

# **The evolution of carbon cycle in tropical forests: integrating ecology and evolution**

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

## **Chapter 2**

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F.C.S and T.R.B. conceived the study, F.C.S, T.R.B. and K.G.D. designed the study; all co-authors contributed to field data collection and/or data management; F.C.S. analysed the data and wrote the chapter.

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### **Chapter 4**

In preparation. Environmental preferences of tropical trees are strongly shaped by evolution.

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## **Abstract**

Present-day patterns of species diversity and their ecological characteristics in the tropics result from more than 100 million years of evolution. The environmental conditions in which species evolved have left a fingerprint on their functional traits, so investigating this legacy may improve our understanding of current patterns of ecosystem function and potentially guide us in managing our resources more wisely as the climate changes. Amazonian forests are ideal for such a study as they play a major role in the global carbon cycle and harbour a remarkable diversity of angiosperm lineages and species with a broad range of ecologies. Here, I linked data from long-term forest inventory plots, environmental conditions, and a newly constructed phylogeny in order to investigate the legacy of evolution on modern-day patterns of ecosystem function and diversity. I show first that evolutionarily related taxa are more similar in their demography and carbon storage and processing ability (i.e. wood density, potential size, growth and mortality-rates) than expected by chance. Thus, the degree of evolutionary history shared between lineages is a good proxy for their carbon traits. Next, using the evolutionary relationships among lineages I find a legacy of evolutionary history on current patterns of whole ecosystem productivity across the Amazon, such that communities with more evolutionarily distinct lineages have greater wood productivity. Finally, I compare the role of heritability versus selection on shaping lineages preferences for certain environments (i.e. soils and climate). I show that there is a tendency for evolutionarily related taxa to have more similar environmental preferences than expected by chance, but that certain kinds of habitat specialization have also occurred repeatedly and independently in many lineages. These findings are important for understanding the future of Amazonian forests under global change and support an evolutionary perspective as an important component of conservation strategies.



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## **Abbreviations**

- AGB - Aboveground Biomass
- AGWP – Aboveground Wood Productivity
- AIC - Akaike Information Criterion
- a.m.s.l – above mean sea level
- BM – Brownian motion
- Ca - calcium
- CEC - Cation Exchangeable Capacity
- CWD – Cumulative Water Deficit
- DNA - Deoxyribonucleic acid
- EDGE – Evolutionary Distinct and Global Endangered
- GLS - Generalised Least Squares
- GR – Genus Richness
- H' - Shannon Index
- HWSD - Harmonised World Soil database
- K – potassium
- MAT – Mean Annual Temperature
- Max.T – Maximum Temperature
- MCMC - Markov Chain Monte Carlo
- Mg - magnesium
- Min.T - Minimum Temperature
- MNTD – Mean Nearest Taxon Distance
- MPD – Mean Pairwise Phylogenetic Distance
- OU - Ornstein-Uhlenbeck
- P - Phosphorus

PCA - Principal Component Analysis

PD - Phylogenetic Diversity

PNC – Phylogenetic Niche Conservatism

POM – Point of measurement

PPCA - Phylogenetic Principal Component Analysis

PS – Phylogenetic Signal

RAINFOR - Amazon Forest Inventory Network

REDD - Reduce Emissions from Deforestation and forest Degradation

ses.MNTD - Standardized Mean Nearest Taxon Distance

ses.MPD - Standardized Mean Pairwise Phylogenetic Distance

ses.PD - Standardized phylogenetic diversity

TEB – Total exchangeable bases

VIF – Variance Inflation Factor

UCLN - Uncorrelated Lognormal

WN – White-Noise

## Chapter 1 : Introduction and background

### 1.1 Introduction

Tropical forests cover just 15% of the Earth's land surface but store over 70% of the world's living biomass (Beer *et al.* 2010; Pan *et al.* 2011) and harbour a plethora of biodiversity, including more than 43 000 tree species (Fine & Ree 2006). These ecosystems play a major role in the global carbon cycle, storing ca. 450 billion tonnes of carbon in their biomass and soil (Pan *et al.* 2011) and processing roughly 40 billion tonnes of carbon per year (Beer *et al.* 2010). The amount of carbon processed and stored in aboveground biomass varies widely among tree species (Fauset *et al.* 2015; Poorter *et al.* 2015a), and it is often suggested that there is a synergy between species diversity and ecosystem functioning within forest communities, or more specifically, that the amount of carbon processed and stored in the living biomass enhances with increasing species diversity (van der Sande *et al.* 2017b). From a conservation perspective, this potentially provides a 'win-win' situation for preserving both carbon and biodiversity in the tropics, as conservation policies designed to mitigate the impacts of climate change through carbon-based payments for ecosystem services, would also conserve high levels of biodiversity (e.g. via national mitigation strategies to Reduce Emissions from Deforestation and forest Degradation - REDD+ ; Miles & Kapos 2008; Venter *et al.* 2009; Gardner *et al.* 2012; Hinsley *et al.* 2015). However, the potential for maximizing the benefits of carbon-based projects whilst also safeguarding species diversity critically depends on the link between biodiversity and ecosystem function.

Evidence from a number of experimental studies at small spatial scales and a restricted number of species show that species diversity promotes productivity and biomass (Naeem *et al.* 1994; Tilman *et al.* 1996; Hector *et al.* 1999; Loreau & Hector 2001; Tilman *et al.* 2001; Cardinale *et al.* 2007; Cardinale *et al.* 2012; Tilman *et al.* 2014; Duffy *et al.* 2017). However, the effect of biodiversity on

ecosystem functioning in more complex, hyperdiverse systems, and at large spatial scales relevant for conservation planning, remains unclear. Recently, numerous studies have attempted to understand how biological diversity in tropical forests is linked to ecosystem function, but they show inconsistent and contrasting results (Chisholm *et al.* 2013; Day *et al.* 2013; Cavanaugh *et al.* 2014; Poorter *et al.* 2015b; Poorter *et al.* 2017; Sullivan *et al.* 2017; van der Sande *et al.* 2017a; van der Sande *et al.* 2017b). At small spatial scales (e.g. 0.04 ha) there is a consistent significant positive relationship between diversity and carbon stocks. However, results at landscape scales (e.g. 1 ha), relevant to informing conservation prioritisation remain controversial. Whilst some recent studies found a weak and positive effect of species richness on carbon storage and uptake (Day *et al.* 2013; Cavanaugh *et al.* 2014; Poorter *et al.* 2015b; Poorter *et al.* 2017), others have found that tree diversity has a negative or negligible effect on ecosystem function (Chisholm *et al.* 2013; Sullivan *et al.* 2017).

One point of agreement among these studies is that variation in functional characteristics is more strongly and consistently associated with wood productivity and biomass than species diversity *per se* (Cavanaugh *et al.* 2014; Poorter *et al.* 2015b; Poorter *et al.* 2017; Sullivan *et al.* 2017; van der Sande *et al.* 2017a). Although some of the key traits that influence the ability of tree species to process and store carbon are well known (e.g. wood density and tree size), the fact that these processes are mediated by combinations of traits (Rawat *et al.* 2015; Shen *et al.* 2016), and that identifying and measuring these traits remains difficult in diverse forests, limits the development of a comprehensive trait-based understanding of how biodiversity influences ecosystem function in tropical forests. The premise of this thesis is that an understanding of the evolutionary relationships among species may help to avoid these limitations and provide a way forward for advancing this field.

Differences in species' functional characteristics that leads to variation in their ability to process and store carbon are a result of evolutionary processes operating over long timescales. The simple assumption that the amount of time that has passed since two species diverged from a common ancestor reflects differences in their functional characteristics (Pagel 1999; Freckleton *et al.* 2002; Blomberg *et al.*

*al.* 2003), suggests that the evolutionary history shared amongst species may be a powerful tool for investigating the link between biodiversity and ecosystem function (Cadotte *et al.* 2008; Cadotte 2013; Cadotte *et al.* 2017b). As such, if over evolutionary timescales species tend to retain their ancestral characteristics, then the phylogenetic distance between species will be related to variation in their functional traits, and evolutionary relatedness can be considered an integrative measure of trait similarity. In other words, phylogeny will be a good proxy for functional diversity (Webb 2000; Webb *et al.* 2002). This link is potentially particularly useful for understanding species ecology in tropical forests because the high diversity of these ecosystems (Fine & Ree 2006; ter Steege *et al.* 2013) means it is impractical to undertake detailed studies of the ecology of all of the many coexisting species (Chave *et al.* 2009; Baraloto *et al.* 2010a; Baraloto *et al.* 2010b).

To assess the value of evolutionary history for understanding present-day patterns of ecosystem function, the first question is whether functional traits that are directly associated with carbon stocks and uptake are more similar amongst sister species. The strength of the link between evolutionary relationships and ecological characteristics can be measured by the extent of phylogenetic signal (Pagel 1999; Blomberg *et al.* 2003). The second chapter of this thesis therefore focuses on exploring the fingerprint of evolution on present-day functional characteristics that directly reflect species' ability to process and store carbon (i.e. wood density, potential tree size, growth and mortality rates). If traits are more similar among closely related lineages then these traits will show a significant phylogenetic signal and evolutionary history will be a good predictor of variation in traits. Additionally, if the amount of shared evolutionary history among species reflects variation in their ecological characteristics, it is possible to assume that phylogenetic distance among lineages represents ecological niche differences. As a result, phylogenetic data will summarize information on numerous traits in an index of ecological and functional relatedness, and allow a more comprehensive analysis of how biodiversity affects ecosystem function.

Previous experimental work has shown that a phylogeny-based approach can provide useful information for understanding the link between diversity and

ecosystem function. For example, experimental studies that manipulate species richness have shown that the degree of evolutionary relatedness amongst species is a better predictor of ecosystem function than species richness itself, or species associated traits (Cadotte *et al.* 2008; Cadotte *et al.* 2009; Cadotte 2013). In experiments using grassland plants, communities with greater evolutionary diversity showed higher biomass production, while communities that shared more closely related species produced less biomass (Cadotte *et al.* 2008). This example demonstrates that evolutionary relationships may integrate the effect of additional axes of trait variation that are not captured by measured traits. Thus, a significant effect of evolutionary diversity on ecosystem function suggests that there may be additional important unmeasured functional characteristics. Although there is some evidence that communities with distantly related lineages promote carbon stocks and productivity on small spatial scales and controlled experiments (Cadotte *et al.* 2009; Srivastava *et al.* 2012; Cadotte *et al.* 2013; Cadotte 2013; Cadotte *et al.* 2017a; Cadotte *et al.* 2017b), scaling up these results to scales relevant to conservation planning is an important challenge. Therefore, in chapter 3, using a new phylogeny including 615 angiosperm genera as a proxy for functional diversity, I assessed the relationship between evolutionary relatedness amongst lineages and two metrics of ecosystem function - aboveground wood productivity and aboveground biomass - across Amazonian forests.

In tropical forests, landscape-scale variation in wood productivity and aboveground biomass are not only driven by traits but also mediated by environmental gradients. Across the Amazon basin there are three main axes of associated edaphic (Baraloto *et al.* 2011; Quesada *et al.* 2012), precipitation (ter Steege *et al.* 2006) and temperature gradients (Toledo *et al.* 2011; Girardin *et al.* 2013; Malhi *et al.* 2017) linked with variation in species composition, their functional characteristics and carbon stocks and productivity. The western/eastern gradient in soil fertility (Figure 1.1a) is an important driver of variation in tree communities, and represents a continuum from forests growing on the more nutrient-rich soils in the western Amazonia where forests generally contain species with low wood density, to the poorer soils in eastern Amazon where forests tend to have more heavy-wooded species (Baker *et al.* 2004b; Chave *et al.*

2006; ter Steege *et al.* 2006). More nutrient-rich soils in the western Amazonian enable the establishment of fast growing species with low wood density, while poorer soils in the eastern Amazon favour slow growing species with higher wood density (Baker *et al.* 2004b; Quesada *et al.* 2012).

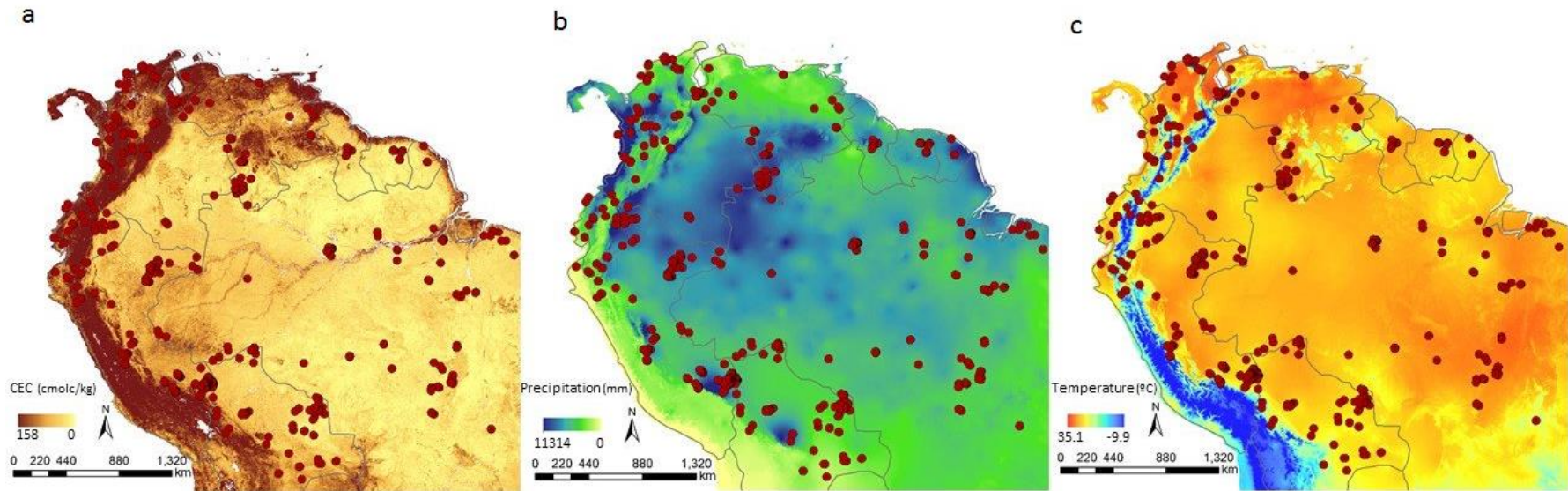
The second major environmental gradient across the basin is associated with dry-season length, and reflects the continuum from wetter and more diverse forests in the north-west to drier and less diverse forests in the south-eastern Amazonia (ter Steege *et al.* 2006) (Figure 1.1b). Differences in species diversity and distribution are broadly determined by precipitation gradient, with a greater number of species (ter Steege *et al.* 2003; Esquivel-Muelbert *et al.* 2017a) and higher carbon stocks and uptake in wetter forests than in drier forests (Malhi *et al.* 2006; Baraloto *et al.* 2011). Additionally, a third major axis of variation in floristic composition and forest structure is the temperature gradient, from warmer lowland forests to cooler mountainous forests in the Andes (Figure 1.1c) (Girardin *et al.* 2013; Malhi *et al.* 2017). Tropical montane forests usually have lower aboveground biomass and wood productivity associated with their variation in species composition (Girardin *et al.* 2013).

