and predictions for the global carbon budget. My work provides a pioneer estimation of SOC stocks from active pastures, secondary forests and mature forests and the comparison of soil types in the Australian Wet Tropics. I have demonstrated that soil organic C stocks in my secondary forests (61.4 ± 18.3 Mg C ha^{-1} for the 0-30 cm depth) are comparable to those reported recently in a meta-analysis on plantations and natural regeneration: 77.6 ± 2.3 Mg ha^{-1} (Marín-Spiotta and Sharma 2013).

Despite assumptions that conversion of mature forests to agricultural land reduces SOC stocks, my results indicate that secondary forests (natural regeneration) can either maintain similar levels of C in soil or recover it after around 30 years of pasture abandonment, depending on the type of soil. As suggested by other studies, soil type is a factor that should be considered in estimates and predictions of SOC stock accrual. Additionally, my results indicate

that increases in species diversity can assist SOC stock recovery during forest succession. Woody plant diversity was found in my study to be an important factor affecting the accumulation of SOC during secondary forest regeneration. I conclude that quantification and predictions of SOC stocks are not trivial, especially during the process of secondary forest regeneration, which itself can be highly stochastic and influenced by multiple factors.

5.6 Supporting material

Table S4. *F*-test (ANOVA type II) to compare soil properties among vegetation and soil types. Significance at α= 0.05: *** *P*<0.0000, ** *P*<0.001, * *P*<0.050, ns= non-significant.

	F-value	
	Vegetation type [df=3,31]	Soil type [df=1,31]
Clay	1.59 ns	45.52 ***
pH	10.68 ***	0.01 ns
tN	8.92 ***	47.80 ***
aP	2.63 ns	4.89 *
tP	2.75 *	66.78 ***
Ca	4.91 *	1.55 ns
Mg	1.18 ns	23.73 ***
Na	5.23 *	7.92 *
K	4.17 *	1.94 ns
C:N	3.41 *	13.51 **

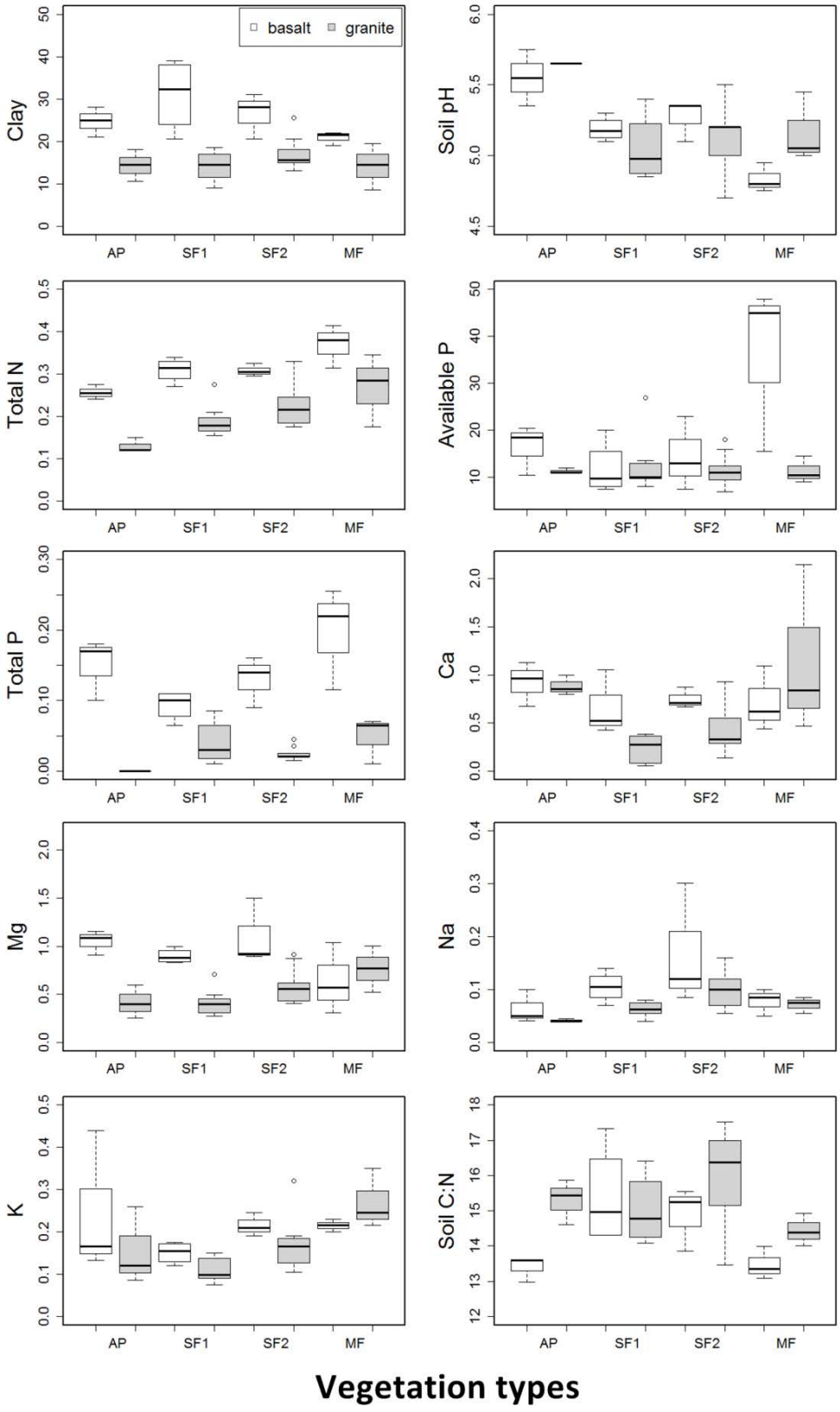

Figure S4. Variation of soil properties along vegetation types: active pastures (AP), secondary forest <30 years since pasture abandonment (SF-1), secondary forest ≥30 years (SF-2) and mature forest (MF) in two soil types (basalt and granite).

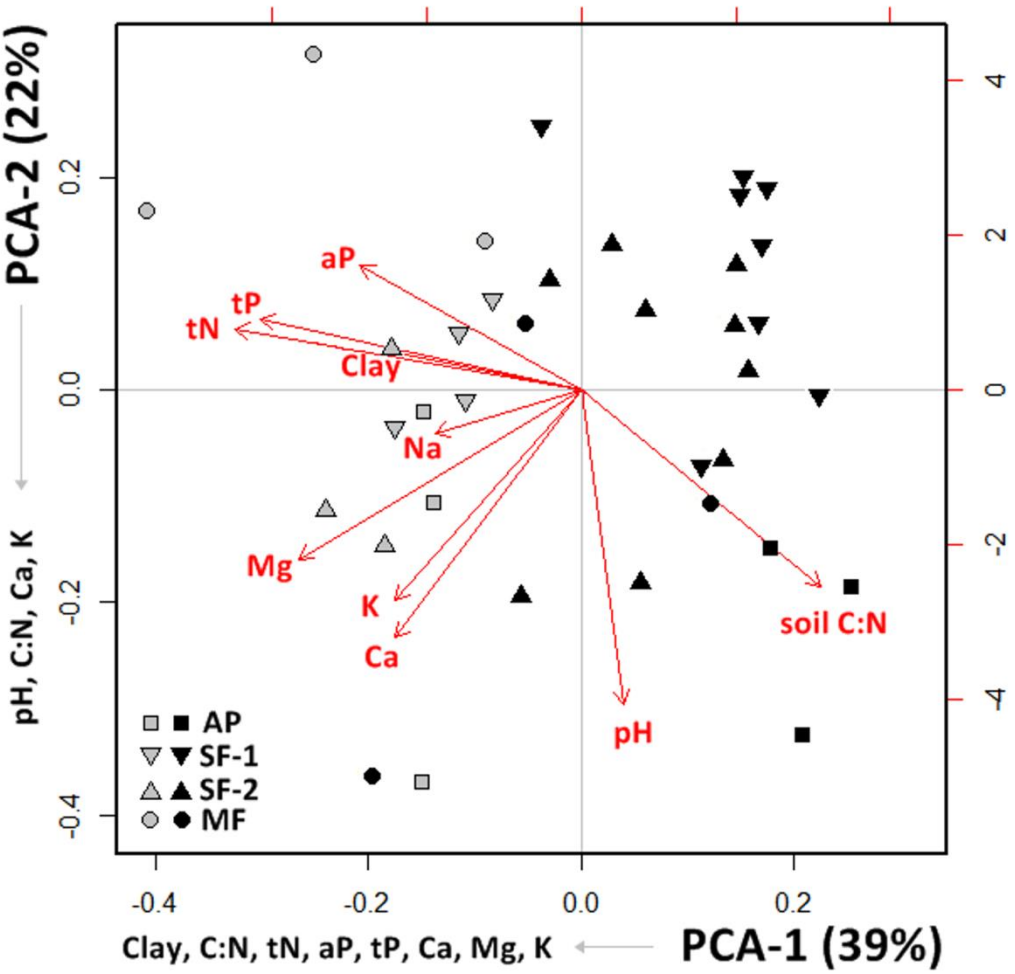

Figure S5. Biplot of the two main axes of a principal component analysis (PCA) with soil properties from active pastures (AP), secondary forest <30 years since pasture abandonment (SF-1), secondary forest ≥30 years (SF-2) and mature forest (MF). Arrows indicate the direction and variables significantly associated with each axis. Significance at α=0.005 (adjusted with Bonferroni's correction for multiple comparisons). Symbols in gray represent sites on basalt, Symbols in black represent sites on granite soils.