Accounting for the variation in environmental conditions is important for understanding the effect of biodiversity on ecosystem function. Therefore I compare the influence of climate and locally collected soil data with the impact of measures of biodiversity in Chapter 3. Preferences of different lineages for certain environmental conditions may also constrain how different groups of species respond to changing environmental conditions, and determine how the ecosystem services provided by tropical forests change in the future. Therefore in Chapter 4, I explore the evolutionary history shared among lineages of tropical trees and their associations with temperature, rainfall, and soil fertility, and ask whether preferences for certain environments are strongly restricted to certain parts of the tree of life.

Historical processes that underlie the origins of plant lineages often leave an imprint on their current environmental preferences (Cavender-Bares *et al.* 2016). Understanding the legacy of evolution on present-day patterns of habitat

association may also help us to understand how different species respond to predicted rises in temperature (Malhi & Wright 2004; Marengo *et al.* 2009; Zelazowski *et al.* 2011; Jimenez-Munoz *et al.* 2016), and increases in the intensity and frequency of droughts (Aragão *et al.* 2007; Phillips *et al.* 2009; Lewis *et al.* 2011). If the evolutionary heritage of a lineage has acted as a major constraint, and environmental niches have evolved little from ancestral conditions, species may struggle to adapt to changing environments. In contrast, if there has been strong selection and environmental preferences are rather distinctive and varied compared to their ancestral states, species may be able to adapt to novel environments. The evolution of habitat preferences has been investigated for a number of plant clades, however these studies are either limited to small spatial scales (Pei *et al.* 2011; Baraloto *et al.* 2012; Yang *et al.* 2014; Zhang *et al.* 2017) or restricted to a few clades (Fine *et al.* 2005; Fine *et al.* 2014; Misiewicz & Fine 2014; Weeks *et al.* 2014). Therefore, in Chapter 4, I investigate the role of evolution in shaping the environmental preferences of 510 lineages across all biomes that occur within northern South America.





**Figure 1.1** Maps of environmental variation across northern South America: a) Cation exchange Capacity (CEC cmolc/kg), b) Precipitation (mm), and c) Temperature (°C). CEC data was extracted from the Soil Grid database, a global gridded soil information map based on interpolation from soil profiles to a 250 m spatial resolution (Hengl *et al.* 2017). Precipitation and temperature were extracted from the WorldClim dataset based on interpolations of climate station data to a 1 km spatial resolution (Hijmans *et al.* 2005). Red dots represent all the forest plots used in this thesis.

## 1.2 Thesis outline

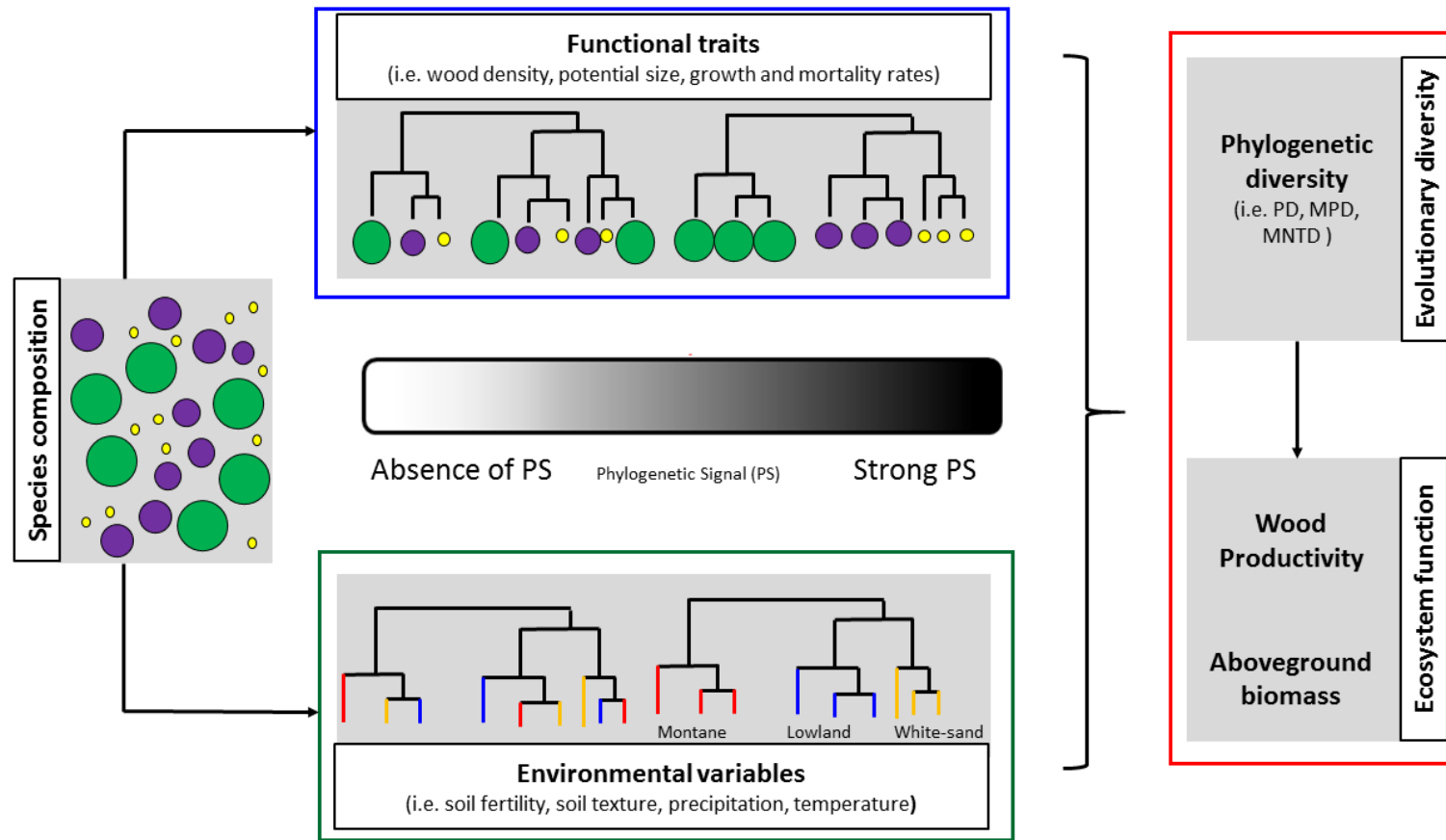
**Chapter 1** In this chapter I review the use of phylogenies for integrating an ecological and evolutionary approach for understanding how historical processes have shaped evolutionary relationships among species. Based on the published literature, I compile previous findings on tropical forests and explore how the legacy of the evolution of tree traits and environmental preferences can be used to understand the processes underlying present-day patterns.

**Chapter 2** This data chapter investigates how the constraints imposed by evolutionary history, or selection determines variation among species in plant traits. I focus on functional traits that underlie species ability to process and store carbon (i.e. wood density, potential tree size, growth and mortality rates) and investigate how different plant life-history strategies have evolved (Figure 1.2 – blue box).

**Chapter 3** This data chapter uses a new constructed phylogeny as a proxy for functional diversity to assess the relationship between evolutionary relatedness amongst lineages and two key metrics of ecosystem function - aboveground biomass and wood productivity - for 90 forest plots in Amazonia (Figure 1.2 – red box).

**Chapter 4** In this data chapter I explore how preferences for certain environmental niches have evolved. I investigate the fingerprint of evolution of preferences for different levels of soil fertility, soil texture, temperature, and precipitation, as these are the most important environmental variables for determining broad-scale patterns in composition (Figure 1.2 box).

**Chapter 5** In the final chapter I conclude the thesis by providing a general overview of the main findings, the implications of the research for conservation prioritization and a series of suggestions for future research.



**Figure 1.2** Conceptual diagram that summarizes the thesis aims. Different coloured boxes represent the different questions answered in the thesis. Blue represents the extent to which traits show a phylogenetic signal (Chapter 2); the red box represents the relationship between phylogenetic diversity and ecosystem functioning (Chapter 3) and the green box represents the role of evolutionary history for shaping environmental preferences (Chapter 4).

### **1.3 Integrating perspectives from ecology and evolutionary biology**

There is a high level of interest in linking datasets on the ecological characteristics of species with datasets on evolutionary relationships to address a wide range of new research questions. Ecological studies typically consist of comparative analyses of current similarities and differences between species, and how they respond to the environment. In contrast, evolutionary studies offer a perspective that considers long-term interactions to gain insights into the relative importance of historical processes. These research areas should not be considered in isolation since ecological and evolutionary process interact and there is a link between local processes and large-scale events (Webb *et al.* 2002; Ricklefs 2004; Wiens & Graham 2005; Hoorn *et al.* 2010; Cavender-Bares *et al.* 2016; Cadotte *et al.* 2017a).

While integrating ecology and evolution perspectives has the potential to elucidate the mechanisms mediating present-day patterns, the paucity of data on species evolutionary relationships, distributions, functional characteristics, and environmental preferences has prevented these links being explored until recently. Only now, with the rapid and recent increase in dated molecular phylogenies for a range of tree groups (Fine *et al.* 2005; Simon *et al.* 2009; Baraloto *et al.* 2012; Fine *et al.* 2014; Dexter & Chave 2016; Dexter *et al.* 2017), their associated traits (e.g. Chave *et al.* 2009; Zanne *et al.* 2009), spatial distribution (ter Steege *et al.* 2013), environmental preferences (Fine *et al.* 2005; Esquivel-Muelbert *et al.* 2017a) and demography (Lopez-Gonzalez *et al.* 2009) is it possible to address these questions within tropical forests.

This expanding research area has already provided valuable information about the mechanisms driving ecosystem processes (Cadotte *et al.* 2009; Srivastava *et al.* 2012; Cadotte 2013; Cadotte *et al.* 2017b), community assembly rules (Baraloto *et al.* 2012; Yang *et al.* 2014), evolution of environmental preferences (Fine *et al.* 2005; Simon *et al.* 2009; Pei *et al.* 2011; Fine *et al.* 2014; Liu *et al.* 2015; Zhang

*et al.* 2017) and species ability to respond to environmental change (Willis *et al.* 2008; Lavergne *et al.* 2013; Quintero & Wiens 2013). However, a key point for understanding how historical processes affect ecological patterns relies on how the evolutionary relationships of species are correlated with their ecological characteristics, but these links are poorly explored for tropical forests.

The link between evolutionary relationships and ecological processes relies fundamentally on the similarities and differences among species (Blomberg *et al.* 2003; Losos 2008a; Cavender-Bares *et al.* 2009; Wiens *et al.* 2010). The strength of similarity and the amount of evolutionary history shared between species depends on when lineages that contain those species diverged from their most recent common ancestor. In particular, as distantly related lineages diverged a longer time ago, they may be expected to be less similar and have contrasting traits, while species that diverged more recently are expected to have more similar traits. The tendency for species to retain ancestral ecological characteristics and for related taxa to share similar traits is termed ‘niche conservatism’ (Wiens & Donoghue 2004; Wiens & Graham 2005; Wiens *et al.* 2010). Closely related lineages do often tend to resemble one another more than distantly related lineages (Blomberg *et al.* 2003; Wiens *et al.* 2010). However, in many clades and for some traits, this trend to retain ancestral characteristics does not exist, and traits may be more labile than expected by chance (Blomberg *et al.* 2003; Revell *et al.* 2008; Wiens *et al.* 2010; Crisp & Cook 2012). Thus, rather than being simply assumed, this tendency of related lineages to share similar ecological characteristics needs to be tested. In fact, investigating the amount of similarity amongst related lineages is an essential first step to detect the signature of past evolutionary processes within contemporary patterns of diversity, composition and their respective traits.

#### **1.4 The extent of similarity amongst related lineages**

Given species’ functional traits, environmental niches and the associated evolutionary relationships among species, there are three main approaches to investigate the extent to which phylogeny is associated with ecological

characteristics. The first and most widely used approach consists of mapping traits onto a phylogeny and measuring the extent of phylogenetic signal (PS) - whether ecological and environmental characteristics are conserved over evolutionary scales, termed 'phylogenetic niche conservatism' (PNC; Pagel 1999; Freckleton *et al.* 2002; Blomberg *et al.* 2003; Wiens *et al.* 2010). A second approach lies in model fitting, which tests which evolutionary model (e.g. BM, WN, OU, Lambda) best fits the observed distribution of functional traits and environmental preferences in relation to the phylogeny (Kozak & Wiens 2010a; Wiens *et al.* 2010). Lastly, a third approach involves observing the disparity in trait values through time by exploring the pattern of trait and environmental variation throughout evolutionary history (Harmon *et al.* 2003; Jonsson *et al.* 2015).

#### **1.4.1 Phylogenetic Niche Conservatism and Phylogenetic Signal**

Phylogenetic niche conservatism (PNC) and phylogenetic signal (PS) are key concepts that link species ecological characteristics and their evolutionary relatedness. In general terms, traits may be conserved, which means that related species are more similar than expected by chance, implying PNC or high phylogenetic signal (Blomberg *et al.* 2003). Alternatively, traits may be labile and thus close relatives may be less similar than expected by chance (Blomberg *et al.* 2003). Investigating PS and PNC addresses questions on how constrained traits or environmental preferences are over evolutionary history. Indeed, investigating the extent of PS may also allow us to understand the processes that determined such patterns. However, these concepts need to be defined clearly (Losos 2008a; Wiens 2008; Wiens *et al.* 2010). Here I define significant PS as the tendency of closely related species to be more ecologically similar and share more related traits than would be expected by chance. Meanwhile, PNC is defined as closely related species being more ecologically similar and sharing more related traits than would be expected under a Brownian Motion (BM) model of evolution (Losos 2008a; Losos 2008b). BM represents a random model of evolutionary change, which assumes constant rates of trait evolution through time and can be measured using either the Blomberg's *K* statistic (Blomberg *et al.* 2003) or the Pagel's Lambda value (Pagel 1999; Freckleton *et al.* 2002). These metrics indicate whether a trait

evolved according to a null BM expectation of neutral drift. When  $K$  or Lambda are significant, traits or ecological niches among related species resemble each other: there is a tendency of closely related species to be more similar than expected by chance. In contrast, non-significant  $K$  or Lambda values indicate that there is no correlation between taxa relatedness and their ecological similarity. Finally,  $K$  or Lambda values greater than expected under a null BM model of evolution (i.e.  $K$  or Lambda  $\geq 1$ ) suggest that phylogenetic distance amongst taxa is equivalent to their divergence time and strongly explains niche or functional similarity; such values have been used as evidence for PNC (Freckleton *et al.* 2002; Losos 2008a; Cooper *et al.* 2010). However, interpretation of niche conservatism through estimates of  $K$  should be done with caution as other processes (such as evolutionary stasis) could lead to  $K$  values much lower than one and still be a result of niche conservatism (Revell *et al.* 2008; Munkemuller *et al.* 2015).

An important debate in the recent literature is whether PNC is simply a pattern, or a process driving community structure (Losos 2008a; Losos 2008b; Wiens 2008; Wiens *et al.* 2010; Crisp & Cook 2012). Wiens and Graham (2005) argued that PNC is a fundamental evolutionary process that creates and provides causal explanations for patterns in ecological data. For example, if climatic niche is phylogenetically conserved, species cannot adapt easily to different environmental conditions and thus it can be seen as process that may lead to local extinction as the climate changes (Wiens *et al.* 2010). However, Losos (2008a) contested this definition and argued that PNC is a pattern resulting from the processes that drive trait evolution.