Table S5. Correlation (Spearman rank correlation coefficients) between NMDS axes 1 and 2 and each one of the most dominant woody plant species ranked by total number of individuals. Ordination using species counts resulted in a good representation of reduced dimensions (k=2, stress=0.17), with significant separation between basalt and granite sites (Permanova: $F_{1, 22}$ = 2.23, *P*=0.013). Only the first ordination dimension (NMDS-1) was associated with stand age (r= 0.75, P<0.0001; NMDS-2 r= -0.35, P=0.09). Proportion of sites of each forest category occupied (%) is shown for the most abundant woody plant species (>30 stems) in the two soil types. SF1 = secondary forest <30 years old, SF2 = secondary forest ≥ 31 years old and M = reference mature forest. **Exotic species*.

Species	**Successional stage**	**Correlation (*r*)**		**Proportion in basalt (%)**			**Proportion in granite (%)**			*Total*
		NMDS-1	NMDS-2	SF1	SF2	M	SF1	SF2	M	
Guioa lasioneura	Early-mid	-0.13	0.33	100.0	100.0	0.0	100.0	100.0	33.3	*377*
Rhodomyrtus pervagata	Mid	**-0.44**	**0.62**	25.0	0.0	0.0	88.9	87.5	0.0	*179*
Neolitsea dealbata	Mid	**0.59**	-0.02	75.0	66.7	66.7	77.8	75.0	33.3	*162*
Alphitonia petriei	Early-mid	**-0.46**	0.02	100.0	33.3	0.0	55.6	62.5	0.0	*146*
*Psidium cattleianum var. cattleianum**	Early-mid	-0.34	-0.37	75.0	66.7	0.0	66.7	37.5	0.0	*135*
Rhodamnia sessiliflora	Mid	0.36	**-0.60**	100.0	100.0	0.0	55.6	50.0	0.0	*93*

Species	**Successional stage**	**Correlation (*r*)**		**Proportion in basalt (%)**			**Proportion in granite (%)**			*Total*
		NMDS-1	NMDS-2	SF1	SF2	M	SF1	SF2	M	
Litsea leefeana	Mid-late	**0.81**	0.11	50.0	100.0	100.0	44.4	87.5	66.7	*73*
Acacia celsa	Early-mid	0.17	**-0.53**	100.0	0.0	0.0	33.3	25.0	0.0	*67*
Cardwellia sublimis	Mid-late	0.01	0.35	0.0	0.0	0.0	0.0	37.5	66.7	*52*
Flindersia brayleyana	Mid-late	**0.73**	0.18	50.0	100.0	33.3	11.1	62.5	0.0	*41*
Glochidion hylandii	Mid	-0.09	-0.14	100.0	100.0	0.0	22.2	75.0	0.0	*41*
Goniothalamus australis	Late	**0.49**	0.07	0.0	66.7	33.3	0.0	12.5	33.3	*41*
Endiandra leptodendron	Late	-	-	0.0	33.3	100.0	11.1	12.5	66.7	*36*
Beilschmiedia tooram	Late	-	-	0.0	33.3	100.0	0.0	12.5	100.0	*35*
Endiandra monothyra subsp. monothyra	Late	-	-	0.0	33.3	100.0	11.1	0.0	100.0	*34*
Acronychia acidula	Mid-late	**0.80**	-0.08	25.0	100.0	33.3	22.2	50.0	33.3	*33*
Lomatia fraxinifolia	Mid-late	0.35	**0.43**	0.0	0.0	0.0	0.0	50.0	0.0	*31*

Table S6 Alternative generalised linear models (family gamma, log=link) to explain variation in SOC stocks in secondary forests with ΔAICc >4. Models are ranked by ΔAICc from lowest to highest.

	Intercept	Age	Basal area	Clay	Comp1	Comp2	Diversity	pH	Soil type	df	logLik	AICc	ΔAICc	weight
Mod5	4.38				0.169	0.024			+	5	-94.77	202.9	6.76	0.021
Mod9	4.15	-0.002	0.001				0.017		+	6	-93.20	203.3	7.23	0.017
Mod3	2.59			-0.003				0.357	+	5	-95.59	204.5	8.41	0.009
Mod8	2.83	0.005		-0.004				0.294	+	6	-94.45	205.8	9.73	0.005
Mod10	4.33	0.002			0.137	-0.005			+	6	-94.74	206.4	10.30	0.004
Mod6	1.46		0.000	0.003	-0.168	-0.248	0.030	0.440	+	9	-90.20	211.3	15.15	0

Chapter 6

General conclusion

This doctoral thesis investigated patterns of secondary forest recovery in two contrasting soil types in the Wet Tropics of Australia. Differences in substrates and their relationships with soil organic carbon and the structure and composition of woody plant communities and the communities of arbuscular mycorrhizal fungi were documented in detail in the previous data chapters. These investigations were a response to knowledge gaps identified in the literature review, where I found that there is surprisingly limited data on the effects of soil type and soil abiotic and biotic conditions on secondary forest regeneration despite its frequent mention of importance in the literature. Therefore, this thesis has contributed to the understanding of secondary forest succession, not only for Australian rainforests but for the field of forest ecology as a whole. In this final chapter, I revisit some of the key findings to provide a general conclusion and some future research directions.

6.1 Plant and fungal communities recover slowly in secondary forests

My central aim was to investigate secondary forest recovery in woody plant and arbuscular mycorrhizal fungi communities, in two dominant, contrasting soil types in the study area (basalt- and granite-derived soils). In Chapter 3, I examined nine different ecological aspects of forest recovery: woody plant alpha diversity, species dominance, numbers of stems, basal area, number of common species, number of rare species, the community composition of woody plants, and functional dispersion and divergence in 33 secondary forest sites, using

stand age, soil types and distance from remnant forest fragments to investigate forest recovery patterns.

Importantly, I found that as succession progressed over time in secondary forests, changes in basal area, species diversity and dominance were dependent on soil type. Although basal area and species alpha diversity increased with stand age in both soil types, in granite soil (less fertile) they seemed to increase at faster rates but from a low baseline in the young secondary forests. In contrast, secondary forests on basalt soils appeared to recover faster initially with respect to the number stems, species diversity and species dominance indices but subsequently plateaued as forests aged. After approximately 30 years, forests on granite accumulated significantly more stems, species diversity and dominance. The positive, steeper and increasing trend of species dominance in granite soil compared with basalt may indicate that dominance in the poorer soil may continue to facilitate species diversity over time. However, species dominance appears to be less important for woody species diversity in secondary forests of approximately 30 years or more which grow on more fertile soils. As a measure of forest recovery, diversity per se is limited, as plateauing may occur in a community but species turnover could still be high and indicative of continuing forest succession. This possibility needs to be explored in future studies as does the composition of the seedling community. Future studies could also experimentally test the role of fertility on species recruitment through the addition of fertilizer to permanent plots in the landscape.

In Chapter 4, I selected a subset of the study sites (n=18 sites in total) to analyse the richness and community composition of arbuscular mycorrhizal fungi (AMF). I described AMF taxa with next generation sequencing and explored its relationships with measures of soil fertility and forest recovery. I found that soil acidity and fertility were more important correlates with the richness and composition of the arbuscular mycorrhizal fungal community than soil texture or vegetation parameters. However, the numbers of AMF taxa responded differently to soil pH and nutrient content. Whereas soil pH was positively related to AMF

richness in both soil types, the influence of soil fertility depends on the soil type. Not surprisingly, since arbuscular mycorrhizal fungi assist trees in the uptake of nutrients, higher levels of P and N in the more fertile soil were accompanied by reduced numbers of AMF taxa. However, in granite I observed the opposite trend. The mechanisms that explain the positive correlation of number of AMF taxa with increasing soil nutrients in granite soils is unknown, but I hypothesized that a minimum fertility level (*e.g.* nutrients and soil organic matter) is necessary to support AMF diversity. The variation in AMF richness along the P gradient regardless of soil types indicates that at intermediate fertility AMF richness is higher.