#### **1.4.2 Fit of different evolutionary models**

Alternatively, a second approach to investigate the signature of evolution is to compare the relative fit of different models of trait or niche evolution (Kozak & Wiens 2006; Cooper *et al.* 2010; Wiens *et al.* 2010). This approach uses the phylogenetic relationships among species (represented in a phylogeny), their ecological characteristics, and a suite of distinct models of evolution. Under the White-Noise (WN) model of evolution, functional traits or environmental niches

are assumed to have evolved independently and this model is generally consistent with an absence of phylogenetic signal. In contrast, the Brownian motion (BM; genetic drift), Ornstein-Uhlenbeck (OU; stabilizing selection) and Lambda models of evolution all indicate that ecological characteristics evolved with an underlying phylogenetic structure (Pagel 1999; Freckleton *et al.* 2002; Kozak & Wiens 2006; Wiens *et al.* 2010; Pyron *et al.* 2015). BM assumes that the correlation structure among ecological characteristics is proportional to the amount of evolutionary history shared among species (Felsenstein 1973). OU with a single optimum provides evidence that some factors constrain ecological characteristics to an optimum (Butler & King 2004), whilst Lambda fits the extent to which the phylogeny predicts covariance among the ecological characteristics (Pagel 1999). A better fit of the OU model over the BM and WN models has been suggested to reflect niche conservatism through evolutionary history. For example, comparing the fit of different evolutionary models to investigate similarity in temperature and precipitation niches of bats (Chiroptera), Peixoto *et al.* (2017) found stronger support for the OU model. The authors investigated the extent of similarity in climatic niches across different phylogenetic scales and the OU model provided the best fit for the Chiroptera as a whole, and in particular for species-rich families. This stronger support for the OU model suggested that climatic niches are conserved through evolutionary history and supports the idea that thermal and precipitation niches have evolved more slowly than expected under the null BM model of evolution (Peixoto *et al.* 2017). In another example, across freshwater arthropods (Colymbetinae), Moriniere *et al.* (2016) also found stronger support for the single optimum OU model for the evolution of climatic niches, suggesting a tendency among species to retain similar environmental preferences during evolution. Finally, the Lambda model of evolution is generally not used in model fitting comparisons as many different processes can lead to it being the selected model (Pagel 1999). However, support for the Lambda model suggests that there is significant phylogenetic signal which could be either due to random BM evolution or due to evolutionary constraints operating within clades. For instance, investigating the extent of similarity in range size amongst tropical tree genera, Dexter and Chave (2016) found that the Lambda model of evolution provided a



better fit compared to the WN and BM models of evolutions. Their results show that sister lineages tend to have more similar range sizes than expected by chance, though divergent selection may have also played a role in shaping lineage variation in range size.

### **1.4.3 Disparity through time**

A third approach consists of investigating disparity through time in trait values. Disparity reflects the proportion of variance that occurs among species within each clade, and analyses of disparity through time allow the portion of niche variation found within clades to be compared with that found among clades (Harmon *et al.* 2003). Higher levels of phylogenetic signal are congruent with low variation within clades and closely related species being more similar to each other than expected by chance. Values of relative disparity through time that are smaller than 1 suggest greater variation among, rather than within, clades, whilst values greater than 1 indicate greater variation within clades in comparison to all the variation across the phylogeny (Harmon *et al.* 2003; Loza *et al.* 2017). Similar to the measurements of phylogenetic signal, relative disparity can be compared with expectations under a null BM model of evolution. For example, comparing the observed patterns of disparity through time of brain shape and body mass in primates, Aristide *et al.* (2015) found that relative disparity was near zero and lower than expected under a null BM model of evolution: disparity dropped to values near zero following the early divergence of primates and showed little variation over time. This result indicates that variation occurs among, rather than within, clades and is consistent with brain shape and body mass being traits that are highly constrained over evolutionary timescales. In contrast, across frogs (*Kaloula*, Microhylidae) the disparity of morphological traits associated with climbing and digging (i.e. the length and width of digits, digit tips and lengths of metatarsal tubercles) exhibit greater variation within subclades, and disparity over time is therefore, on average greater than expected under a null BM (Blackburn *et al.* 2013).

#### 1.4.4 Evolutionary processes underlying ecological patterns

Multiple fundamental evolutionary processes and interactions such as heritability, convergence, selection, dispersal and extinction may lead to certain patterns that should maintain or constrain the ancestral niche, and therefore determine whether PNC occurs (Blomberg *et al.* 2003; Wiens & Donoghue 2004; Revell *et al.* 2008; Crisp & Cook 2012). Overall, under the assumption that PNC provides information on species niche similarity, it seems more reasonable to consider PNC as a pattern generated by different processes during evolution.

Heritability is one of the processes that drives niche conservatism and refers to the genetic contribution to the tendency to retain the ancestral characteristic. If closely related species share heritable traits and environmental preferences with their ancestors, as lineages diverge, those characteristics will become more similar within clades than they are among clades, and sister lineages will also be more similar (Wiens *et al.* 2010; Crisp & Cook 2012).

Selection can drive divergence among lineages that occur under different environmental conditions and therefore also affect PNC. Natural selection is assumed to drive divergence among lineages, promoting evolutionary change, speciation and reducing the extent of similarity amongst related lineages (Wiens 2004). For example, in white-sand forests in the Peruvian Amazonia, among 20 species from six genera, selection has been the major factor determining species fitness on the nutrient-poor soils in the presence of herbivores (Fine *et al.* 2006). As nutrient availability is limited in white-sand forests, Fine *et al.* (2006) found that herbivore pressure had led to high investment in plant defences. Thus, selection and divergence had caused species from white-sand forests to have a higher allocation to defence than their congeners in nutrient-rich clay forests. This process resulted in a weak pattern of niche conservatism for traits associated with plant defence.

Convergence represents the evolution of similar biological attributes under similar environmental conditions. For example, succulent plants from widely different families in Africa (Euphorbiaceae) and North America (Cactaceae) evolved from different ancestors but developed similar growth forms and adaptations, reflecting

convergence as an adaptive response to similar environment pressures (Ezcurra *et al.* 2006). Low levels of convergence might be linked to a strong pattern of PNC, while high convergence results in trait similarity among distantly related lineages. Thus, in this example, succulent plants in different continents have undergone high convergence, and show similar traits, but succulence as a trait would show low PNC.

Dispersal is an important determinant of species distribution and dispersal limitation may lead to a pattern of niche conservatism with closely related species sharing similar traits (Crisp & Cook 2012). For example, seasonally dry tropical forests have few widespread woody species, causing high  $\beta$ -diversity between different forest fragments (Pennington *et al.* 2006; Pennington *et al.* 2009). High dispersal limitation between dry forests explains the patterns of low floristic similarity between these areas. Indeed, the fact that clades restricted to dry forests are not found outside of these dry biomes suggests high PNC in woody plants of Neotropical seasonally dry tropical forests (Pennington *et al.* 2009).

Finally, extinction may play an important role determining niche conservatism and some patterns of PNC may be a result of extinction, rather than the trait being highly conserved (Crisp & Cook 2012). For example, studying traits related to adaptation to fire in 101 species of *Pinus*, He *et al.* (2012) found that, although Pinaceae has a 237 Ma evolutionary history, fire-adapted traits have only been found for the last 126 Ma. Many of the fossil lineages are not present in the extant clades, suggesting that those lineages were unable to adapt to new fire regimes and went extinct. As these taxa became extinct, this could have led to a pattern of niche conservatism in the fire-adaptive traits (Crisp & Cook 2012). However, the direction of the extinction effect on the extent of phylogenetic signal will depend on which species die-out.

## **1.5 Scale dependence**

In addition to the underlying processes, the scale of study is also likely to affect whether measurements of the extent of similarity among related lineages will be

observed (Cavender-Bares *et al.* 2006; Swenson *et al.* 2007; Cadotte *et al.* 2009; Cavender-Bares *et al.* 2009; Krasnov *et al.* 2011). In particular, patterns of similarity may not be detected at small spatial and taxonomic scales. In local assemblages, the co-occurring species represent just a small proportion of clades and to infer patterns of niche conservatism typically requires larger spatial scales including more taxa. For example, in 55 plots (0.1 ha) in north central Florida, Cavender-Bares *et al.* (2006) investigated how spatial and taxonomic scale affected phylogenetic structure in plants. They showed that when communities were narrowly defined as just one single lineage (e.g. *Quercus*), closely related species tend to be less functionally similar in terms of maximum height, maximum hydraulic conductivity, transpiration rate, and vulnerability to cavitation during drought, than when including more lineages. Similarly, by extending their analysis from north central Florida communities to communities across the whole state of Florida, Cavender-Bares *et al.* (2006) showed that niche conservatism tends to be more prevalent at larger scales. Communities for the entire state of Florida include a greater number and variety of community types, a higher degree of environmental heterogeneity and also encompass a larger number of taxa (Cavender-Bares *et al.* 2006). The ability to detect phylogenetic signal will therefore vary with spatial scale, either due to changes in the species pool or dictated by how environmental heterogeneity changes with scale. At small spatial scales, competitive interactions are stronger and group of species that are already environmentally filtered may not co-occur (Ricklefs 1987). Additionally, because biogeographical processes that involve dispersal, extinction, and speciation occur at large scales, they may be more relevant to consistently detect the signature of different ecological and evolutionary processes.

## **1.6 Inferences from current patterns**

The strength of the link between trait variation and phylogenetic relatedness has a wide range of implications. The presence of phylogenetic signal suggests that measures of phylogenetic distances among species that occur within a community (e.g. phylogenetic diversity) can serve as a proxy for their functional diversity

(reviewed in Mouquet *et al.* 2012). If phylogenetic signal exists for important functional traits, then communities with low phylogenetic diversity will include species with high overlap in their ecological characteristics. This pattern may result in strong interspecific competition limiting species abundances (Srivastava *et al.* 2012). In contrast, communities with high phylogenetic diversity will include species with dissimilar ecological characteristics and lower niche overlap. Overall, the effectiveness of using evolution as a proxy for ecosystem ecology will depend critically on the strength of phylogenetic signal of the relevant traits (Losos 2008a; Cavender-Bares *et al.* 2009; Srivastava *et al.* 2012). Furthermore, if evolutionary history is a good predictor of trait data it may also allow us to avoid measuring a number traits for every single species: if traits are more similar among closely related lineages, it is possible to make predictions of trait values for species where data are not available.

Investigating the role of evolution for shaping present-day environmental preferences is also important to understand the mechanisms that originate and maintain species diversity. Specifically, the extent of similarity amongst related lineages may also enable us to distinguish whether ecological speciation or geographical isolation are important drivers of diversification (Wiens 2004a; Wiens 2004b; Wiens & Donoghue 2004). For example, under ecological speciation, strong environmental pressure imposes niche divergence amongst related lineages and promotes diversification (Gentry 1981; Fine *et al.* 2005; Simon *et al.* 2009; Fine *et al.* 2013; Fine *et al.* 2014; Misiewicz & Fine 2014). Divergence in sister lineages under contrasting environmental pressures therefore results in habitat specialization, with closely related species found in adjacent, distinct environments (Fine *et al.* 2005; Misiewicz & Fine 2014). In this context, niches are not conserved and environmental preferences are randomly distributed over the phylogeny. In contrast, if long-distance dispersal (Dexter *et al.* 2017) or physical barriers (Haffer 1969; Hoorn *et al.* 2010) have been important for promoting species diversification, geographic isolation between habitats promotes divergence and limits gene flow among areas. Populations will gradually diverge to originate new species with a high degree of similarity, and habitat preferences

will be conserved, resulting in environmental niches clustered within the phylogeny (Peterson *et al.* 1999; Wiens 2004a, 2007).

Lastly, different levels of PS or PNC may also affect species ability to adapt in the face of predicted climatic and anthropogenic changes. Through time, species evolve, adapt, or become locally or globally extinct when facing stressful conditions. Some taxa may have the evolutionary potential to adapt to environmental changes and persist (Bell & Collins 2008) while other taxa may be unable to move or evolve fast enough and may become vulnerable to extinction (Quintero & Wiens 2013). Alternatively, species may die out locally and shift their geographical distribution to remain within their ancestral environment (Ackerly 2003; Parmesan & Yohe 2003). In particular, the prevalence of niche conservatism or strong phylogenetic signal would suggest that environmental niches have evolved little from their ancestral state and species may struggle to adapt to changing environments (Wiens & Donoghue 2004; Wiens & Graham 2005; Wiens *et al.* 2010; Lavergne *et al.* 2013). Therefore, their only possible response may be to migrate and track their most suitable environment conditions (Feeley *et al.* 2011a; Feeley *et al.* 2011b; Feeley & Rehm 2012; Jump *et al.* 2012; Duque *et al.* 2015). In contrast, the presence of low phylogenetic signal would suggest that species may be able to adapt to current environmental changes.

If closely related species share similar environmental preferences, species' responses to environmental change may be biased towards particular lineages, whereas, if environmental preferences are randomly distributed over the phylogeny, it is likely to protect evolutionary diversity from being eroded. For instance, Willis *et al.* (2008) studied species responses to climate change over the past 100 years among 473 tree species. They found that traits associated with flowering-time response to temperature (i.e. the ability of species flowering time to track short-term seasonal temperature changes) did show a phylogenetic signal. Thus, rather than individual species randomly declining in abundance, the pattern was biased against certain clades. Species where flowering times were not able to track climate changes were clustered in the phylogeny and decreased significantly in population size, indicating that there is a phylogenetic selective pattern shaping

species abundance and composition in the face of climate change (Willis *et al.* 2008).

## **1.7 Similarity amongst related lineages in tropical trees**

The links between ecological characteristics and phylogeny are potentially particularly important in tropical forests because the broad environmental gradients found in these ecosystems (ter Steege *et al.* 2006; Quesada *et al.* 2010; Moulatlet *et al.* 2017), high tree and evolutionary diversity (Gentry 1982, 1988b, a; ter Steege *et al.* 2013; Honorio Coronado *et al.* 2015) and the widely varying functional characteristics (Chave *et al.* 2006; Baraloto *et al.* 2010a) mean it is difficult to understand the ecology of each of the many coexisting species in these ecosystems. In such complex ecosystems, evolutionary relationships may be useful for understanding variation in species' functional characteristics and environmental preferences. However, the presence of niche conservatism or strong phylogenetic signal in tropical forest is controversial, and it is still uncertain to what extent it varies among traits.

### **1.7.1 PNC and PS of tropical tree traits**

Previous studies of PS in tropical forests, focusing on a wide variety of morphological traits (e.g. specific leaf area, seed mass, trunk xylem, tree height) and at different spatial scales (Chave *et al.* 2006; Baraloto *et al.* 2012; Swenson *et al.* 2012; Yang *et al.* 2014; Liu *et al.* 2015; Hietz *et al.* 2017), have failed to find consistent patterns. Different studies have contrasting results: whilst some traits show low but significant phylogenetic signal (Baraloto *et al.* 2012; Swenson *et al.* 2012; Yang *et al.* 2014; Dexter & Chave 2016), others have found that traits are randomly dispersed over the phylogeny (Uriarte *et al.* 2010; Fan *et al.* 2012) and it is still uncertain to what extent phylogenetic signal varies. For example, in tropical forest plots in French Guiana among 668 tree species, 17 leaf and trunk functional traits (e.g. specific leaf area, leaf nutrients, wood density, and trunk bark thickness) showed a significant phylogenetic signal, suggesting that phylogenetic distance is associated with variation in these traits. In contrast, in

Asian tropical forest among 40 species, seven functional traits (e.g. wood density, vessel density, potential hydraulic conductivity) did not display a significant phylogenetic signal, suggesting that there is no functional trait similarity amongst related lineages (Fan *et al.* 2012).