The differences I observed between soil types in the community composition of both woody plants and arbuscular mycorrhizal fungi add empirical evidence to the theories of forest succession in poor and fertile soils proposed by Connell and Slatyer (1977) and Janos (1980), respectively. Connell and Slatyer (1977) proposed that variations in soil nutrient and moisture could regulate species coexistence, and potentially the trajectories of secondary forest regeneration, by mechanisms of facilitation and tolerance. Similarly, Janos (1980) suggested that plant communities on more fertile soils would demonstrate lower dependence on the mycorrhizal association, which would result in fewer fungal hyphae in the soil. My results indicate that the arbuscular mycorrhizal fungi community is less diverse in more fertile soil, but mature forests provide the best evidence. Secondary forests, although demonstrating different community composition, had similar mycorrhizal diversity. Examination of species-specific interactions between plants and mycorrhizal fungi, and measures of fungal species abundance from these secondary forests would help to elucidate the mechanisms involved in the composition of and links between plant and fungal communities across soils of different fertility.

Basalt and granite soils shared a third of the total number of woody species (35.9%), indicating that soil fertility can shape plant communities at this local scale (Grime 2006). However, unlike woody plant communities, more than half (60.3%) of the mycorrhizal taxa

were shared by the two soil types. Additionally, the virtual taxa recorded in this study comprise one quarter of the world's known mycorrhizal taxa. These results support the notion that arbuscular mycorrhizal fungi can associate with different plant species, with little or no species-specificity (Brundrett 2004). However, basal groups of fungi were also found in my sites and these may be more closely-linked to the plant community. The tropical rainforests of north-eastern Australia are recognized as communities comprised of high numbers of 'primitive' plants. Phylogenetic relationships among plants and arbuscular fungi should be explored in the future, which may bring new insights to the strategies of these plants to cope with environmental changes.

6.2 Secondary forests offer great opportunities as soil carbon pool

It has become evident that secondary forests need to be included in estimations and predictions about the global C budget (Lugo and Brown 1992, Letcher and Chazdon 2009, Grace *et al*. 2014). In Chapter 5 I analysed the changes in soil carbon stocks during forest succession in the two soil types. For this study, I also selected a subset of the secondary forests (33 sites) and included six sites on active pastures close to the secondary and mature forest sites. I found that soil carbon stocks in secondary forests were comparable to those in the active pasture and in some cases to mature forests. However, the C isotopic composition (measured as the variation in ^{12}C to ^{13}C) in pastures differed between secondary and mature forests. The two soil types had slightly different rates of soil carbon accumulation and isotopic composition during forest succession, but soil properties and vegetation characteristics seem to be better predictors of changes in C than forest age (measured as years since pasture abandonment).

Based on these results I suggest that soil carbon stocks are dynamic and can accumulate quite rapidly in secondary forests on granite soils, therefore, estimations of C

stocks can be improved by considering differences in soil types. A key finding from Chapter 5 was related to the contrasting patterns of SOC stock during forest succession in the different soil types. In the poorer soil (granite), SOC stocks seem to respond more promptly to increases in soil fertility, basal area and woody species diversity, whereas in the more fertile soil (basalt) SOC stock does not increase significantly with the same parameters. However, basalt soil seemed more resistant to pasture use as, in this soil type, estimates of SOC stocks for secondary forests were usually similar to mature forest sites. The ability of SOC stocks to recover in secondary forests on granite soils and the high levels of SOC found in basalt soils provide good news as there is a desperate requirement to sequester C from the atmosphere in the face of global climate change (FCCC 2015).

Nonetheless, the conclusion about whether secondary forests are recovering rapidly depends on the type of ecological feature in which we are interested. If the aim is to recover and protect biological and functional diversity, a few decades may not be sufficient. Alternatively, if the aim is to improve carbon stocks, either in above-ground biomass or soil carbon stocks, positive results could be achieved in relatively short periods of time - between 20 to 30 years. My results agree with other studies across the tropics which have shown that within two to three decades secondary forests are able to increase basal area (a proxy to above-ground biomass) and soil carbon stocks similar to levels of mature forests if abandoned lands are relatively close (<1000m) to remnant forest fragments (Marín-Spiotta and Sharma 2013, Sloan *et al*. 2016).

6.3 Final statements

In summary, the nutritional and textural distinction between soil types remains apparent during forest succession, indicating that the major edaphic properties of some parent materials are only marginally affected or unaffected after long-term agricultural use. Not

surprisingly, woody plant communities, mycorrhizal fungi and soil carbon stocks seem to respond to soil type differences at the local scale. Nonetheless, continued investigation of the interactions of plants, fungi and carbon stocks and experimentation into the regeneration process of tropical forests will likely produce ever more interesting and practical ecological evidence to better understand and manage tropical forests. The research reported in this thesis has produced outcomes that should add to the ecological understanding of secondary forests, with a special focus on the Wet Tropics of Australia, where the agricultural lands are relatively old (100 years) and secondary forests have received less attention compared with other forests in the world.

Concerns about tropical rainforest loss and attention to topics involving ecosystem regeneration need to continue. Despite primary forests being considered irreplaceable (Gibson *et al*. 2011), my results indicate that old secondary forests can potentially become biologically and functionally rich systems with relatively high conservation value (Chazdon 2014, Breugel *et al*. 2013). To allow secondary forests to reach communities similar to mature forests, human actions, such as enrichment of forests with late successional and rarer species, are likely to be needed. With high rates of forest loss and slow forest recovery globally (Hansen *et al*. 2013), there is an imminent risk of landscapes being totally transformed into degraded, less heterogeneous forests that are less resilient or resistant to disturbance (Walker 1992, Gunderson 2000). For instance, tropical cyclones are predicted to become more intense in northeast Australia due to accelerated changes in the global climate (Hughes 2003). The vulnerability of secondary forests should be a matter of concern and the subject of future research.

References

Ackerly, D.D., 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecol. Monog. 74:25–44.

Abbott, L.K., Robson, a. D., 1991. Factors influencing the occurrence of vesicular-arbuscular mycorrhizas. Agric. Ecosyst. Environ. 35, 121–150.

Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L., Marcano-Vega, H., 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Rest. Ecol. 8, 328–338.

Aide,T.M., Zimmerman, J.K., Rosario, M., Marcano, H., 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica 28, 537–548.

Allen, M.F., Swenson, W., Querejeta, J.I., Egerton-Warburton, L.M., Treseder, K.K., 2003. Ecology of mycorrhizae: conceptual framework for complex interactions among plants and fungi. Ann. Rev. Phyt. 41, 271–303.

Allen, J.C., 1985. Soil response to forest clearing in the United States and the tropics: geological and biological factors. Biotropica 17, 15–27.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Aust. Ecol., 26: 32–46.

Avio, L., Pellegrino, E., Bonari, E., Giovannetti, M., 2006. Functional diversity of arbuscular mycorrhizal fungal isolates in relation to extraradical mycelial networks. New Phytol. 172, 347–57.

Bakker, J.D., Wilson, S.D., 2004. Using ecological restoration to constrain biological invasion. J. Appl. Ecol. 41, 1058–1064.

Barbier, E.B. 1997. The economic determinants of land degradation in developing countries. Phil. Trans. R. Soc. Lond. B. 352, 891-889.

Bauhus, J., Khanna, P.K., Hopmans, P., Weston, C., 2002. Is soil carbon a useful indicator of sustainable forest soil management?—a case study from native eucalypt forests of south-eastern Australia. For. Ecol. Manag. 171, 59–74.

Bazzaz, F., 1979. The physiological ecology of plant succession. Ann. Rev. Ecol. Syst. 10, 351–371.

Beauregard, F., De Blois, S., 2014. Beyond a climate-centric view of plant distribution: Edaphic variables add value to distribution models. PLoS One 9, e92642.

Becknell, J.M., Powers, J.S., 2014. Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. Can. J. For. Res. 613, 604–613.

Benayas, J.M.R., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: an overview of drivers and consequences. CAB Rev Perspect. Agric. Vet. Sci. Nutr. Nat. Resour. 2, 1–14.

Berthrong, S.T., Jobbágy, E.G., Jackson, R.B., 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. Ecol. Appl. 19, 2228–2241.

Bever, J.D., 2002. Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. Proc. Biol. Sci. 269, 2595–601.

Blaser, J., Sarre, A., Poore, D., Johnson, S., 2011. Status of Tropical Forest Management, International Tropical Timber Organization.

Bolan, N.S., 1991. A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant Soil 134, 189–207.

Breugel, M. Van, Hall, J.S., Craven, D., Bailon, M., Hernandez, A., Abbene, M., Breugel, P. Van, 2013. Succession of ephemeral secondary forests and their limited role for the conservation of floristic diversity in a human-modified tropical landscape. PLoS One 8, 1–13.

Brown, S., Lugo, A.E., 1990. Tropical secondary forests. J. Trop. Ecol. 6, 1–32.

Brundrett, M., 2004. Diversity and classification of mycorrhizal associations. Biol. Rev. 79, 473–95.

Bunker, D.E., Declerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L., Sankaran, M., Naeem, S., 2005. Species loss and aboveground carbon storage in a tropical forest. Science 310, 1029–31.

Bureau of Meteorology (BOM). 2014. Rainfall figures for Millaa Millaa and Malanda, Queensland, Australia. Accessed September 2014. http://www.bom.gov.au/climate/data/index.shtml

Bureau of Meteorology (BOM). 2016. Rainfall figures for Millaa Millaa and Malanda, Queensland, Australia. Accessed April 2016. http://www.bom.gov.au/cyclone/history/eastern.shtml

Burrows, R.L., Pfleger, F.L., 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. Can. J. Bot. 80, 120–130.

Buschbacher, R., Uhl, C., Serrão, E.A.S., 1988. Abandoned Pastures in Eastern Amazonia . II . Nutrient Stocks in the Soil and Vegetation. J. Ecol. 76, 682–699.

Cáceres, M. De, 2013. How to use the indicspecies package (ver. 1.7.1). R Proj. 29.

Callaway, R.M., 1995. Positive interactions among plants. Bot. Rev. 61, 306–349.

Callaway, R.M., Walker, L.R., 1997. Competition and Facilitation: A Synthetic Approach to Interactions in Plant Communities. Ecology 78, 1958–1965.

Cameron, K.C., Di, H.J., Moir, J.L., 2013. Nitrogen losses from the soil/plant system: a review. Ann. Appl. Biol. 162, 145–173.

Chapin III, S. F., 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11, 233–260.

Chapin III, S., McFarland, J.F., McGuire D., Euskirchen, E.S., Ruess, R.W., Kielland, K., 2009. The changing global carbon cycle: linking plant-soil carbon dynamics to global consequences. J. Ecol. 97, 840–850.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. Ecol. Let. 12, 351-366.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., ter Steege, H., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecol. Appl. 16, 2356 – 2367.

Chazdon, R.L. 2014. Second growth: the promise of tropical forest regeneration in an age of deforestation. Chicago: University of Chicago Press. 472 p. ISBN: 9780226118079.

Chazdon, R.L., 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320, 1458–60.

Chazdon, R.L., Letcher, S.G., van Breugel, M., Martinez-Ramos, M., Bongers, F., Finegan, B., 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. Philos. Trans. R. Soc. B Biol. Sci. 362, 273–289.

Chen, G., Yang, Y., Yang, Z., Xie, J., Guo, J., Gao, R., Yin, Y., Robinson, D., 2016. Accelerated soil carbon turnover under tree plantations limits soil carbon storage. Sci. Rep. 6, 19693. DOI 10.1038/srep19693.

Chinea, J.D. 2002. Tropical forest succession on abandoned farms in the Humacao Municipality of eastern Puerto Rico. For. Ecol. Manag., 167(1-3), 195–207.

Christensen, N.L., Peet, R.K., 1984. Convergence during secondary forest succession. J. Ecol. 72, 25–36.

Clark, D.B., Palmer, M.W., Clark, D.A., 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology 80, 2662–2675.

Coley, P.D., Bryant, J.P., Chapin, FS. 1985. Resource availability and plant antiherbivore defense. Science 230: 895-899.

Condit, R., Asthon, P., Bunyavejchewin, S., Dattaraja, H.S., Davies, S. 2006. The importance of demographic niches to tree diversity. Science 313:98-101.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science. 199, 1302–1310.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. Am. Nat. 111, 1119–1144.

Coomes, D.A, Allen, R.B., 2007. Effects of size, competition and altitude on tree growth. J. Ecol. 95, 1984-1097.

Coomes, D.A, Grubb, P.J., 2003. Colonization, tolerance, competition and seed-size variation within functional groups. Trends in Ecol Evol. 18, 283-291.

Corlett, R.T., 1994. What is secondary forest? J. Trop. Ecol. 10, 445–447.

Coughlan, A.P., Dalpé, Y., Lapointe, L., Piché, Y., 2000. Soil pH-induced changes in root colonization, diversity, and reproduction of symbiotic arbuscular mycorrhizal fungi from healthy and declining maple forests. Can. J. For. Res. 30, 1543–1554.

Cramer, V. a, Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol. Evol. 23, 104–12.

Dalling, J.W., Denslow, J.S., 1998. Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest , Panama. J. Veg. Sci. 9, 669–678.

Dalling, J.W., Hubbell, S.P., 2002. Seed size , growth rate and gap microsite conditions as. J. Ecol. 557–568.

Davidson, E. a, Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

Davidson, E.A., Carvalho, C.J.R. de, Vieira, I.C.G., Figueiredo, R. de O., Moutinho, P., Ishida, F.Y., Santos, M.T.P., Benito, G.J., Kalif, K., Sabá, R.T., 2004. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecol. Appl. 14, 150-163.

Davison, J., Moora, M., Opik, M., Adholeya, A., Ainsaar, L., Ba, A., Burla, S., Diedhiou, A.G., Hiiesalu, I., Jairus, T., Johnson, N.C., Kane, A., Koorem, K., Kochar, M., Ndiaye, C., Partel, M., Reier, U., Saks, U., Singh, R., Vasar, M., Zobel, M., 2015. Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. Science. 349, 970–973.

Davison, J., Öpik, M., Zobel, M., Vasar, M., Metsis, M., Moora, M., 2012. Communities of arbuscular mycorrhizal fungi detected in forest soil are spatially heterogeneous but do not vary throughout the growing season. PLoS One 7, e41938.

Dawud, S.M., Raulund-Rasmussen, K., Domisch, T., Finér, L., Jaroszewicz, B., Vesterdal, L., 2016. Is Tree Species Diversity or Species Identity the More Important Driver of Soil Carbon Stocks, C/N Ratio, and pH? Ecosystems, online DOI 10.10007/s10021-016-9958-1.

Defries, R.S., Foley, J.A., Asner, G.P., 2004. Land-use choices: balancing human needs and ecosystem function. Front. Ecol. Environ. 2, 249–257.

Dent, D.H., DeWalt, S.J., Denslow, J.S., 2013. Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. J. Veg. Sci. 24, 530–542.

Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A, Zak, M. R., 2004. The plant traits that drive ecosystems: Evidence from three continents. J. Veg Sci 15, 295-304.

Dighton, J., 2009. Mycorrhizae, in: Mutualism and Commensalism. Elsevier, pp. 153–162.

Dixon, R.K., Solomon, a M., Brown, S., Houghton, R. a, Trexier, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–90.

do Nascimento, L.M., de Sá Barretto Sampaio, E.V., Rodal, M.J.N., Lins-e-Silva, A.C.B., 2014. Secondary succession in a fragmented Atlantic Forest landscape: evidence of structural and diversity convergence along a chronosequence. J. For. Res. 501–513.

Dufrêne, M., Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monog. 67: 345-366.

Dwyer, J.M., Fensham, R.J., Buckley, Y.M., 2010. Agricultural legacy, climate, and soil influence the restoration and carbon potential of woody regrowth in Australia. Ecol. Appl. 20, 1838–50.

Ehrenfeld, J.G., Ravit, B., Elgersma, K., 2005. Feedback in the Plant-Soil System. Ann. Rev. Environ. Resour. 30, 75–115.

Ellert, B.H., Janzen, H.H., Vandenbygaart, A.J., Bremer, E., 2008. Measuring changes in soil organic carbon storage. In: Carter, M.R., Gregorich (Eds.), Soil Sampling Methods of Analysis, 2nd ed. Canadian Society of Soil Science, CRS Press, pp. 25-38.

Ellison, A.M., 2001. Interspecific and intraspecific variation in seed size and germination requirements of Sarracenia (Sarraceniaceae). Am. J. Bot. 88, 429-437.

FAO, Food and Agriculture Organization of the United Nations. 2005. The importance of soil organic matter. FAO Soils Bulletin 80. 77p.

FCCC, 2015. Paris Agreement. In: Change FCoC (ed), vol. FCCC/CP/2015/L.9. United Nations, Paris.

Fearnside, P.M., Barbosa, R.I., 1998. Soil carbon changes from conversion of forest to pasture in Brazilian Amazonia. For. Ecol. Manag. 108, 147–166.

Feldpausch, T.R., Prates-Clark, C.D.C., Fernandes, E.C.M., Riha, S.J., 2007. Secondary forest growth deviation from chronosequence predictions in central Amazonia. Glob. Chang. Biol. 13, 967–979.

Feldpausch, T.R., Rondon, M.A., Fernandes, E.C.M., Riha, S.J., Wandelli, E., 2004. Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. Ecol. Appl. 14, 164–176.

Fernandes, D.N., Sanford, R.L.J., 1995. Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. Conserv. Biol. 9, 915–922.

Finegan, B., 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. Trends Ecol. Evol. 11, 119–124.

Fischer, C.R., Janos, D.P., Perry, D.A., Linderman, R.G., Sollins, P., 1994. Mycorrhiza Inoculum Potentials in Tropical Secondary Succession Mycorrhiza Inoculum Potentials in Tropical Secondary Succession1. Biotropica 26, 369–377.