These results illustrate the different patterns found for different traits in tropical forests. Two main points need to be considered in light of these results: i) which traits are most important and, ii) the scale of the study. The specific traits investigated in previous studies (specific leaf area; foliar K, N, C, P, chlorophyll; leaf thickness; trunk bark thickness; trunk xylem density) reflect specific aspects of plant function. In contrast, life-history traits (e.g. turnover rates, maximum growth, and mean size) may be more functionally relevant as they provide integrated measures of tree performance and better reflect life-history strategies. Moreover, the scale of study is also likely to affect whether phylogenetic signal will be observed, and previous studies were conducted at small spatial scales and only included a limited set of environmental conditions.

### **1.7.2 PNC and PS of the environmental preferences of tropical trees**

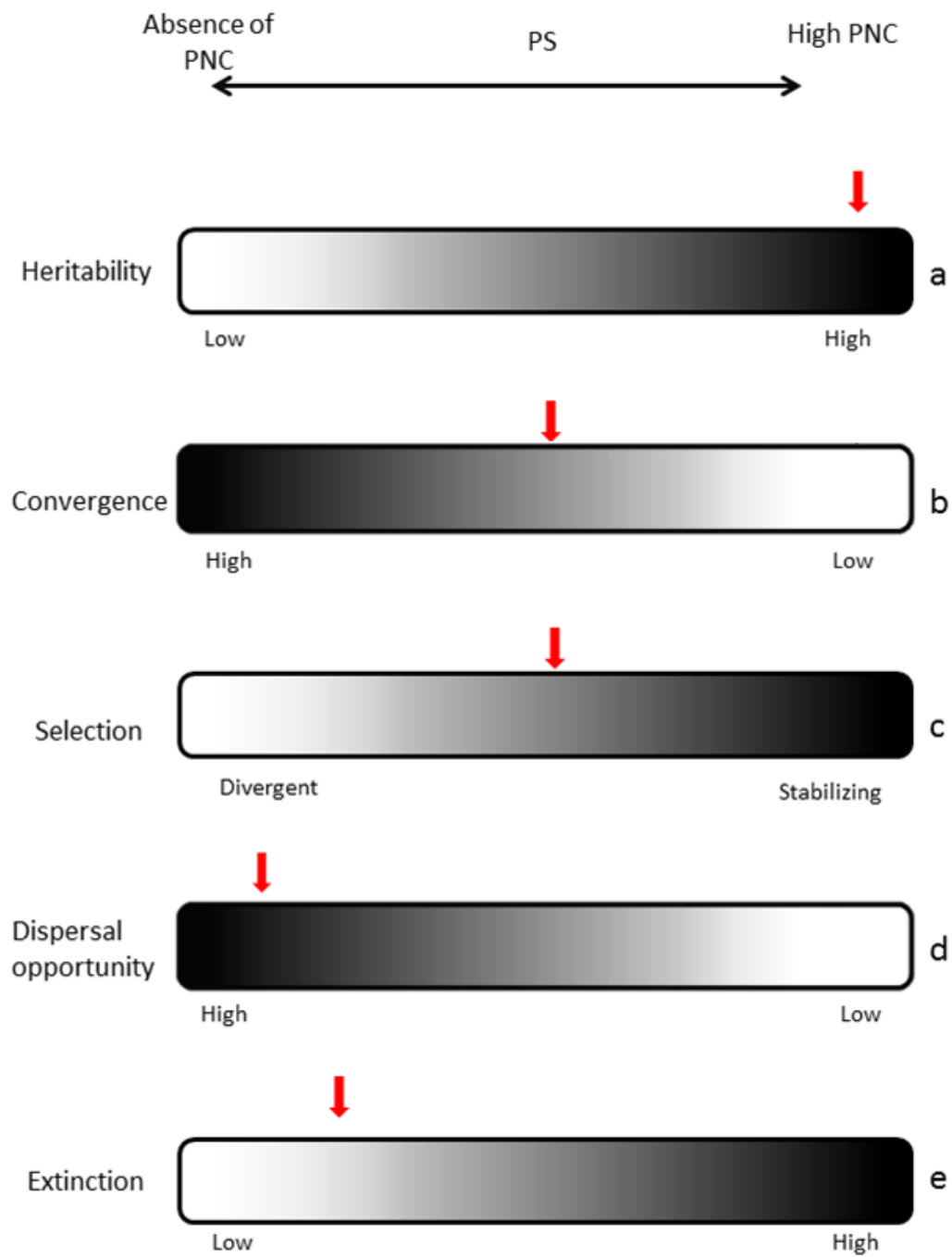
The extent of similarity of environmental preferences among tropical trees has also been used to understand the mechanisms that generate and maintain species diversity. Several studies have previously investigated the fingerprint of evolution on environmental niche preferences of tropical trees. However, these studies are either focused on specific clades (Fine *et al.* 2005; Fine *et al.* 2014; Misiewicz & Fine 2014) or limited to small spatial scales (Schreeg *et al.* 2010; Zhang *et al.* 2017). For instance, investigating environmental preferences in *Crepidospermum*, *Protium*, and *Tetragastris* of the monophyletic tribe Protieae in the Western Amazon, Fine *et al.* (2005) found that edaphic specialization is an important driver of species diversity and distribution. Among 35 species in the Protieae, 74% were significantly associated with only one soil type (i.e. white-sand, clay, and terrace) and no species occurred in all habitat types. Additionally, closely related species did not tend to share similar edaphic preferences, suggesting that adaptations to different edaphic heterogeneity had contributed to generating the high diversity of this group. The finding that white-sand and clay specialist



species are randomly distributed over the phylogeny show that adaptations for certain environments have evolved independently and at multiple times over evolutionary timescales. In contrast, across 183 woody species in a subtropical tree community in China, preferences for specific environments were clustered in the phylogeny, showing that closely related species tend to share similar habitats (Pei *et al.* 2011). The significant phylogenetic signal for habitat preference indicates that niche conservatism was a more important process underlying the assembly of this community.

### 1.7.3 Evolutionary processes underlying trait variation in tropical trees

Overall, multiple processes have acted simultaneously during the evolution of tropical forest trees and these processes may favour the existence of either high or low levels of similarities of functional tree traits and environmental niches between related species (Figure 1.3). For example, if traits are inherited from their ancestors, high heritability may induce strong PS or niche conservatism (Figure 1.3a). In contrast, strong convergent or divergent evolution may reduce the extent of phylogenetic signal. Adaptation to distinct environmental conditions (e.g. white sand, terra-firme, and swamp forests) may either lead to convergent evolution among distantly related lineages, or divergent selection across related lineages. Considering the wide range of environmental gradients across the Amazon basin and the role of habitat specialization in the diversification process (Fine *et al.* 2005) I expect that both convergent evolution (Figure 1.3b) and divergent selection (Figure 1.3c) may reduce the extent of PS. Dispersal limitation will also influence the extent of similarity among related lineages. High dispersal opportunity over geological timescales across Amazonia (Dexter *et al.* 2017) could potentially reduce the extent of PS among lineages (Figure 1.3d). Extinction also plays a role in governing patterns of niche conservatism. Many Amazon rainforest lineages survived strong fluctuations in climate over the Quaternary, including the cooler and drier conditions of the of last glacial maximum (Anhufo *et al.* 2006). Due to low levels of extinction in these lineages, low levels of PS may also be expected (Figure 3e). Therefore, because many rainforest lineages survived fluctuations in climate, I expect low levels of extinction that could lead to low levels of phylogenetic signal (Figure 1.3e). Overall, high PS may suggest that high heritability is more important in driving the evolutionary trajectory of tropical forests. In contrast, absence of PS may suggest that greater selection, dispersal opportunity, and extinction have been more important processes driving the evolution of extant taxa.



**Figure 1.3** Evolutionary and ecological causes of the presence or absence of niche conservatism: The red arrows represent the expected trend in niche conservatism for Amazonian trees at genus level, according to the different processes (adapted from Crisp and Cook, 2012).

Moreover, I acknowledge that interpretation of the processes underlying the extent of similarity among related lineages must be done with caution. Measuring the amount of PS or PNC does not directly explain which processes are responsible for the final pattern. However, it has many implications for understanding community structure and ecosystem processes (Wiens *et al.* 2010).

## **1.8 Diversity and ecosystem function**

Evolutionary history may be valuable for understanding variation in ecosystem function in tropical forests, in addition to understanding the mechanisms that underlie the maintenance of species diversity and distributions. Generally it has been found that ecosystem functioning increases with higher species richness (Tilman *et al.* 1996; Tilman *et al.* 2001; Cardinale *et al.* 2012; Cavanaugh *et al.* 2014; Poorter *et al.* 2015b; van der Sande *et al.* 2017b), and biodiversity loss has a negative effect on ecosystem function (Cardinale *et al.* 2012). For example, to test how differences in species richness impact biomass production, Tilman *et al.* (1996) conducted a grassland field experiment from a pool of 24 species in 147, 0.5 x 0.5 m, plots. Among seven different treatments, ecosystem productivity increased with species richness and diversity. In general, higher biomass and carbon stocks are commonly found in more diverse assemblages, while less carbon content is frequently observed in monoculture or lower diversity areas (Tilman *et al.* 1996; Tilman *et al.* 2001; Liang *et al.* 2016).

Different species contribute in different ways to the storage and processing of carbon. The two main mechanisms proposed to explain the effect of biodiversity on ecosystem processes are niche complementarity and the selection effect. Niche complementarity assumes that diverse groups of species have a higher variety of functional traits and can better utilize the available resources, which increases ecosystem function (Cardinale *et al.* 2007; Cardinale *et al.* 2012; Tilman *et al.* 2014). Thus, in more diverse communities, species complementarity in their use of resources and production of biomass is more efficient than in less diverse areas. In contrast, the selection effect states that the presence of particular highly productive species controls ecosystem processes, and that these key species are

more likely to be found in hyperdiverse communities. Both these underlying mechanisms may also act together (Loreau & Hector 2001). For example, across 111 experiments that manipulated species richness to investigate how diversity affect biomass, Cardinale *et al.* (2006) found that on average more diverse communities tended to maximize biomass. Higher stocks were found in more diverse communities that were more likely to be dominated by the most productive species, providing consistent evidence for the selection effect. In contrast, Cadotte (2013) found support for the complementarity effect when investigating the relationship between biodiversity and productivity across 100 grassland experimental plots. However, even though these studies made substantive progress on understanding the relationship between biodiversity and ecosystem function, they have mainly focused on small spatial scales and controlled experiments, and it is therefore difficult to expand these results to natural and hyperdiverse ecosystems over large scales (Tilman *et al.* 1996; Tilman *et al.* 2001; Cardinale *et al.* 2006; Cardinale *et al.* 2007; Cardinale *et al.* 2012; Cadotte 2013).

Recently, a number of studies have attempted to understand how diversity in tropical forests is linked to ecosystem function (Chisholm *et al.* 2013; Day *et al.* 2013; Cavanaugh *et al.* 2014; Poorter *et al.* 2015b; Poorter *et al.* 2017; Sullivan *et al.* 2017). Overall, at fine spatial scales (e.g. 0.1 and 0.04 ha) there is a positive and significant biodiversity-carbon relationship (Chisholm *et al.* 2013; Poorter *et al.* 2015b; Sullivan *et al.* 2017; van der Sande *et al.* 2017a). However, results for larger spatial scales relevant for conservation planning are less clear (Table 1.1). For example, among one hectare plots, some studies show a positive carbon-diversity relationship across the Neotropics (294 plots -Poorter *et al.* 2015b), in the pantropics (59-Cavanaugh *et al.* 2014) and in Central Africa (33-Day *et al.* 2013), whilst others detected no global relationship (668-Chisholm *et al.* 2013) or no relationship within the tropics (366-Sullivan *et al.* 2017). In a recent meta-analysis of 38 empirical studies assessing biodiversity-ecosystem functioning in tropical forests, van der Sande *et al.* (2017b) argued that in 64% of the investigated relationships, biodiversity was significantly associated with carbon stocks and uptake. However, the authors used the term biodiversity in a broader

sense, including trait diversity (wood density, specific leaf area), community mean traits, and forest structural attributes (e.g. basal area, number of individuals), and their results were mainly driven by the prevalent effect of structural attributes and trait diversity. In essence, variation in forest structural characteristics (e.g. wood density and tree size) are a more consistent and important driver of ecosystem functioning than diversity *per se* at these scales (Cavanaugh *et al.* 2014; Poorter *et al.* 2015b; Poorter *et al.* 2017; Sullivan *et al.* 2017). Importantly, whilst different studies show contrasting results for biodiversity-ecosystem functioning relationships at landscape scales, the importance of functional characteristics and structural variables persist with different plot sizes.

**Table 1.1** Summary of studies assessing the relationship between biodiversity and ecosystem functioning including tropical forests. On the effect: ‘+’ indicates a positive diversity-ecosystem functioning relationship and blank spaces indicate that there is no relationship. Plot size with ‘NA’ indicates this information is not available for the study.

Reference	Geographical scope	Number of plots	Plot Size	Ecosystem functioning metric	Diversity - Ecosystem function relationship
Poorter et al., 2017	Neotropics	201	1 ha	Productivity	
Poorter et al., 2017	Neotropics	201	1 ha	Biomass	+
Poorter et al., 2017	Neotropics	201	1 ha	Growth of recruits	
Sullivan et al., 2017	Pan Tropical	360	1 ha	Biomass	
Sullivan et al., 2017	Pan Tropical	6536	0.04 ha	Biomass	+
Poorter et al., 2015	Neotropics	294	1 ha	Biomass	+
Poorter et al., 2015	Neotropics	1975	0.04 ha	Biomass	+
Liang et al., 2016	Tropical and Temperate	777126	NA	Productivity	+
Cavanaugh et al., 2014	Pan Tropical	59	1 ha	Biomass	+
Chilson et al., 2013	Tropical and Temperate	688	1 ha	Biomass	
Chilson et al., 2013	Tropical and Temperate	17200	0.04 ha	Biomass	+
Chilson et al., 2013	Tropical and Temperate	688	1 ha	Productivity	
Chilson et al., 2013	Tropical and Temperate	17200	0.04 ha	Productivity	+
Day et al., 2013	Central Africa	33	1 ha	Biomass	+

The link between biodiversity and both wood productivity and aboveground biomass is mediated by plant functional characteristics. Species' ecological characteristics have been shown to play an important role in determining productivity and aboveground carbon stocks in tropical tree communities (Baker *et al.* 2004b; Banin *et al.* 2012; Banin *et al.* 2014; Fauset *et al.* 2015). In particular, wood density and potential tree size are good predictors of regional-scale patterns of aboveground biomass. For instance, regional-scale patterns of aboveground biomass across the Amazon basin are associated with variation in wood density: forest communities in the central and eastern Amazonia have roughly 16% more carbon than communities in the west, due to the presence and greater abundance of species with higher wood density (Baker *et al.* 2004b). Furthermore, there may also be unmeasured functional characteristics that promote ecosystem function. For example, in temperate forests, variation in crown architecture among species (e.g. height, crown width and shape) has been proposed to increase productivity due to a more efficient use of space (Reich 2012; Pretzsch 2014; Jucker *et al.* 2015; Schmid & Niklaus 2017; Williams *et al.* 2017). Species with different crown architectures distribute their branches and leaves in complementary height layers of the canopy, leading to denser and more packed canopies, which in turn allow higher light interception and promote productivity (Williams *et al.* 2017). However, identifying and measuring all traits that most strongly promote ecosystem services is a challenge in diverse tropical forests. If traits associated with carbon stocks and productivity do show a PS, an alternative approach is therefore to use the evolutionary relatedness amongst species as a proxy for their functional similarity.