Flynn, D.F.B., Uriarte, M., Crk, T., Pascarella, J.B., Zimmerman, J.K., Aide, T.M., Caraballo Ortiz, M. a., 2010. Hurricane Disturbance Alters Secondary Forest Recovery in Puerto Rico. Biotropica 42, 149–157.

Fortini, L.B., Bruna, E.M., Zarin, D.J., Vasconcelos, S.S., Miranda, I.S., 2010. Altered resource availability and the population dynamics of tree species in Amazonian secondary forests. Oecologia 162, 923–34.

Fortunel, C., Paine, C.E.T., Fine, P.V. a, Kraft, N.J.B., Baraloto, C., 2014. Environmental factors predict community functional composition in Amazonian forests. J. Ecol. 102, 145–155.

Fox, J., Weisberg, S. 2011. An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage.

Frawley, K.J., 1987. The Maalan group settlement North Queensland 1954: an historical geography. University of New South Wales Department of Geography & Oceanography Monograph series No. 2.

Fyllas, N., Patino, S., Baker, T.R., Nardoto, G.B., Martinelli, L., Quesada, C., Paiva, R., Schwarz, M., Horna, V., Mercado, L.M., others, 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. Biogeosciences 6, 2677–2708.

Geist, H.J., and Lambin, E.F. 2002. Proximate causes and underlying driving forces or tropical deforestation. BioScience. 52, 143-150.

Gehring, C. a, Connell, J.H., 2006. Arbuscular mycorrhizal fungi in the tree seedlings of two Australian rain forests: occurrence, colonization, and relationships with plant performance. Mycorrhiza 16, 89–98.

George, E., Marschner, H., Jakobsen, I., 1995. Role of Arbuscular Mycorrhizal Fungi in Uptake of Phosphorus and Nitrogen From Soil. Crit. Rev. Biotechnol. 15, 257–270.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.

Gilmore, M.A., 2005. Kill, cure or strangle: the history of government intervention in three key agricultural industries on the Atherton Tablelands, 1895-2005. Ph.D. thesis, James Cook University, Cairns, Australia.

Givnish, T.J., 1999. On the causes of gradients in tropical tree diversity. J. Ecol. 87, 193–210.

Gleason, S.M., Read, J., Ares, A., Metcalfe, D.J., 2010. Species–soil associations, disturbance, and nutrient cycling in an Australian tropical rainforest. Oecologia 162, 1047–1058.

Gleason, S.M., Williams, L.J., Read, J., Metcalfe, D.J., Baker, P.J., 2008. Cyclone effects on the structure and production of a tropical upland rainforest: Implications for life-history tradeoffs. Ecosystems 11, 1277–1290.

Goldsmith, G.R., Comita, L.S., Chua, S.C., 2011. Evidence for arrested succession within a tropical forest fragment in Singapore. J. Trop. Ecol. 27, 323–326.

Goosem, M., Paz, C., Fensham, R., Preece, N., Goosem, S., Laurance, S.G.W., 2016. Forest age and isolation affect the rate of recovery of plant species diversity and community composition in secondary rain forests in tropical Australia. J. Veg. Sci.

Goosem, S. and Tucker, N.I.J., 2013. Repairing the Rainforest (second edition). Wet Tropics Management Authority and Biotropica Australia Pty. Ltd. Cairns, 158 pp.

Goosem, S., Morgan, G., Kemp, J.E. ,1999. Wet tropics. In: P. Sattler, R. Williams. The conservation status of Queensland's bioregional ecosystems. Brisbane: Environmental Protection Agency. p. 7/1–7/73.

Gotelli, N., Colwell, R., 2011. Estimating species richness. Biol. Divers. Front. Meas. Assess. 39–54.

Grace, J., Mitchard, E., Gloor, E., 2014. Perturbation in the carbon budget of the tropics. Glob. Chang. Biol 20, 3238-3255.

Greacen, E., Sands, R., 1980. Compaction of forest soils. A review. Aust. J. Soil Res. 18, 163.

Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. J. Veg. Sci. 17, 255–260.

Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. For. Ecol. Manag. 148, 185–206.

Guggenberger, G., Zech, W., 1999. Soil organic matter composition under primary forest, pasture, and secondary forest succession, Región Huetar Norte, Costa Rica. For. Ecol. Manag. 124, 93–104.

Gunderson, L.H., 2000. Ecological resilience — in theory and application. Ann. Rev. Ecol. Syst. 31, 425–439.

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta-analysis. Glob. Chang. Biol. 8, 345–360.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., McCulloh, K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126, 547-461.

Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V, Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-Century forest cover change. Science 342, 850–853.

Harrell Jr. F.E., 2014. rms: Regression Modeling Strategies. R package version 4.2-0, URL http://CRAN.R-project.org/package=rms.

Hattenschwiler, S., Tiunov, A. V., Scheu, S., 2005. Biodiversity and Litter Decomposition in Terrestrial Ecosystems. Ann. Rev. Ecol. Evol. Syst. 36, 191–218.

Helgason, T., Merryweather, J.W., Young, J.P.W., Fitter, A.H., 2007. Specificity and resilience in the arbuscular mycorrhizal fungi of a natural woodland community. J. Ecol. 95, 623–630.

Herre, E.A., Kyllo, D., Mangan, S., Husband, R., Mejia, L.C., Eom, A.-H., 2005. An overview of arbuscular mycorrhizal fungal composition, distribution and host effects from a tropical moist forest, in: Burslem, D.F.R.P., Pinard, M.A., Hartley, S.E. (Eds.), Biotic Interactions in

the Tropics: Their Role in the Maintenance of Species Diversity. Cambridge University Press, Cambridge, pp. 204–225.

Herrera, B., Finegan, B., 1997. Substrate conditions, foliar nutrients and the distributions of two canopy tree species in a Costa Rican secondary rain forest. Plant Soil 191, 259–267.

Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. Trends Ecol. Evol. 24, 599–605.

Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.

Holl, K.D., Loik, M.E., Lin, E.H. V., Samuels, I. a., 2000. Tropical Montane Forest Restoration in Costa Rica: Overcoming Barriers to Dispersal and Establishment. Rest. Ecol. 8, 339–349.

Hooper, E., Legendre, P., Condit, R., 2004. Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. Ecology 85, 3313–3326.

Hooper, E., Legendre, P., Condit, R., 2005. Barriers to forest regeneration of deforested and abandoned land in Panama. J. Appl. Ecol. 42, 1165–1174.

Houghton, R., 1995. Land-use change and the carbon cycle. Glob. Chang. Biol. 1, 275–287.

Howorth, R.T., Pendry, C. a., 2006. Post-cultivation secondary succession in a Venezuelan lower montane rain forest. Biodiv. Conserv. 15, 693–715.

Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon , and nutrient dynamics of secondary forests in a humid tropical region of México. Ecology 80, 1892–1907.

ITTO, 2002. ITTO guidelines for the restoration , management and rehabilitation of degraded and secondary ITTO guidelines for the restoration , management and rehabilitation of. Organization 84.

Janos, D.P., 1980. Mycorrhizae influence tropical succession. Biotropica 12, 56–64.

Jeffries, P., Gianinazzi, S., Perotto, S., Tarnau, K., Barea, J.-M., 2003. The contribution of arbuscular mycorrhizal fungi in sustainable maintenance of plant health and soil fertility. Biol. Fertil. Soils 37, 1–16.

John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M., Foster, R.B., 2007. Soil nutrients influence spatial distributions of tropical tree species. Proc. Natl. Acad. Sci. U. S. A. 104, 864–9.

Johnson, C.M., Vieira, I.C.G., Zarin, D.J., Frizano, J., Johnson, A.H., 2001. Carbon and nutrient storage in primary and secondary forests in eastern Amazonia. For. Ecol. Manag. 147, 245–252.

Johnson, C.M., Zarin, D.J., Johnson, A.H., 2000. Post-disturbance aboveground biomass accumulation in global secondary sorests. Ecology 81, 1395–1401.

Johnson, E. a., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. Ecol. Lett. 11, 419–431.

Kaiser, K., Guggenberger, G., 2003. Mineral surfaces and soil organic matter. Eur. J. Soil Sci. 54, 219–236.

Kappelle, M., Kennis, P.A.F., Devries, R.A.J., 1995. Changes in diversity along a successional gradient in a Costa-Rican upper montane Quercus forest. Biodiv. Conserv. 4, 10–34.

Kardol, P., Bezemer, T.M., van der Putten, W.H., 2006. Temporal variation in plant-soil feedback controls succession. Ecol. Lett. 9, 1080–8.

Kauffman, J.B., Hughes, R.F., Heider, C. 2009. Carbon pool and biomass dynamics associated with deforestation, land use, and agricultural abandonment in the Neotropics. Ecol. Appl. 19, 1211-1222.

Kernaghan, G., 2005. Mycorrhizal diversity: Cause and effect? Pedobiologia (Jena). 49, 511–520.

Kerridge, P.C., Andrew, C.S., Mwtha, G.G., 1972. Plant nutrient status of soils of the Atherton Tableland , North Queensland. Aust. J. Exp. Agric. Anim. Husb. 12, 618–627.

Klanderud, K., Mbolatiana, H.Z.H., Vololomboahangy, M.N., Radimbison, M.A., Roger, E., Totland, Ø., Rajeriarison, C., 2010. Recovery of plant species richness and composition after

slash-and-burn agriculture in a tropical rainforest in Madagascar. Biodiv. Conserv. 19, 187–204.

Knops, J.M.H. and Tilman. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. Ecology 81, 88-98.

Laganière, J., Angers, D.A., Paré, D., 2010. Carbon accumulation in agricultural soils after afforestation: A meta-analysis. Glob. Chang. Biol. 16, 439–453

Lal, R., 2004. Soil carbon sequestration to mitigate climate change. Geoderma 123, 1–22.

Lal, R., 2005. Forest soils and carbon sequestration. For. Ecol. Manag. 220, 242–258.

Laliberté, A.E., Shipley, B., Laliberté, M.E., 2012. Package " FD " 1–27

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305.

Lamb, D., 2011. Natural Regeneration and Secondary Forests, in: Regreening the Bare Hills. Springer Science, pp. 157–209.

Lamb, D., Erskine, P.D., Parrotta, J. a, 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–32.

Lambers, H., Raven, J.A., Shaver, G.R., Smith, S.E., 2008. Plant nutrient-acquisition strategies change with soil age. Trends Ecol. Evol. 23, 95–103.

Langsrud, Ø., 2003. ANOVA for unbalanced data: Use Type II instead of Type III sums of squares. Stat. Comput. 13, 163–167.

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K.S., Cannon, C.H., Cao, M., Carroll, R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E., Donnelly, M.A., Edwards, D., Edwards, F., Farwig, N., Fashing, P., Forget, P.-M., Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W., Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A.R., McClearn, D., Mudappa, D., Nielsen, M.R.,

Pearson, R., Pitman, N., van der Ploeg, J., Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero, F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm, R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Carlos Arias-G., J., Arroyo, L., Ashton, M., Auzel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O., Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Brühl, C.A., Bunyavejchewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C.J., Clavijo, J., Congdon, R., Corlett, R., Dattaraja, H.S., Dave, C., Davies, G., de Mello Beisiegel, B., de Nazaré Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton, M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone Willis, J., Goodale, U., Goodman, S., Guix, J.C., Guthiga, P., Haber, W., Hamer, K., Herbinger, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes, B., Janovec, J., Janzen, D., Jiangming, M., Jin, C., Jones, T., Justiniano, H., Kalko, E., Kasangaki, A., Killeen, T., King, H., Klop, E., Knott, C., Koné, I., Kudavidanage, E., Lahoz da Silva Ribeiro, J., Lattke, J., Laval, R., Lawton, R., Leal, M., Leighton, M., Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E., Lugo, A., Lwanga, J., Mack, A.L., Martins, M., Scott McGraw, W., McNab, R., Montag, L., Myers Thompson, J., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M., Novotny, V., O'Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N., Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G., Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rödel, M.-O., Rothman, J., Round, P., Sakai, S., Sanaiotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M.R., Smith, T.B., de Almeida, S.S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner, K.E., Sukumar, R., Surbeck, M., Tobler, M., Tscharntke, T., Turkalo, A., Umapathy, G., van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Verea, C., Volkmer de Castilho, C., Waltert, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D., Whitney, K., Wilkie, D., Williams, S., Wright, D.D., Wright, P., Xiankai, L., Yonzon, P., Zamzani, F., 2012. Averting biodiversity collapse in tropical forest protected areas. Nature 489, 290–294.

Leps, J., Rejmanek, M., 1991. Convergence or Divergence - What Should We Expect from Vegetation Succession. Oikos 62, 261–264.

Letcher, S.G. and Chazdon, R.L. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica, 41 (5), 608-617.

Lindenmayer, D.B., Fischer, J., Felton, A., Crane, M., Michael, D., Macgregor, C., Montague-Drake, R., Manning, A., Hobbs, R.J., 2008. Novel ecosystems resulting from landscape transformation create dilemmas for modern conservation practice. Conserv. Lett. 1, 129–135.

Lohbeck, M., Poorter, L., Martínez-Ramos, M., Rodriguez-Velázquez, J., van Breugel, M., Bongers, F., 2014. Changing drivers of species dominance during tropical forest succession. Funct. Ecol. 28, 1052–1058.

Lohbeck, M., Poorter, L., Paz, H., Pla, L., van Breugel, M., Martínez-Ramos, M., Bongers, F., 2012. Functional diversity changes during tropical forest succession. Perspect. Plant Ecol. Evol. Syst. 14, 89–96.

Long, W., Yang, X., Li, D., 2012. Patterns of species diversity and soil nutrients along a chronosequence of vegetation recovery in Hainan Island, South China. Ecol. Res. 27(3), 561–568.

López-Ulloa, M., Veldkamp, E., de Koning, G.H.J., 2005. Soil carbon stabilization in converted tropical pastures and forests depends on soil type. Soil Sci. Soc. Am. J. 69, 1110–1117.

Lugo, A.E. and Brown, S. 1992. Tropical forests as sinks of atmospheric carbon. For. Ecol. Manag. 54, 239-255.

Lugo, A.E., 2004. The outcome of alien tree invasions in Puerto Rico. Front. Ecol. Environ. 2, 265–273.

Lugo, A.E., 2009. The Emerging Era of Novel Tropical Forests. Biotropica 41, 589–591.

Lugo, A.E., Helmer, E., 2004. Emerging forests on abandoned land: Puerto Rico's new forests. For. Ecol. Manag. 190, 145–161.

Maggs, J., Hewett, B., 1993. Organic C and nutrients in surface soils from some primary rainforests, derived grasslands and secondary rainforests on the Atherton Tableland in North East Queensland. Aust. J. Soil Res. 31, 343–350.

Magurran, A.E., 2004 Measuring biological diversity. Oxford: Blackwell Science.

Maherali, H., Klironomos, J.N., 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316, 1746–8.

Malcolm, D.T., Nagel, B.K.A., Sinclair, I., Heiner, I.J., 1999. Land Resources Bulletin. Department of Natural Resources Queensland, Brisbane. 241p.

Malhi, Y., Adu-Bredu, S., Asare, R.A., Lewis, S.L., Mayaux, P. 2013. African rainforests: past, present and future. Phil. Trans. R. Soc. B 368, 20120312.

Marín-Spiotta, E., Sharma, S., 2013. Carbon storage in successional and plantation forest soils: a tropical analysis. Glob. Ecol. Biogeo. 22, 105–117.

Marín-Spiotta, E., Ostertag, R., Silver, W.L., 2007. Long-Term Patterns in Tropical Reforestation : Plant Community Composition and Aboveground Biomass Accumulation. Ecol. Appl. 17, 828–839.

Martin, P.A., Newton, A.C., Bullock, J.M., 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proc. R. Soc. B Biol. Sci. 280, 1–8.

McGroddy, M.E., Silver, W.L., 2011. Biogeochemical cycling in tropical forests, in: Bush, M.B., Flenley, J.R., Gosling, W.D. (Eds.), Tropical Rainforest Responses to Climatic Change. Springer-Verlag, Berlin, Heidelberg, pp. 1–27.

McLauchlan, K., 2006. The nature and longevity of agricultural impacts on soil carbon and nutrients: A review. Ecosystems 9, 1364–1382.

Meiners, S.J., Cadotte, M.W., Fridley, J.D., Pickett, S.T.A., Walker, L.R., 2015. Is successional research nearing its climax? New approaches for understanding dynamic communities. Funct. Ecol. 29, 154–164.

Mesquita, R.C.G., Ickes, K., Ganade, G., Williamson, G.B., 2001. Alternative successional pathways in the Amazon Basin. J. Ecol. 89, 528-537.

Metcalfe, D.J., Ford, A.J., 2009. A re-avaluation of Queensland's Wet Tropics based on "primitive" plants. Pacif Cons. Biol 15, 80-86.

Mitchell, C.E., Agrawal, A. a, Bever, J.D., Gilbert, G.S., Hufbauer, R. a, Klironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G., Seabloom, E.W., Torchin, M.E., Vázquez, D.P., 2006. Biotic interactions and plant invasions. Ecol. Lett. 9, 726–40.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global biodiversity conservation: the critical role of hotspots, in: Biodiversity Hotspots.

Mokany, K.,Raison, R.J., Prokushkin, A.S. 2006. Critical analysis of root:shoot ratios in terrestrial biomes. Glob Chan Biol. 12, 84-96.

Muñiz-Castro, M.A., Williams-Linera, G., Benayas, J.M.R., 2006. Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico. J. Trop. Ecol. 22, 431-440.

Munroe, K.D., van Berkel, D.B., Verburg, P.H., Olson, J. 2013. Alternative trajectories of land abandonment: causes, consequences and research challenges. Cur. Op. Environ. Sustain. 5, 471-476.