## **1.9 Phylogeny as an index**

If traits have a PS or PNC, phylogenetic structure will reflect species niche similarity and may be used as a proxy to investigate the legacy of historical processes. A common metric to represent evolutionary relatedness among species is phylogenetic diversity (PD). PD is a metric that may be expressed as the sum of all phylogenetic branch lengths connecting species together within an assemblage



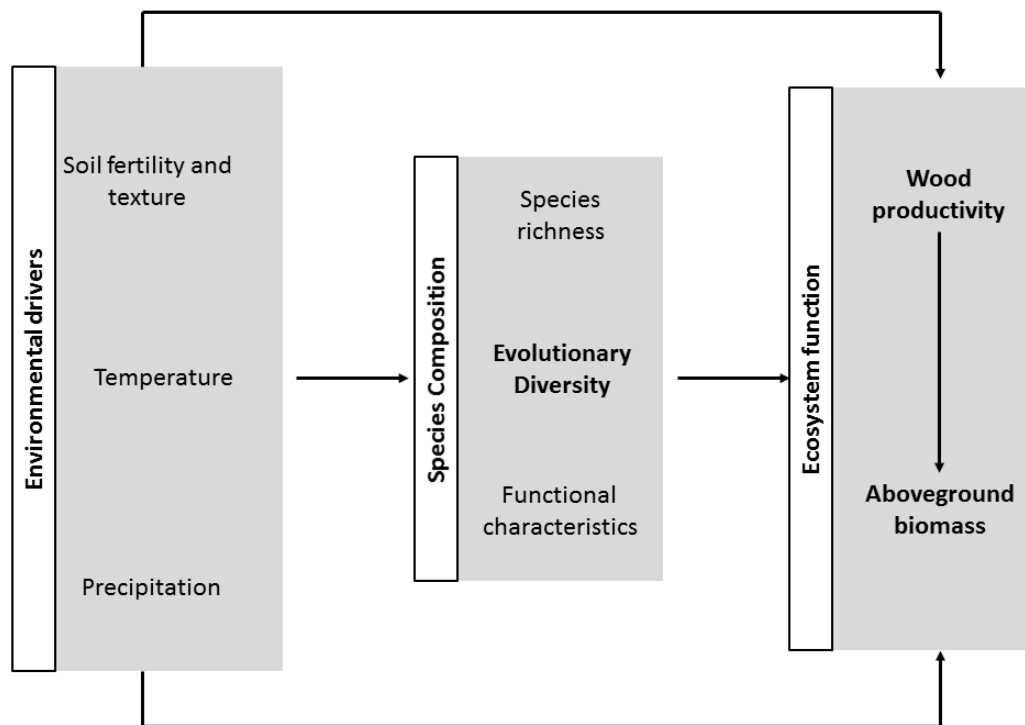
(Faith 1992). This continuous measurement summarises trait information, species richness and composition in a single index (Mouquet *et al.* 2012; Srivastava *et al.* 2012; Tucker *et al.* 2016; Cadotte *et al.* 2017a) and has been widely used in the recent literature to understand patterns of community phylogenetic structure, and as a proxy for functional characteristics (Forest *et al.* 2007; Cadotte *et al.* 2008; Cadotte *et al.* 2009; Flynn *et al.* 2011; Cadotte *et al.* 2013; Cadotte 2013; Honorio Coronado *et al.* 2015). Two additional metrics that have been proposed to represent different facets of evolutionary diversity are the mean phylogenetic distance between all species within a community (MPD), and the mean nearest taxon distance (MNTD), which is calculated based on the mean evolutionary distance between each species and its closest relative (Webb 2000; Webb *et al.* 2002; Tucker *et al.* 2016). MPD is strongly affected by the presence of early diverged clades and represents the proportion of the major lineages of organisms, whereas MNTD is more influenced by presence of closely related species in any given community (Webb *et al.* 2002). PD, MPD and MNTD all attain higher values in communities comprised of more distantly related individuals.

### **1.9.1 Phylogenetic diversity as a proxy for ecosystem function**

Empirical studies have shown that different facets of evolutionary diversity are useful predictors of ecosystem function (Maherali & Klironomos 2007; Cadotte *et al.* 2009; Srivastava *et al.* 2012; Cadotte *et al.* 2013; Cadotte *et al.* 2017b). For example, in experiments using grassland plants, 97 (4 m<sup>2</sup>) plots were seeded with 1, 2 or 4 plant species (from a pool of 17 species) with communities that comprised species with short, medium or large phylogenetic distances between them (Cadotte 2013): plots with short PD included sister species, while plots with large PD included distantly related lineages. Assemblages with greater PD showed higher biomass production, while assemblages with closely related species produced less biomass, and PD was a better predictor of biomass production when compared to other measurements of taxonomic diversity. Cadotte (2013) argued that in assemblages with closely related species there may have been negative interactions due to competition for resources or pathogen sharing among related species, either of which may have reduced productivity.

However, in the same grassland experiment, PD was a better predictor of productivity than functional traits (e.g. specific leaf area, seed weight and height) suggesting an additional contribution of unmeasured traits that are significantly related to phylogeny (e.g. root architecture or root morphology) (Cadotte *et al.* 2009). Overall, these examples demonstrate that evolutionary relationships may account for a proportion of functional diversity not captured in measured traits.

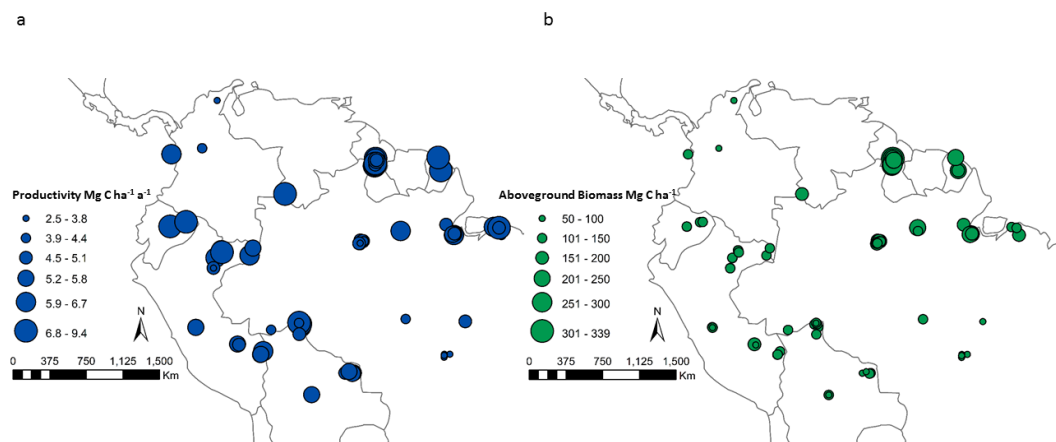
Overall, the potential of PD to predict ecosystem function has been poorly studied, and only examined in experiments conducted with low diversity, which do not represent the complexity of tropical forests. In addition, none of the small-scale studies have considered the direct effect of environmental variables that also affect ecosystem function at large spatial scales (Figure 1.4).



**Figure 1.4** Diagram of environmental effects (climate and soil) on phylogenetic diversity and therefore on ecosystem function. Arrows point to response variables. Higher phylogenetic diversity is expected to increase biomass production and carbon storage.

## 1.10 Environmental determinants of AGWP and AGB

Aboveground wood productivity (AGWP) and aboveground biomass (AGB) vary widely across tropical forests. Within the Amazon, AGWP estimates range from 2.5 to 9.4 Mg C ha<sup>-1</sup> a<sup>-1</sup> and AGB from 50 to 339 Mg C ha<sup>-1</sup> for all trees ≥ 10 cm diameter at breast height (Figure 1.5). Overall, AGWP is substantially higher in Western Amazon and the Guiana Shield, while much lower values are found in forests on the Brazilian Shield (Phillips *et al.* 2004; Johnson *et al.* 2016). By contrast, AGB is generally lower in Western Amazon and the Brazilian Shield, whilst greater AGB is found in forests on the Guiana Shield and East Central Amazon (Baker *et al.* 2004b; Malhi *et al.* 2006; Johnson *et al.* 2016). The spatial variation of AGWP is largely determined by edaphic and climatic gradients (Malhi *et al.* 2004; Phillips *et al.* 2004; Quesada *et al.* 2012), whilst variation in AGB is mainly determined by variation in stem mortality rates (Johnson *et al.* 2016).



**Figure 1.5** Variation in wood productivity (a) and carbon storage (b) across the Amazon basin and Guiana Shield. Sizes of dots are proportional to the magnitude of each variable.

Variation in AGWP has been shown to be strongly positively correlated with soil fertility, and to a lesser extent, negatively associated with temperature (Quesada *et al.* 2012). The positive effect of soil fertility in AGWP is mainly driven by total phosphorus, with forest plots nearer the Andes having higher phosphorus and cation exchange capacity (Quesada *et al.* 2010; Quesada *et al.* 2011; Quesada *et al.*

*al.* 2012) due to recent sediment deposition from the Andean uplift (Hoorn *et al.* 2010). In contrast, older and more weathered soils in the central and eastern Amazon have lower phosphorus concentrations and are associated with lower AGWP (Aragao *et al.* 2009; Quesada *et al.* 2012). The effect of phosphorus on increasing AGWP is directly associated with photosynthetic rates; as phosphorus is a vital element of adenosine triphosphate (ATP) and sugar phosphates, low levels of phosphorus may limit photosynthesis and consequently decrease productivity (Kitayama *et al.* 2004; Domingues *et al.* 2010). The pervasive negative effect of temperature may be associated with decreasing in photosynthetic rates or increasing respiration rates at higher temperatures (Lloyd & Farquhar 1996, 2008). Under high temperatures, there is an increase in the vapour pressure deficit, reducing stomatal conductance and consequently leading to a reduction in photosynthesis and carbon assimilation (Lloyd & Farquhar 2008). However, despite the importance of environmental variables for driving very large-scale patterns of AGWP and AGB, within moist tropical forests the effect of AGWP on AGB is weak, and AGB is ultimately largely determined by variation in stem mortality rates (Johnson *et al.* 2016). Tree death is a highly stochastic process, mediated by disturbance events and plant traits such as wood density and growth rates (Chao *et al.* 2008).

## **1.11 Quantifying environmental variables**

Climate variables, including precipitation and temperature, are readily available at 1 km resolution (e.g. WorlClim Hijmans *et al.* 2005) and have been widely used as potential confounding factors in analyses investigating the relationship between taxonomic metrics of diversity and ecosystem functioning (Poorter *et al.* 2015b; Poorter *et al.* 2017; Sullivan *et al.* 2017; van der Sande *et al.* 2017a; van der Sande *et al.* 2017b). However, the inclusion of edaphic properties is still a major problem. Although there are a number of soil maps currently available (e.g. Nachtergaele *et al.* 2012; Hengl *et al.* 2014; Hengl *et al.* 2017) their low resolution and accuracy represent a major practical problem (as reviewed in Moulatlet *et al.* 2017). One of the challenges to quantify soil properties is the

spatial scale which they operate. The most commonly used soil maps are the Harmonised World Soil database (HWSD; Nachtergaele *et al.* 2012) and the Soil Grid map (Hengl *et al.* 2014; Hengl *et al.* 2017) which have spatial resolutions of 1 km and 250 m respectively. However, unlike climate data that can be more readily interpolated, soil properties are not continuous in space and vary at small spatial scales of 0.1-1 km, limiting the spatial accuracy of these maps. An additional limitation on using large-scale soil maps are the variables that are available to use as a proxy for soil fertility (Lloyd & Veenendaal 2016; Moulatlet *et al.* 2017). In particular, Soil Grid provides cation exchangeable capacity (CEC) as a proxy for soil fertility. CEC combines information about the concentrations of different soil cations (e.g. calcium, magnesium, potassium, and aluminium) in a single index and does not provide information on specific soil nutrients. Because CEC includes the contribution of potentially toxic aluminium ions, it does not provide an ecologically relevant variable to infer soil fertility in tropical forests (Lloyd & Veenendaal 2016; Moulatlet *et al.* 2017). Moreover, a number of studies have shown that phosphorus is the most relevant edaphic property associated with ecosystem functioning (Aragao *et al.* 2009; Cleveland *et al.* 2011; Mercado *et al.* 2011; Quesada *et al.* 2012) and soil phosphorus is not available in any of the large-scale digital maps. Although edaphic variables at a local scale are challenging to collect, ecologically relevant soil properties are difficult to estimate without direct local measurements.

## **1.12 Data sources**

### **1.12.1 Inventory data**

This thesis used tree inventory data available from ForestPlots.net, through the RAINFOR project (Amazon Forest Inventory Network - Lopez-Gonzalez *et al.* 2009). Forest plots were established during 1975-2010 across the major climatic and edaphic gradients in the Neotropics (Figure 1.1). Each plot includes living trees  $\geq 10$  cm diameter, records of tree mortality and identifications of recruits using uniform and standardized protocols. The number of plots used in each data

chapter varied according to the selection criterion for each analysis. For Chapter 2, I used 577 inventory plots in closed-canopy forest plots. In Chapter 3, I used 90 plots from lowland moist forests on well-drained soils across the Amazon Basin. Lastly, in Chapter 4, I used 788 plots including the Amazon and adjacent biomes. (Appendix 1 - please see detailed methods in each chapter for the specific reasoning and selection criteria for each analysis).

### **1.12.2 Environmental data**

In order to understand the role of environmental variation in explaining the results found here, for each plot I used temperature and precipitation data extracted from the WorldClim dataset (Hijmans *et al.* 2005), cumulative water deficit (the difference between precipitation and evapotranspiration) from Chave *et al.* (2014) and soil data from Quesada *et al.* (2010). All climate variables (i.e. precipitation, temperature, and cumulative water deficit) are derived from interpolations of monthly weather station data from 1950 to 2000 at a resolution of 1km<sup>2</sup>. Soil sampling was carried out following standard protocols detailed described by Quesada *et al.* (2010). Here, I used soil data from 0-30 cm depth collected in 160 forest plots. From homogeneous plots with flat topography 5 soil samples were taken across the plot. In areas with higher spatial variability up to 12 samples were taken within the plot (Quesada *et al.* 2010).

### **1.12.3 Phylogenetic data**

In order to understand the role of evolution for present day patterns of diversity and carbon processing and storage, I used different sources of phylogenetic data. In Chapter 2, I used a recently developed genus-level phylogeny of tropical trees (Dexter & Chave 2016) and species-level phylogenies of the genus *Inga* (Dexter *et al.* 2017) and the tribe Protieae (Burseraeae) (Fine *et al.* 2014). For Chapters 3 and 4, I developed a new time calibrated molecular genus-level phylogeny based on two chloroplast DNA gene regions: *rbcL* and *matK*. The phylogeny comprises 1122 genera found in South America tree communities and includes all major angiosperm clades (details of the methods of phylogenetic reconstruction are given in Chapter 3).

The main analyses in this thesis were done at genus-level due to the availability of the phylogenetic data at this taxonomic scale. Most angiosperm phylogenies are poorly sampled at the species-level (Nieto-Blázquez *et al.* 2017) and the relationships between many species are still unresolved (Hodkinson & Parnell 2007). Thus, generating a species-level phylogeny considering the high diversity of the Amazon and adjacent biomes (Gentry 1982, 1988b; ter Steege *et al.* 2013) would be unfeasible in the time-frame of this thesis. A possible alternative approach would have been to use the genus-level phylogeny, but include polytomies within each genus to include the species within each clade (e.g. Kress *et al.* 2010; Uriarte *et al.* 2010; Jetz *et al.* 2012). However, this approach could strongly inflate estimates of phylogenetic signal (Davies *et al.* 2012; Molina-Venegas & Rodriguez 2017) and underestimate phylogenetic diversity (Swenson 2009), leading to misleading interpretations of many ecological and evolutionary processes.

## **1.13 Research aim and objectives**

### **1.13.1 Thesis aim**

The introduction and background above have shown that the legacy of historical processes on present day patterns of diversity, their respective functional characteristics, and ecosystem functioning remains largely unexplored in diverse tropical forests. In this thesis, I focus on investigating the legacy of evolution on the current patterns of biodiversity, carbon processing, and storage in tropical forests.

### **1.13.2 Thesis objectives**

**Objective 1: Explore the extent to which closely related lineages share similar abilities to process and store carbon.**

1.1 Compile wood density data and calculate life-history traits (i.e. potential size, maximum and mean growth and mortality rates) using data from a large network of inventory plots across the Neotropics;

1.2 Examine how different traits associated with carbon processing and storage are correlated;

1.3 Quantify the phylogenetic signal of the different traits to determine how the variation in the ability of different taxa to process and store carbon is correlated with their phylogenetic relatedness.

**Objective 2: Test the association between taxonomic and evolutionary metrics of diversity, and two key measures of ecosystem function - wood productivity and aboveground biomass.**

2.1. Estimate common and phylogenetic diversity metrics for tropical tree communities from permanent inventory plots;

2.2 Calculate wood productivity and carbon storage for the same tropical tree communities;

2.3 Compile environmental variables that directly affect carbon processing in tropical forests (i.e. soil and climate);

2.4 Compile functional attributes that are associated with carbon processing and storage (i.e. mean wood density and potential tree size);

2.5. Assess the effect of tree diversity on carbon uptake and stocks.

**Objective 3: Investigate the role of evolution in shaping environmental preferences in tropical forests.**

3.1 Compile the abundance of taxa within each tropical tree community from a large forest plots network;

3.2 Calculate the temperature, precipitation, and edaphic niche preference for each taxon across the Neotropics;

3.3 Investigate how the preferences for different environmental gradients are correlated;

3.4 Quantify the extent to which closely related taxa occupy similar habitats, using data on temperature, precipitation, and soil variation through:

3.4.1 Quantifying the phylogenetic signal of these environmental preferences;



3.4.2 Comparing the fit of four different evolutionary models (White-Noise, Brownian motion, Ornstein-Uhlenbeck, and Lambda) for the environmental preferences;

3.4.3 Investigating disparity of environmental preferences through time: explore the variation for the environmental preferences among clades versus within clades;

3.5 Compare the strength of PS across different environmental variables.



## **Chapter 2 : Evolutionary heritage influences Amazon tree ecology**

### **Abstract**

Lineages tend to retain ecological characteristics of their ancestors through time. However, for some traits, selection during evolutionary history may have also played a role in determining trait values. To address the relative importance of these processes requires large-scale quantification of traits and evolutionary relationships amongst species. The Amazonian tree flora comprises a high diversity of angiosperm lineages and species with widely differing life-history characteristics, providing an excellent system to investigate the combined influences of evolutionary heritage and selection in determining trait variation. I used trait data related to the major axes of life-history variation among tropical trees (e.g. growth and mortality rates) from 577 inventory plots in closed-canopy forest, mapped onto a phylogenetic hypothesis spanning >300 genera including all major angiosperm clades to test for evolutionary constraints on traits. I found significant phylogenetic signal for all traits, consistent with evolutionarily related genera having more similar characteristics than expected by chance. Although there is also evidence for repeated evolution of similar, pioneer and shade tolerant life-history strategies within independent lineages, the existence of significant phylogenetic signal allows clearer predictions of the links between evolutionary diversity, ecosystem function and the response of tropical forests to global change.

## 2.1 Introduction

Evolutionary heritage may act as a major constraint on the ecological roles that species in a lineage can occupy. Even under a random model of trait evolution where functional traits drift in state over time (e.g. a Brownian motion model), it is expected that closely related species have similar functional trait values and similar ecologies due to their shared common ancestry (Blomberg *et al.* 2003; Losos 2008a). However, both divergent selection and convergent evolution lead to weaker relationships between species relatedness and their ecological similarity (Blomberg *et al.* 2003; Revell *et al.* 2008; Crisp & Cook 2012). Hence, although it is often assumed that close relatives are more similar because they retain the ecological characteristics of their ancestors, in many clades the ancestral character state may not be conserved. Thus, rather than being simply assumed, the tendency of closely related species to have similar ecological characteristics needs to be tested.

The strength of the link between trait variation and phylogenetic relatedness has a wide range of implications for understanding ecological and evolutionary processes and can be measured by the magnitude of phylogenetic signal (PS) (Blomberg *et al.* 2003; Losos 2008a). For example, if a selected trait has significant PS, the relatedness of species can help to understand the underlying mechanisms that drive community structure (Webb *et al.* 2002; Baraloto *et al.* 2012; Yang *et al.* 2014). The presence of significant PS also suggests that the sum of phylogenetic distances among species that occur within a community (i.e. phylogenetic diversity) is a useful proxy for functional diversity and that, in turn, phylogenies of tree taxa may contribute to understanding ecosystem function (Cadotte *et al.* 2008; Cadotte 2013). In addition, if trait values are more similar than expected by chance among closely related lineages, it will be possible to predict the trait values for species where trait data are not available.

To understand the relative importance of evolutionary heritage versus selection in determining trait variation requires large-scale quantification of traits and evolutionary relationships amongst species. The Amazonian tree flora comprises a

high diversity of angiosperm lineages and species with widely differing life-history characteristics, providing an excellent system to investigate these processes. Previous studies of the degree of phylogenetic signal among traits of tropical trees, such as seed mass, leaf structure and chemistry, trunk characteristics and range size, have shown variable results (Uriarte *et al.* 2010; Baraloto *et al.* 2012; Yang *et al.* 2014; Dexter & Chave 2016). For example, some studies show significant PS (Baraloto *et al.* 2012; Yang *et al.* 2014; Dexter & Chave 2016), while for the same traits other studies have failed to detect any PS, with closely related species exhibiting rather different trait values (Uriarte *et al.* 2010; Fan *et al.* 2012). A key limitation of many of these studies is the limited spatial and phylogenetic scale of study, as well as the resolution of the phylogeny that they have used (Davies *et al.* 2012). Here, I explore patterns of PS at large spatial and phylogenetic scales using a sequence-based phylogeny to test whether there are significant levels of PS for four key traits related to the major axes of life-history variation among tropical trees: tree growth and mortality rates, wood density and potential tree size. These traits are related to resource acquisition and allocation, defence, and dispersal ability (Enquist *et al.* 2007; Swenson & Enquist 2007) and represent important axes of functional variation which drive variation in plant performance and function in many ecosystems (Nascimento *et al.* 2005). Moreover, those traits are strongly related to differences in carbon fluxes and storage among species (Fauset *et al.* 2015). As a result, understanding PS in these traits may help to understand and model ecosystem processes in such highly diverse tropical forests such as Amazonia, which may harbour more than 16,000 tree species (ter Steege *et al.* 2013).

Studying PS at large spatial scales is important because the scale of study affects the strength of PS. At small scales, patterns of PS can be obscured because co-occurring species represent just a small fraction of the species richness of clades (Krasnov *et al.* 2011; Burns & Strauss 2012). Small spatial scales encompass limited environmental variation, so the species pool is limited to representatives of different lineages that may have similar ecological traits and environmental requirements: this pattern results in a lower range in traits and low PS. The strength of this effect depends on how environmental variability changes with

spatial scale, on the degree of habitat specialization by species and the proportion of clades that are sampled in small-scale studies (Baraloto *et al.* 2012; Yang *et al.* 2014). However, in general, larger spatial scales incorporate greater environmental heterogeneity and encompass a larger number of lineages with a wider range of trait values. Inferring patterns of PS that are more representative of evolutionary trends therefore typically requires measurement across large spatial scales, including a wide range of environmental conditions and taxa from a broad array of clades (Cavender-Bares *et al.* 2009).

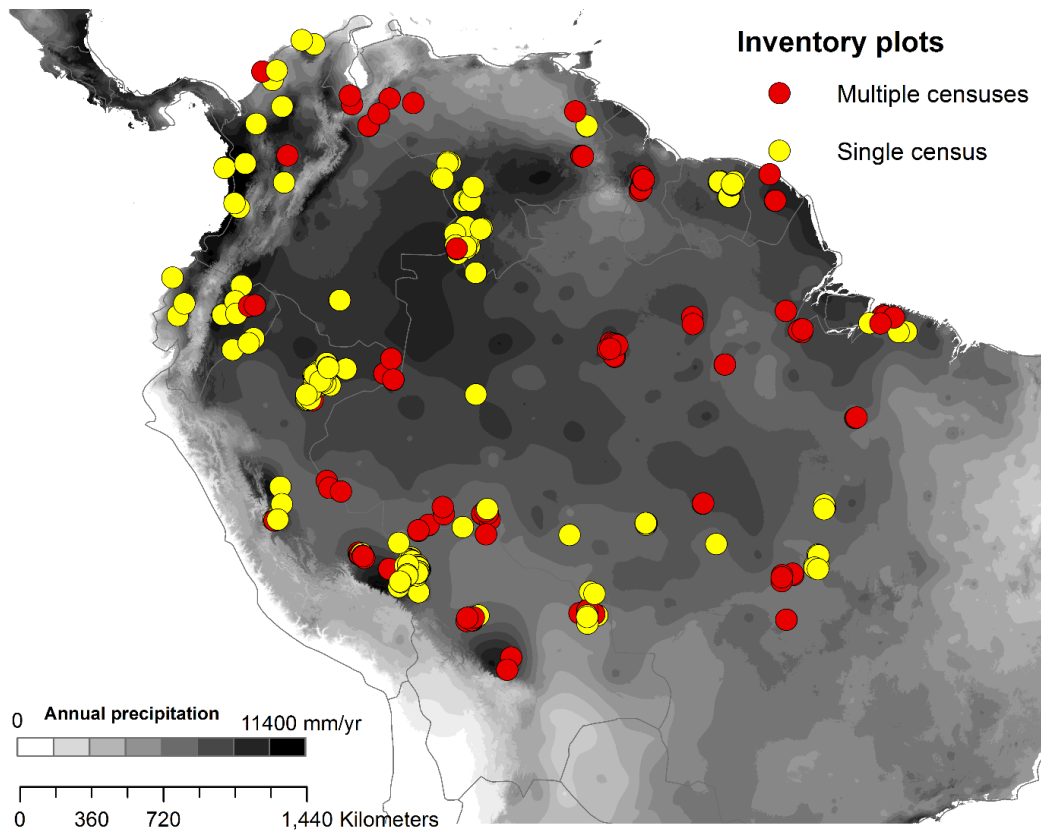
The patterns of PS also depend on traits under investigation and their specific evolutionary history. Some traits may exhibit phylogenetic conservatism where traits in specific lineages are constrained to certain trait values. For example, complex traits, such as growth and mortality, may depend in complex ways on multiple, interacting gene loci (El-Lithy *et al.* 2004; Conner & Hart 2005) which impose strong constraints on trait variation. Alternatively, traits may show no PS because they are under strong selective pressure and/or because they show phenotypic plasticity in response to environmental conditions (Geber & Griffen 2003; Burns & Strauss 2012).

Here, I use a large dataset of several hundred permanent forest plots that occur across a wide range of the environmental conditions from all nine Amazonian countries (Lopez-Gonzalez *et al.* 2011), to quantify key demographic traits of more than 300 lineages of tropical trees, and explore the PS of these traits using recently published molecular genus- (Dexter & Chave 2016) and species-level phylogenies (Fine *et al.* 2014; Dexter *et al.* 2017). By exploring how traits are correlated and the strength of PS, my goal is to address the fundamental question of whether repeated convergent and divergent evolution of life-history strategies has erased phylogenetic signal for life-history-related traits in tropical trees, or whether phylogenetic information can be used to understand ecosystem function in the world's most diverse and ecologically important forest.

## 2.2 Methods

### 2.2.1 Plot data

This study used inventory data from all trees and palms  $\geq 10$  cm diameter (DBH) in 577 forest plots from the RAINFOR forest plot network (Figure 2.1; Appendix 1) across lowland closed-canopy South American tropical forests. This network is centred on Amazonia and includes plots in forests on the Guiana Shield, in the Choco and northern South America; however, hereafter for simplicity I refer to this sampling region as ‘Amazonia’. Plots are located in old growth, unlogged forests and range in size from 0.04 to 25 ha (most being 1 ha). They span a precipitation gradient from 1300 to 7436 mm yr<sup>-1</sup> (Hijmans *et al.* 2005), a broad range of soil types (Quesada *et al.* 2010; Quesada *et al.* 2012), and are found below 500 m in elevation. Data were extracted from the ForestPlots.net database which curates tree-by-tree records from RAINFOR and other plot networks (Lopez-Gonzalez *et al.* 2009; Lopez-Gonzalez *et al.* 2011).



**Figure 2.1** Map of location of 577 selected plots in lowland tropical South America over a backdrop of the precipitation gradient (Annual precipitation, from the WorldClim dataset). The map shows plots, with annual precipitation greater than 1300 mm year<sup>-1</sup> and altitude less than 500 m. Yellow circles – single census, plots used exclusively for wood density and potential tree size; red circles – multi censuses, plots used for wood density, potential tree size, growth and mortality rates.

For productivity and mortality analyses, I used a subset of 257 repeated census plots with a minimum monitoring period of 2 years from 1962 to 2014. Mean census interval length is 4.4 years and plot mean total monitoring period is 9.9 years. During each census, all surviving trees and palms were measured, dead trees were documented, and new trees with  $\geq 10$  cm dbh were recorded. More detailed measurement methods and plot characteristics have been previously published (Baker *et al.* 2004a; Phillips *et al.* 2004). All recorded species and genus names were checked and standardized using the Taxonomic Name Resolution Service (Boyle *et al.* 2013). All trees and palms not identified to genus-level were excluded (7.9% of stems).



### 2.2.2 Trait data

Trait mean values of potential tree size, mean and maximum growth rates, mortality rates, and wood density were calculated at both the genus and species-level. Main analyses were performed at the genus-level and covered all genera present in a recently published genus-level phylogeny for Amazonian trees (Dexter & Chave 2016). Species-level trait data for those clades where I had species-level phylogenies with sufficient sampling of species in the dataset (>20 species): Burseraceae (Fine *et al.* 2014) and *Inga* (Dexter *et al.* 2017), were used to investigate whether patterns of PS at the genus-level were consistent with species level patterns. Species-level trait data were also used to account for intrageneric variation in the genus-level analyses of PS: the species-level data were used to calculate the standard error of each trait within each genus and these values were incorporated into the calculations of PS (described below) (Ives *et al.* 2007). In the methods below, all the details are given for trait values calculated at the genus-level; similar calculations and methods were used at the species-level.