Nepstad, D.C., Uhl, C. Serrão, E.A.S., 1991. Recuperation of a degraded Amazonian landscapes: Forest recovery and agricultural restoration. Ambio 20, 248-255.

Nicol, G.W., Leininger, S., Schleper, C., Prosser, J.I., 2008. The influence of soil pH on the diversity, abundance and transcriptional activity of ammonia oxidizing archaea and bacteria. Environ. Microbiol. 10, 2966–2978.

Norden, N., Mesquita, R.C.G., Bentos, T. V., Chazdon, R.L., Williamson, G.B., 2011. Contrasting community compensatory trends in alternative successional pathways in central Amazonia. Oikos 120, 143–151.

Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.-H., Vílchez-Alvarado, B., 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. Ecol. Lett. 12, 385–394

Ordoñez, J.C., van Bodegom, P.M., Witte, J.-P.M., Wright, I.J., Reich, P.B., Aerts, R., 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. Glob. Ecol. Biogeogr. 18, 137–149.

O'Sullivan, M.F., Simota, C., 1995. Modelling the environmental impacts of soil compaction: a review. Soil Till. Res. 35, 69–84.

Oksanen, J., Blanchet, F.G., Kindt R., Legendre P., Minchin P.R., O'Hara, R.B., Gavin L. Simpson G.L., Solymos P., Stevens, M.H.H., Wagner H. 2013. Vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Öpik, M., Vanatoa, a., Vanatoa, E., Moora, M., Davison, J., Kalwij, J.M., Reier, Ü., Zobel, M., 2010. The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). New Phytol. 188, 223–241.

Pan, Y., Birdsey, R. a, Fang, J., Houghton, R., Kauppi, P.E., Kurz, W. a, Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, a D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–93.

Parsons, S. a., Congdon, R. a., 2008. Plant litter decomposition and nutrient cycling in north Queensland tropical rain-forest communities of differing successional status. J. Trop. Ecol. 24.

Pascarella, J.B., Aide, T.M., Serrano, M.I., Zimmerman, J.K., 2000. Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. Ecosystems 3, 217-228.

Peña-Claros, M., 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. Biotropica 35, 450–461

Peltzer, D.A., Wardle, D.A., Allison, V.J., Baisden, W.T., Bardgett, R.D., Chadwick, O.A., Condron, L.M., Parfitt, R.L., Porder, S., Richardson, S.J., Turner, B.L., Vitousek, P.M., Walker, J., Walker, L.R., 2010. Understanding ecosystem retrogression. Ecol. Monogr. 80, 509–529.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Ann. Rev. Ecol. Syst. 18, 293–320.

Picone, C., 2000. Diversity and abundance of arbuscular-mycorrhizal fungus spores in tropical forest and pasture. Biotropica 32, 734–750.

Pinheiro, J., Bates, B., DebRoy, S., Sarkar D., R Development Core Team, 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-113.

Piotto, D., Montagnini, F., Thomas, W., Ashton, M., Oliver, C., 2009. Forest recovery after swidden cultivation across a 40-year chronosequence in the Atlantic forest of southern Bahia, Brazil. Plant Ecol. 205, 261–272.

Porter, A.W.M., Robson, A.D., Abbott, L.K., 1987. Field survey of the distribution of vesicular-arbuscular mycorrhizal fungi in relation to soil pH. J. Appl. Ecol. 24, 659–662.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., de Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M.,

van der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. Nature 1–15.

Post, W.M., Kwon, K.C., 2000. Soil carbon sequestration and land-use change: processes and potential. Glob. Chang. Biol. 6, 317–327.

Posada, R.H., Madriñan, S., Rivera, E.L., 2012. Relationships between the litter colonization by saprotrophic and arbuscular mycorrhizal fungi with depth in a tropical forest. Fungal Biol. 116, 747–755.

Prach, K., Walker, L.R., 2011. Four opportunities for studies of ecological succession. Trends Ecol. Evol. 26, 119–123.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rayment, G.E. and Lyons, D.J. 2011. Soil chemical methods: Australasia. CSIRO Publishing, Collingwood, Vic. 495 p. ISBN 9780643067684.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C., Bowman, W.D., 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80, 1955-1969.

Robinson, D., Fitter, A., 1999. The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. J. Exp. Bot. 50, 9–13.

Ruiz-Jaen, M.C., Mitchell Aide, T., 2005. Restoration Success: How Is It Being Measured? Restor. Ecol. 13, 569–577.

Sayer, E.J., 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol. Rev. Camb. Philos. Soc. 81, 1–31.

Schedlbauer, J.L., Kavanagh, K.L., 2008. Soil carbon dynamics in a chronosequence of secondary forests in northeastern Costa Rica. For. Ecol. Manage. 255, 1326–1335.

Schrumpf, M., Schulze, E.D., Kaiser, K., Schumacher, J., 2011. How accurately can soil organic carbon stocks and stock changes be quantified by soil inventories? Biogeosciences 8, 1193–1212.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Baraloto, C., Carlucci, M.B., Cianciaruso, M. V., Dantas, V. de L., Bello, F. de, Duarte, L.D.S., Fonseca, C.R., Freschet, G.T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama, C., Katabuchi, M., Kembel, S.W., Kichenin, E., Kraft, N.J.B., Lagerström, A., Bagousse-Pinguet, Y. Le, Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J.M., Peltzer, D.A., Pérez-Ramos, I.M., Pillar, V.D., Prentice, H.C., Richardson, S., Sasaki, T., Schamp, B.S., Schöb, C., Shipley, B., Sundqvist, M., Sykes, M.T., Vandewalle, M., Wardle, D.A., 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol. Lett. 18, 1406–1419.

Silver, W.L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M., Cosme, R., 2000. Effects of Soil Texture on Belowground Carbon and Nutrient Storage in a Lowland Amazonian Forest Ecosystem. Ecosystems 3, 193–209.

Slik, J.W.F., 2006. Estimating species-specific wood density from the genus average in Indonesian trees. J Trop Ecol 22, 481-482.

Sloan, S., Goosem, M., Laurance, S.G., 2015. Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region. Landsc. Ecol. 4, 1-18.

Smith, S.E., Jakobsen, I., Gronlund, M., Smith, F.A., 2011. Roles of Arbuscular Mycorrhizas in Plant Phosphorus Nutrition: Interactions between Pathways of Phosphorus Uptake in Arbuscular Mycorrhizal Roots Have Important Implications for Understanding and Manipulating Plant Phosphorus Acquisition. Plant Physiol. 156, 1050–1057.

Smith, J., Kop, P. Van De, Reategui, K., Lombardi, I., Sabogal, C., Diaz, A., 1999. Dynamics of secondary forests in slash-and-burn farming: interactions among land use types in the Peruvian Amazon. Agric. Ecosyst. Environ. 76, 85–98.

Srivastava, D.S., Vellend, M., 2005. Biodiversity-ecosystem function research: is it relevant to conservation? Annu. Rev. Ecol. Evol. Syst. 36, 267–294.

Staddon, P.L., 2004. Carbon isotopes in functional soil ecology. Trends Ecol. Evol. 19, 148–154.

Standish, R.J., Cramer, V.A., Wild, S.L., Hobbs, R.J., 2007. Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in Western Australia. J. Appl. Ecol. 44, 435-445.

Stürmer, S.L., Siqueira, J.O., 2011. Species richness and spore abundance of arbuscular mycorrhizal fungi across distinct land uses in western Brazilian Amazon. Mycorrhiza 21, 255–67.

Suding, K.N., Gross, K., 2006. The dynamic nature of ecological systems: multiple states and restoration trajectories, in: Falk, D.A., Palmer, M.A., Zedler, J.B. (Eds.), Foundations of Restoration Ecology. Island Press, Washington, D.C., p. 379.

Swaine, M.D., Whitmore, T.C., 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75, 81–86.

Tesfaye, M.A., Bravo, F., Ruiz-Peinado, R., Pando, V., Bravo-Oviedo, A. 2016. Impact of changes in land use, species and elevation on soil organic carbon and total nitrogen in Ethiopian Central Highlands. Geoderma 261:70-9.

Tilman, D., 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol. Monogr. 57, 189–214.

Thuiller, W., 2013. On the importance of edaphic variables to predict plant species distributions - limits and prospects. J. Veg. Sci. 24, 591–592.

Tng, D.Y.P., Goosem, M.W., Paz, C.P., Preece, N.D., Goosem, S., Fensham, R.J., Laurance, S.G.W., 2015. Characteristics of the Psidium cattleianum invasion of secondary rainforests. Aust Ecol. DOI 10.1111/aec.12319

Tng, D.Y.P., Jordan, G.J., Bowman, D.M.J.S., 2013. Plant traits demonstrate that temperate and tropical giant eucalypt forests are ecologically convergent with rainforest not savanna. PLoS One 8(12):e84378.

Treseder, K.K., Cross, A., 2006. Global Distributions Mycorrhizal of Arbuscular Fungi 9, 305–316.