Potential tree size, mean, and maximum growth rates were all calculated in terms of tree diameter, basal area, and biomass for each genus with at least 20 individuals across multiple censuses.

Potential tree size was estimated as the 95<sup>th</sup> percentile of the size distribution of all trees within each genus. For trees with multiple measurements, I selected the maximum size across different censuses to define these distributions. Tree aboveground biomass (AGB) per stem was calculated using the pan-tropical, three parameter allometric equation (diameter, wood density and  $E$ ) of Chave *et al.* (2014), which assumes that tree diameter-height relationships depend linearly on bioclimatic variables ( $E$ ), where  $E$  is a measurement of environmental stress based on measures of temperature seasonality and precipitation seasonality derived from the WorldClim dataset (Hijmans *et al.* 2005) and a measure of Cumulative Water Deficit extracted from a global gridded dataset (Chave *et al.* 2014). Palm biomass was estimated using a palm-specific allometric equation based on diameter (Goodman *et al.* 2014).

For each genus, I computed both mean growth rate and the 95<sup>th</sup> percentile of growth rates, to represent maximum growth rates within each genus, across all stems. To calculate these parameters, mean stem-level growth rate was first estimated as the mean growth per year across multiple censuses and maximum stem-level growth as the maximum growth rate per year calculated across multiple censuses. Trees with mean negative growth rates (0.9% of stems) were excluded in order to normalize the data (similar to Feeley *et al.* 2007). Palms, which do not have secondary growth, nine trees exhibiting diameter growth greater than 80 mm yr<sup>-1</sup> which likely represent recording errors and stems where diameter measurements were not made using a tape measure (0.12 % of all stems) were also excluded. If a change in the point of measurement (POM) was made during the measurement record of any given tree, growth rates were calculated using the arithmetic mean of the diameter measured at the original POM and the diameter at the new POM (Talbot *et al.* 2014).

Mortality rates were estimated for all genera with a minimum of 100 individuals in the plot data, based on the number of individuals found alive in the initial and final censuses of each plot. To estimate average mortality rates within each genus, the survival probability of individual trees within each clade was modelled as an exponentially declining function of the monitoring period whilst accounting for variation in tree size (Lines *et al.* 2010; Baker *et al.* 2014).

To account for the wide range of environmental conditions across plots (Figure 1.2), I used mixed models to calculate genus-level values of potential tree size, mean and maximum growth rates and mortality rates while accounting for systematic variation in these parameters among plots (Baker *et al.* 2014) (please, see detailed methods for calculating trait intrinsic value in Appendix 2.1).

Wood density data were extracted from the Global Wood Density database (Chave *et al.* 2009; Zanne *et al.* 2009) and average values calculated for each genus in the phylogeny (Baker *et al.* 2004b).

### 2.2.3 Trait correlations

To identify relationships amongst genus-level traits, I conducted a Phylogenetic Principal Component Analysis (PPCA) (Revell 2012) including genera where a complete set of trait data were available. PPCA incorporates the expected correlation among traits due to their shared evolutionary history into the principal component analyses (Revell 2009). Trait values were standardized to a mean of zero and unit variance to ensure that each trait contributed equally to the PPCA.

### 2.2.4 Phylogenetic Signal

In order to estimate phylogenetic signal (PS) for traits, I used Blomberg's  $K$  (Blomberg *et al.* 2003). This metric quantifies the amount of variance in an observed trait in relation to the expected trait variance under a BM model of evolution (Blomberg *et al.* 2003; Losos 2008a; Revell *et al.* 2008; Crisp & Cook 2012). Under this model of evolution, trait values drift randomly over time, with small changes being more likely than large changes within a given unit of time (trait values at  $t_1$  are chosen from a normal distribution centred on the trait value at  $t_0$ ). This model generates trait data where the covariance among trait values for taxa is proportional to the duration of their shared evolutionary history (Revell *et al.* 2008). Values of  $K$  equal to 0 indicate that there is no phylogenetic signal, whilst  $K$  equal to 1 indicates high phylogenetic signal and is the expected value under a BM model of evolution. Intermediate values ( $0 < K < 1$ ) indicate intermediate levels of phylogenetic signal. To assess significance in  $K$ , I recalculated  $K$  on the tree with randomized tips a thousand times, and compared the simulated values with the observed value of  $K$ . If the observed value fell outside the range given by 2.5-97.5 percentiles of the simulated values, this value was considered significant.

I accounted for intra-generic trait variation in the calculation of  $K$  by measuring the standard error for each genus, treating individual genera as species and intrageneric variation as intraspecific variation *sensu* (Ives *et al.* 2007). For genera where the standard error could not be computed, I assigned the mean value of the standard error for all genera with estimates for multiple species (Ives *et al.* 2007).

Including this within-genus variation allows to account for uncertainty in trait estimation (e.g. population variation and measurement error), improve parameter estimation and reduce bias in the calculation of PS (Blomberg *et al.* 2003; Ives *et al.* 2007).

I also calculated PS using Pagel's  $\lambda$  (Freckleton *et al.* 2002) in order to explore whether results were dependent on the particular method used to calculate phylogenetic signal (Appendix 2.2).

### **2.2.5 Sensitivity analysis**

To investigate whether results were affected by the spatial scale of study, I repeated the analyses using 26 plots within 55 km of each other near Manaus. Similarly, to verify whether results were affected by the use of genus-level data, I conducted the same analyses at the species level for the genus *Inga* and the Proteaceae (Bursaceae). Likewise, to investigate whether the number of lineages included in the analyses affected the extent of PS, I repeated the calculations of PS with just the genera with a complete set of trait values (214).

Statistical analyses were performed in the R 3.1.1 program (Team 2014), using *ape* (Paradis *et al.* 2004), *phytools* (Revell 2012) and *data.table* (Dowle *et al.* 2014) packages.

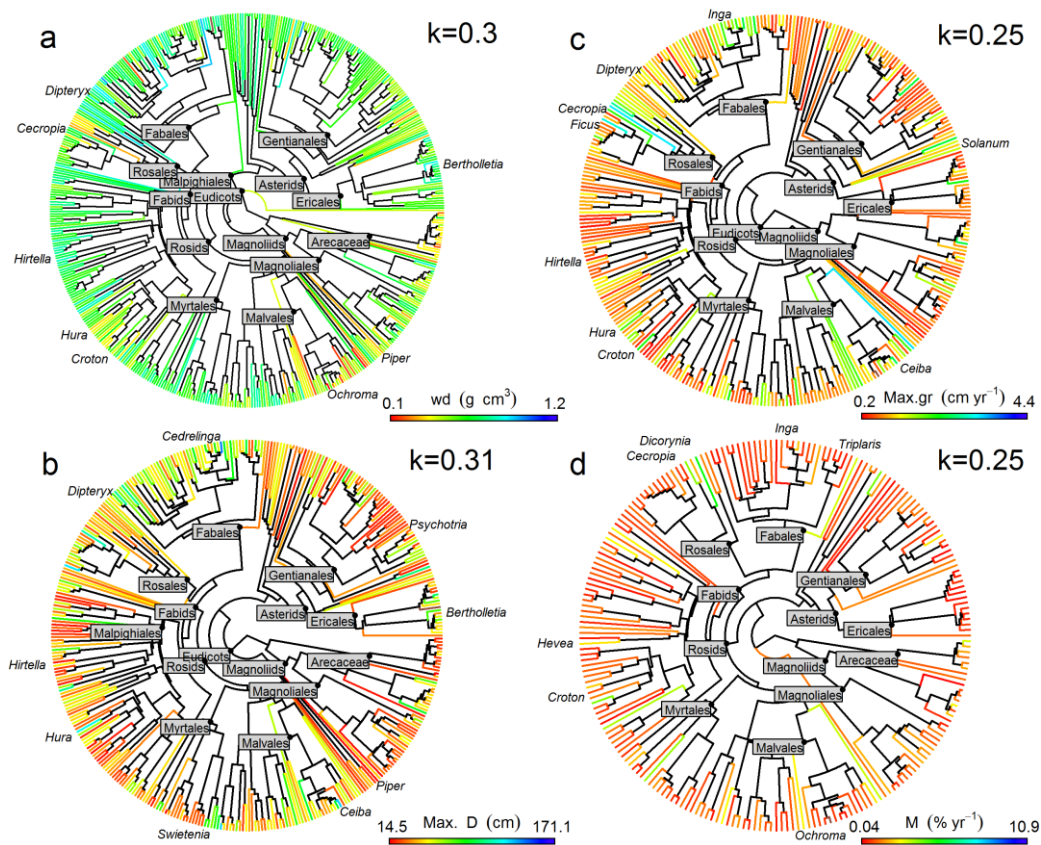
## **2.3 Results**

### **2.3.1 Trait data**

All traits measured varied substantially among genera (Table 2.1; Figure 2.2): wood density varied eight-fold, potential size in tree diameter 12-fold, potential size in biomass 814-fold, maximum growth rates in tree diameter 23-fold, mean diameter growth rates 35-fold, and mortality rates 275-fold. Overall, the trait values after correcting for environmental variation and those estimated directly from the database without accounting for variation among plots were highly correlated with each other ( $p < 0.001$  in all cases and  $\tau$  ranging from 0.59-0.79)

**Table 2.1** Summary of trait data including number of genera per trait, number of species, and number of individuals used for selection criterion, minimum, maximum and mean trait values per genera. In addition, phylogenetic signal for absolute trait values, accounting for intragenetic variation, environmental variation, and both environmental and intragenetic variation. Phylogenetic signal measured using Blomberg's *K*. \*\*\**p*<0.001; \*\**p*<0.05; \**p*<0.1.

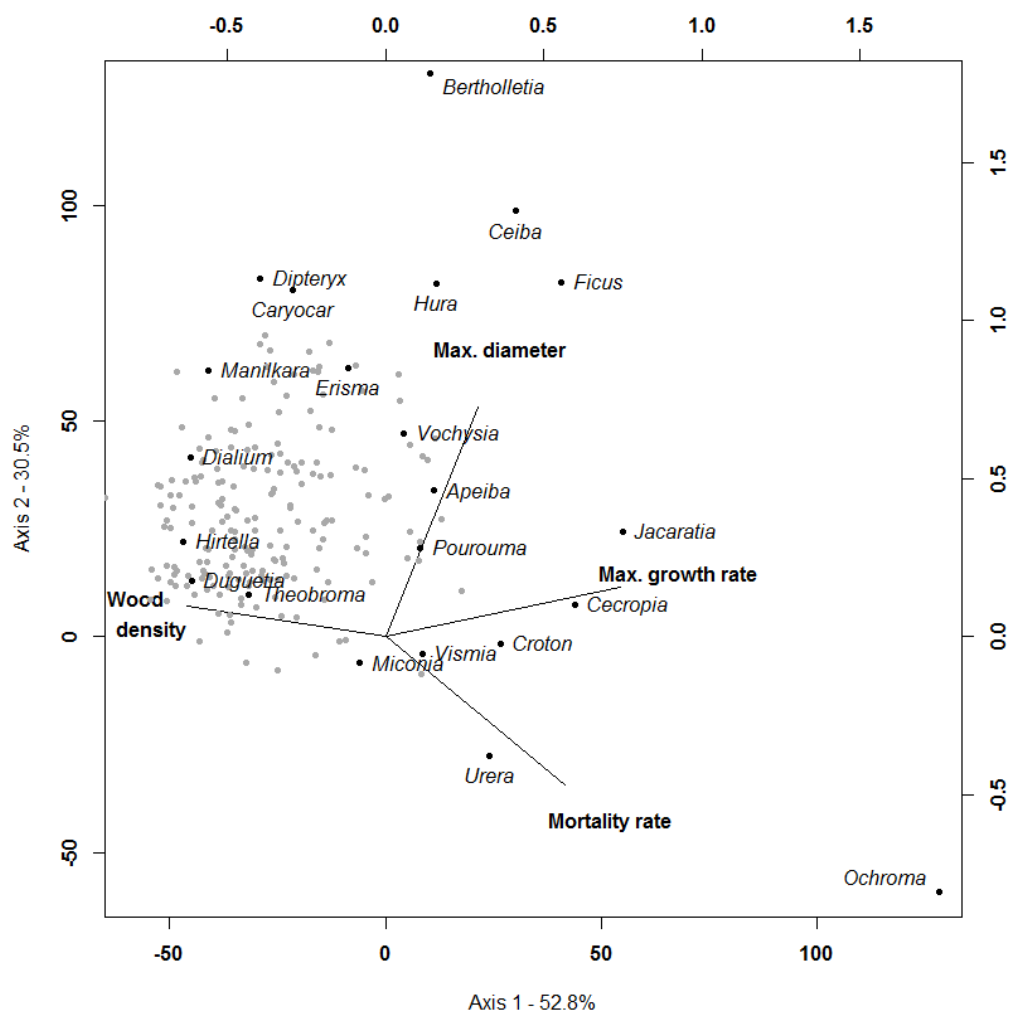
		Units	N° ind	N° Genera	N° Species	Range	Mean	Phylogenetic Signal ( <i>K</i> )			
								Intragenetic variation		Environmental variation	
Traits							no	yes	no	yes	
Wood density	wd	g.cm <sup>3</sup>	-	497	1324	0.15-1.21	0.61	0.26***	0.30***	-	-
	Maximum diameter	cm	244362	383	1412	14.5-171.1	45.94	0.23***	0.31***	0.20***	0.29***
	Maximum diameter * wd	-	244362	383	1412	4.94-154.69	28.08	0.27***	0.34***	0.25***	0.32***
Potential size	Maximum basal area	m <sup>2</sup>	244362	383	1412	0.02-2.3	0.21	0.23***	0.31***	0.21**	0.26***
	Maximum basal area * wd	-	244362	383	1412	0.01-0.13	0.13	0.26***	0.32***	0.23***	0.29***
	Maximum biomass	kg	244362	383	1412	54.63-44443.1	2760.6	0.25***	0.28***	0.22***	0.28***
Growth rates	Maximum growth in diameter	cm	134303	329	1024	0.19-4.38	0.93	0.19***	0.25***	0.18***	0.25***
	Maximum growth in basal area	m <sup>2</sup>	134303	329	1024	0.003-0.03	0.005	0.22***	0.32***	0.21***	0.29***
	Maximum growth in biomass	kg	134303	329	1024	0.21-95.23	6.17	0.25***	0.39***	0.23***	0.33***
	Mean growth in diameter	cm	133656	327	1000	0.05-1.74	0.26	0.18***	0.25***	0.19***	0.29***
	Mean growth in basal area	m <sup>2</sup>	133656	327	1000	0-0.01	0	0.20***	0.27***	0.19***	0.29***
Mortality	Mean growth in biomass	kg	133656	327	1000	0.15-21.76	1.67	0.23***	0.30***	0.19***	0.25***
	Mean stem mortality	%	156495	221	306	0.04-10.98	1.08	0.17**	0.25**	-	-
PPCA1	-		-	214	-	-	-	0.18**	-	-	-
PPCA2	-		-	214	-	-	-	0.21***	-	-	-



**Figure 2.2** Phylogeny (based on *rbcL* and *matK* plastid gene) of 497 Amazonian tree and palm genera . Number of genera varied in the different phylogenies according to the selection criterion for each trait (see Material and Methods). Branches are coloured according to (a) wood density ( $wd$   $g \cdot cm^3$ ), (b) potential tree size in diameter (Max D  $cm$ ), (c) maximum tree growth in diameter (Max gr  $cm^{-1}$ ) and (d) mortality rates ( $\% yr^{-1}$ ). Continuous traits were coloured using a continuous colour gradient, with colour codes indicate the wide range of trait values, from blue to red, indicating higher and lower trait values respectively. Phylogenies for each trait with all tips labelled are available in the (Appendix 2.3).