Trumbore, S.E., Davidson, E.A., Camargo, P.B., Nepstad, D.C., and Martinelli, L.A. 1995. Belowground cycling of carbon in forests and pastures of eastern Amazonia. Glob Biogeochem Cycles 9 (4), 515-528.

Tuomisto, H., Zuquim, G., Cárdenas, G., 2014. Species richness and diversity along edaphic and climatic gradients in Amazonia. Ecography 37, 1034–1046.

Uhl, C., 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75, 377–407.

van Aarle, I.M., Olsson, P.A., Söderström, B., 2002. Arbuscular mycorrhizal fungi respond to the substrate pH of their extraradical mycelium by altered growth and root colonization. New Phytol. 155, 173–182.

Van Geel, M., Ceustermans, A., Van Hemelrijck, W., Lievens, B., Honnay, O., 2015. Decrease in diversity and changes in community composition of arbuscular mycorrhizal fungi in roots of apple trees with increasing orchard management intensity across a regional scale. Mol. Ecol. 24, 941–952.

van der Heijden, M.G. a, Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11, 296–310.

van der Heijden, M.G. a, Streitwolf-Engel, R., Riedl, R., Siegrist, S., Neudecker, A., Ineichen, K., Boller, T., Wiemken, A., Sanders, I.R., 2006. The mycorrhizal contribution to plant productivity, plant nutrition and soil structure in experimental grassland. New Phytol. 172, 739–52.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396, 69–72.

Van Veen, J.A., Kuikman, P.J., 1990. Soil structural aspects decommposition of organic matter by micro-organisms. Biogeochemistry 11, 213–233.

Venables, W.N., Ripley, B.D, 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Verheye, W., 2008. Soils of the humid and sub-humid tropics, in: Verheye, W. (Ed.), Land Use, Land Cover and Soil Sciences. UNESCO-EOLSS Publishers., Oxford, UK.

Villéger S., Mason, W.H.N., Mouillot, D., 2012. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290-2301.

Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen — phosphorus interactions. Ecol. Appl. 20, 5–15.

Von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., 2007. SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. Soil Biol. Biochem. 39, 2183–2207.

Vyšná, V., Dyer, F., Maher, W., Norris, R., 2014. Have you checked for charcoal? Assessment of soil condition using soil organic carbon. Eur. J. Soil Sci. 65, 264–273.

Walker, L.R., Wardle, D. a., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. J. Ecol. 98, 725–736.

Walker, B.H., 1992. Biodiversity and ecological redundancy. Biol. Conserv. 6, 18–23.

Weaver, P.L., Birdsey, R.A., Lugo, A.E., 1987. Soil Organic Matter in Secondary Forests of Puerto Rico. Biotropica 19, 17-23.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. Ann. Rev. Ecol. Syst. 33, 125-159.

Whittaker, R.H., 1973. Evolution and measurement of species diversity. Taxon 21, 213-251.

Wijdeven, S.M.J., Kuzee, M.E., 2000. Seed Availability as a limiting factor in forest recovery processes in Costa Rica. Rest. Ecol. 8, 414–424.

Williams-Linera, G., 1983. Biomass and Nutrient Content in Two Successional Stages of Tropical Wet Forest in Uxpanapa, Mexico. Biotropica 15, 275–284

Williamson, G.B., Bentos, T. V., Longworth, J.B., Mesquita, R.C.G., 2012. Convergence and divergence in alternative successional pathways in Central Amazonia. Plant Ecol. Divers. 1-8.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821-827.

Yeo, W.L.J., Fensham, R.J., 2014. Will Acacia secondary forest become rainforest in the Australian Wet Tropics? For. Ecol. Manag. 331, 208–217.

Zangaro, W., Nishidate, F.R., Vandresen, J., Andrade, G., Nogueira, M.A., 2007. Root mycorrhizal colonization and plant responsiveness are related to root plasticity, soil fertility and successional status of native woody species in southern Brazil. J. Trop. Ecol. 23, 53.

Zangaro, W., Rostirola, L.V., de Souza, P.B., de Almeida Alves, R., Lescano, L.E.A.M., Rondina, A.B.L., Nogueira, M.A., Carrenho, R., 2013. Root colonization and spore abundance of

arbuscular mycorrhizal fungi in distinct successional stages from an Atlantic rainforest biome in southern Brazil. Mycorrhiza 23, 221–33.

Zanini, K. J., Bergamin, R. S., Machado, R. E., Pillar, V. D., & Müller, S. C., 2014. Atlantic rain forest recovery: Successional drivers of floristic and structural patterns of secondary forest in Southern Brazil. J. Veg. Sci, 25, 1056-1068.

Zarin, D.J., Ducey, M.J., Tucker, J.M., Salas, W. a., 2001. Potential biomass accumulation in Amazonian regrowth forests. Ecosystems 4, 658–668.

Zimmerman, J.K., Pascarella, J.B., Aide, T.M., 2000. Barriers to Forest Regeneration in an Abandoned Pasture in Puerto Rico. Rest. Ecol. 8, 350-360.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Met. Ecol. Evol. 1, 3-14.

Appendix

HOT TOPICS IN ECOLOGY http://www.ecolsoc.org.au/hot-topics/invader-dark-side

Invader from the dark side

Shade-tolerant weed threatens Australian World Heritage Rainforests

Synthesis by DYP Tng, MW Goosem, CP Paz, and SGW Laurance, James Cook University

- Weeds are often associated with high light and disturbed habitats but shade-tolerant weeds are gaining attention as serious invaders of rainforests worldwide
- The shade-tolerant Cherry Guava (Psidium cattleianum) is emerging as a serious invader of rainforest understoreys in the Wet Tropics of North Queensland, and is well-known to have the potential to displace native vegetation.
- The prognosis for control is good but incisive action is needed.

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Characteristics of the *Psidium cattleianum* invasion of secondary rainforests

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Abstract Strawberry guava (*Psidium cattleianum*) is a shade-tolerant shrub or small tree invader in tropical and subtropical regions and is considered among the world's top 100 worst invasive species. Studies from affected regions report deleterious effects of strawberry guava invasion on native vegetation. Here we examine the life history demographics and environmental determinants of strawberry guava invasions to inform effective weed management in affected rainforest regions. We surveyed the vegetation of 8 mature rainforest and 33 successional sites at various stages of regeneration in the Australian Wet Tropics and found that strawberry guava invasion was largely restricted to successional forests. Strawberry guava exhibited high stem and seedling densities, represented approximately 8% of all individual stems recorded and 20% of all seedlings recorded. The species also had the highest basal area among all the non-native woody species measured. We compared environmental and community level effects between strawberry guava-invaded and non-invaded sites, and modelled how the species basal area and recruitment patterns respond to these effects. Invaded sites differed from non-invaded sites in several environmental features such as aspect, distance from intact forest blocks, as well as supported higher grass and herb stem densities. Our analysis showed that invasion is currently ongoing in secondary forests, and also that strawberry guava is able to establish and persist under closed canopies. If left unchecked, strawberry guava invasion will have deleterious consequences for native regenerating forest in the Australian Wet Tropics.

Key words: community species diversity, biological invasion, *Psidium cattleianum*, secondary rainforest, shade-tolerant invader, strawberry guava.

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Forest age and isolation affect the rate of recovery of plant species diversity and community composition in secondary rain forests in tropical Australia

Miriam Goosem, Claudia Paz, Rod Fensham, Noel Preece, Stephen Goosem & Susan G. W. Laurance

Keywords
Forest age; Forest isolation; Forest regeneration; Forest remnants; Pasture; Secondary forest; Species composition; Species richness; Successional trajectories; Tropical rain forest

Nomenclature
Bostock & Holland (2013)

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Abstract

Questions: Which factors affect the diversity and species composition of tropical secondary rain forests in a region with little information regarding their contribution to global biodiversity? Can older secondary forests approach the diversity and composition of mature forests following 100 yr of pasture use?

Location: Tropical secondary rain forest, northeast Australia.

Methods: We identified trees, shrubs and vines ≥2.5 cm DBH in a chronosequence comprising 33 sites, aged 3–60 yr since the formation of closed canopy (9–69 yr since pasture abandonment) and compared them with eight sites in nearby mature forest remnants.

Results: Species richness and community composition were strongly influenced by secondary forest age but did not attain values of mature forest. Sites in close proximity to mature forests had higher plant richness, whereas low soil fertility appeared to depress species recruitment. Thus, multiple factors operated in secondary forest community assembly. Unusual tree community patterns that suggest accelerated or slowed successional trajectories were observed at several sites.

Conclusions: Secondary forests in our study region contained important plant diversity for conservation, particularly in older sites, however, even the oldest secondary forests (60 yr) did not converge with the species composition and diversity of mature forests. The protection of mature forest tracts and remnants must be a priority if we are to maintain high levels of plant diversity in tropical landscapes, conserve rare species and facilitate the recruitment of plant species in recovering forests.

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