### **2.3.2 Trait relationships**

Trait associations among lineages were analysed with a phylogenetic principal component analysis (PPCA): eighty-three percent of the variation in the four-dimensional space was accounted for by the first two axes (Figure 2.3). The first axis (PPCA1) explained 52.8% of the variation and shows strong positive loadings for mortality and maximum growth rates, whilst wood density was negatively associated with this axis (Appendix 2.4). PPCA1 thus represents a continuum from pioneer and light demanding lineages with low wood density and fast demographic traits (e.g. high mortality and growth rates) to non-pioneer lineages with high wood density and slow demographic rates. The second axis (PPCA2) explained 30.5% of the variation and was associated more closely with potential tree size, and reflects the variation from individuals of understory genera, to individuals of canopy and emergent lineages (Figure 2.3).



**Figure 2.3** Phylogenetic Principal Component Analyses (PPCA) for the first two principal components with PC loadings for the four traits studied here: Wood density, potential tree size in terms of diameter (Max. Diameter), potential growth rates in terms of diameter (Max. growth rate) and annual mortality rates (Mortality rate.). Points represent 221 genera of trees; position of 22 key genera marked in bold and named.

### 2.3.3 Phylogenetic signal

All traits and the first two PPCA axes exhibited significant PS, with closely related genera being more similar than expected by chance, using either Bloomberg's  $K$  (Table 2.1) or Pagel's  $\lambda$  (Appendix 2.2). Because estimates of Pagel's  $\lambda$  and Blomberg's  $K$  are strongly correlated and most studies of



phylogenetic signal in tropical trees have focused on the  $K$  metric rather than  $\lambda$ , results and discussion are focused on the calculations using Blomberg's  $K$ -value.

Traits showed significant and similar values for  $K$ , varying from 0.25 to 0.39 and from 0.18 to 0.27, with and without accounting for intrageneric variation respectively. These  $K$ -values indicate that evolutionarily related genera tend to be more similar to each other, but less than expected under a BM model of evolution (Table 2.1). Finally, removing the environmental contribution to trait variation did not substantially alter the magnitude of PS (Table 2.1).

### **2.3.4 Sensitivity analyses**

Although selecting just the Manaus plot data significantly reduced the number of genera, species, and individual trees included in the analyses, PS at smaller spatial scales showed similar patterns to PS calculated using the whole dataset (Appendix 2.5). Similarly, reducing the number of lineages to genera for which all trait values were available, showed congruent patterns of PS (Appendix 2.5). In addition, all traits showed similar or slightly higher Blomberg's  $K$  values for just *Inga* or *Protieae* than for all taxa together (Appendix 2.5).

## **2.4 Discussion**

This is the first study, to my knowledge, to investigate the extent of phylogenetic signal (PS) for traits that quantify the main axes of life-history variation in survival and growth of trees at such a large phylogenetic and spatial scale. The results presented here demonstrate that for Amazonian forests, closely related genera have similar life-history strategies, with all traits showing similar levels of PS (Table 2.1; Figure 2.2; Appendix 2.5). The similar level of PS found across all the different, correlated traits suggests that the main axes of life-history variation among lineages of Amazonian trees may represent the result of repeated evolution of a suite of coordinated functional characteristics.

### 2.4.1 Relationships amongst Traits

Strong correlations among traits were represented by two major axes of variation, which are likely to be associated with adaptations to horizontal and vertical light gradients. Ecological differences among species adapted to gaps versus the shaded understory or to the understory versus the canopy are well-established as the principal axes of functional variation among tropical forest tree species (Denslow 1987; Kitajima & Poorter 2008). The first axis runs from pioneer and light demanding genera with low wood density and fast demographic traits (e.g. high mortality and high growth rates) to shade tolerant genera with heavy wood and slow demographic traits. The second axis represents variation in tree size and contrasts understorey genera, from lineages of canopy trees. For example, these axes distinguish *Cecropia* and *Croton*, classic pioneers with low wood density and fast demographic traits, from *Hirtella* - a typically dense-wooded and slow-growing understory genus of trees. Lineages of emergent trees which all achieve very large potential tree sizes (e.g. *Bertholletia*, *Ceiba*, *Hura*, *Dipteryx*), are also distinguished in this analysis by their different wood densities and growth rates (Figure 2.3).

### 2.4.2 Phylogenetic Signal

The results in this chapter demonstrate significant levels of PS among demographic and structural traits of tropical trees, with Blomberg's  $K$  ranging from 0.25 to 0.39. This pattern suggests that evolutionary relationships provide useful information about the ecological similarity of these lineages. However, while the analyses of PS presented here shows that evolutionarily related lineages have more similar traits than expected by chance, their values are lower than expected under a pure BM model of evolution (Table 2.1; Figure 2.2) under which  $K$ -values would be close to 1. PS can be lower than expected under BM if there is convergent evolution across distantly related lineages and/or divergent selection among closely related groups (Revell *et al.* 2008; Crisp & Cook 2012). This result therefore suggests that there has been repeated convergent evolution and/or divergent selection, along the two main axes of variation identified by the PPCA

analysis (Figure 2.3). This finding suggests that adaptations to light gaps, or understorey and canopy light environments, have repeatedly evolved within multiple lineages of tropical trees as shown by the different pioneer and shade tolerant genera within a series of unrelated families (e.g. *Cecropia* versus *Brosimum* (Urticaceae/Moraceae), *Vismia* versus *Calophyllum* (Clusiaceae), and *Inga* versus *Dipteryx/Parkia* (Fabaceae; Figure 2.2).

### 2.4.3 Sensitivity analyses

The PS found here for trees across lowland closed-canopy South American forests is generally stronger than previously reported in the literature for tropical forests in smaller-scale analyses (Appendix 2.6). In previous studies, some traits showed low but significant PS (Baraloto *et al.* 2012; Yang *et al.* 2014; Dexter & Chave 2016), while others have even found that traits are randomly dispersed over the phylogeny (Uriarte *et al.* 2010; Fan *et al.* 2012). However, although  $K$ -values are standardized to allow comparison between traits and phylogenetic trees (Blomberg *et al.* 2003; Revell *et al.* 2008), direct comparisons of PS are affected by differences in the spatial and taxonomic scale of the studies, the number of lineages and the use of different kinds of phylogenies.

A first issue for comparing the extent of PS among studies is variation in spatial scales. However, here I show that the higher PS in the present study is unlikely to be an artefact of the large spatial scale used here: restricting the analyses to 26 plots around Manaus shows consistent patterns, with similar levels of PS for all traits compared to analyses for the whole Amazon (Appendix 2.5).

Secondly, different numbers of lineages in different studies may play a role in determining variation in the extent of PS. Although Blomberg's  $K$  is efficient at detecting the strength of similarity among closely related lineages for sample sizes greater than 20 (Blomberg *et al.* 2003), the ability to detect different levels of PS may increase with larger sample sizes (Kamilar & Cooper 2013). In order to address this issue, I conducted a set of analyses restricted to genera for which all trait values were available (214 genera). Since estimates of  $K$  are highly consistent when fewer genera were included (Appendix 2.5), it appears that the number of

lineages is unlikely to have caused the observed trends of high levels of PS for the traits investigated here.

Thirdly, most previous studies (Uriarte *et al.* 2010; Baraloto *et al.* 2012; Fan *et al.* 2012; Swenson *et al.* 2012; Yang *et al.* 2014) were conducted at the species-level, and taxonomic scale can also affect the degree of PS. Phylogenetic signal in any trait may vary at different taxonomic scales; a single trait can have high similarity at one level (e.g. genus level) but this pattern can break down at higher or lower taxonomic levels (Kamilar & Cooper 2013). Here, the phylogenetic signal of these traits at the species level within the *Protieae* and *Inga* were similar or slightly greater than for the genus-level results (Appendix 2.5), suggesting that the results reported here are consistent at finer taxonomic levels. However, since the analyses conducted here at low taxonomic levels were limited to two lineages it remains to be fully tested whether the result indeed holds within all clades of Neotropical trees.

Finally, the use of different kinds of phylogenies is likely to affect the extent of similarity among related species that is reported in different studies (Appendix 2.6). Much previous work was carried out using community-level phylogenies, restricted to locally co-occurring species (Baraloto *et al.* 2012; Swenson *et al.* 2012) and in many cases using unresolved phylogenies with relationships represented as polytomies (Fan *et al.* 2012). Such community level phylogenies may lack sister lineages for many clades that may be critical to effectively measure PS. In addition, the use of trees with many polytomies, e.g. those which add genera and species as polytomies onto backbone family-level trees (Webb & Donoghue 2005), leads to uncertainty in phylogenetic signal estimates (Davies *et al.* 2012). More importantly, phylogenetic sampling may play a major role in determining the extent of PS. Although the genus level phylogeny used here is far from complete, the analyses conducted here, do encompass a far wider range of lineages than previous studies, including the major angiosperm lineages present in the Amazon basin.

Our results demonstrate that there is significant PS for key demographic and structural traits in tropical forests. This finding opens the way for clearer

predictions of how evolutionary diversity relates to ecosystem structure and function, and how different drivers will, in turn, affect the evolutionary diversity of Amazonian forests. For example, this study suggests that community-level measures of evolutionary relatedness among species are likely to be good predictors of the structure and functioning of these ecosystems (Cadotte *et al.* 2008; Cadotte 2013). These results also indicate that changes in environmental conditions or disturbance regimes that favour particular life-history strategies will ultimately erode evolutionary diversity (Santos *et al.* 2014; Ribeiro *et al.* 2016), although the presence of some convergent evolution across lineages may prevent significant loss of phylogenetic diversity over some scales of anthropogenic disturbance (Arroyo-Rodriguez *et al.* 2012). Results reported here may therefore help to resolve why different studies of the effect of disturbance on phylogenetic diversity have obtained contrasting results (Arroyo-Rodriguez *et al.* 2012; Ribeiro *et al.* 2016): in particular, this study suggests that investigating the PS of traits that influence species ability to persist after disturbance within the species pool of interest will be critical to understand how disturbance will alter phylogenetic diversity. Finally, these results also suggest that any long-term changes in the evolutionary diversity of intact Amazonian forests may help to uncover functional shifts in these diverse ecosystems. Overall, the phylogenetic structure of life-history strategies within Amazon tree communities described in this study helps to provide a predictive framework to understand how such complex systems will respond to global change and anthropogenic disturbance.



## **Chapter 3 : Impacts of tree diversity on tropical forest function**

### **Abstract**

Higher levels of taxonomic and evolutionary diversity are expected to boost ecosystem function, from both theoretical and experimental studies. However, the relative importance of these different aspects of diversity for driving variation in ecosystem function at large scales in diverse forest ecosystems has not been explored. Here, using 90 inventory plots across lowland, *terra firme*, Amazonian forests, and a new molecular phylogeny including 615 angiosperm genera, I investigated the association between taxonomic and evolutionary metrics of diversity, and two key measures of ecosystem function, wood productivity, and aboveground biomass, for the world's largest and most diverse tropical forest. I show that both taxonomic and evolutionary diversity are significant independent predictors of wood productivity: Amazon forests that contain more evolutionarily distinct lineages and a higher proportion of rare species have higher productivity. In contrast, diversity was not an important predictor of variation in biomass probably because variation in tree mortality rates, rather than wood productivity, largely determines biomass stocks. These results demonstrate how the evolutionary relationships of tree species in diverse forest stands can determine ecosystem function. As the models accounted for wood density and tree size, results found here indicate that additional evolutionarily correlated traits, which remain to be identified, have significant effects on biodiversity-ecosystem function relationships in tropical forests.

### 3.1 Introduction

Different dimensions of biodiversity can play important and independent roles in determining ecosystem function (Maherali & Klironomos 2007; Cadotte *et al.* 2009; Cadotte 2013). In experimental studies of temperate grasslands, higher levels of taxonomic and evolutionary diversity are associated with increased ecosystem function (Cadotte *et al.* 2008; Cadotte *et al.* 2009; Cadotte 2013). In particular, because evolutionary dissimilarity is hypothesised to relate to niche complementarity, the amount of evolutionary diversity, measured by the evolutionary history represented within a group of species, is a better predictor of productivity than the number of species (Cadotte *et al.* 2008; Cadotte *et al.* 2009; Cadotte *et al.* 2013). However, the extent to which evolutionarily diverse communities maximize function at large scales in complex tropical forest ecosystems remains to be explored. Equally, the importance of evolutionary diversity compared to traditional taxonomic measures remains unknown for the world's most diverse ecosystems.

The amount of evolutionary history represented by species within a community and how that evolutionary history is distributed among individuals and species may be useful predictors of how diversity affects ecosystem function because it tends to reflect phenotypes of multiple ecological traits (Webb 2000; Webb *et al.* 2002; Srivastava *et al.* 2012; Coelho de Souza *et al.* 2016), including those that are extremely difficult to measure. For instance, in an experimental study of grassland communities, evolutionary diversity was a better predictor of productivity than some easily measured functional traits (e.g. specific leaf area, seed weight and height), suggesting an additional contribution of unmeasured traits that are significantly related to phylogeny, such as root architecture or root morphology, on shaping complementary functions and maximizing productivity (Cadotte *et al.* 2009). As a result, evolutionary diversity metrics may be a particularly useful way to understand how diversity influences ecosystem function in hyperdiverse communities, especially where identifying and measuring the key traits for all species is difficult. However, although a wealth of functional traits



that might shape ecosystem function have been recently collected in such diverse forests, only easy to measure ‘soft traits’ such as specific leaf area and wood density (Chave *et al.* 2006; Baraloto *et al.* 2010b) have generally been included, and the link between these traits and ecosystem functions such as productivity is relatively weak (Fauset *et al.* 2015). Evolutionary diversity metrics might encompass the breadth of functional diversity that has not been measured across this hyperdiverse region and therefore may be more informative about how much species contribute to ecosystem function.

The evolutionary diversity of a community can be measured in different ways to reflect distinct aspects of biodiversity (Faith 1992; Webb *et al.* 2002; Tucker *et al.* 2016), and these metrics may all relate in different ways to variation in functional traits, life-history strategies, and as a result ecosystem function (Cadotte *et al.* 2009; Srivastava *et al.* 2012; Cadotte *et al.* 2013; Cadotte 2013). Phylogenetic diversity (PD) is a measure of the total evolutionary history, or amount of the tree of life present in a given community and is quantified as the sum of the branch lengths, which are measured in units of time of a phylogeny representing all species in a given community (total lineage diversity) (Faith 1992). A second aspect of evolutionary diversity is to what extent communities are dominated by closely related species (neighbour lineage diversity), which can be quantified by mean nearest taxon distance (MNTD) (Webb 2000; Webb *et al.* 2002). Finally, an additional dimension of the evolutionary history of a community is whether communities contain a balanced proportion of the major lineages of organisms (basal lineage diversity) (Swenson 2009; Honorio Coronado *et al.* 2015), which can be represented by the mean phylogenetic distance (MPD) between all pairs of species (Webb *et al.* 2002). MPD is strongly affected by branch lengths at the deepest nodes of the phylogeny and the relative abundance of major clades in the community (Honorio Coronado *et al.* 2015). Both of these metrics attain higher values in communities comprised of more distantly related individuals.

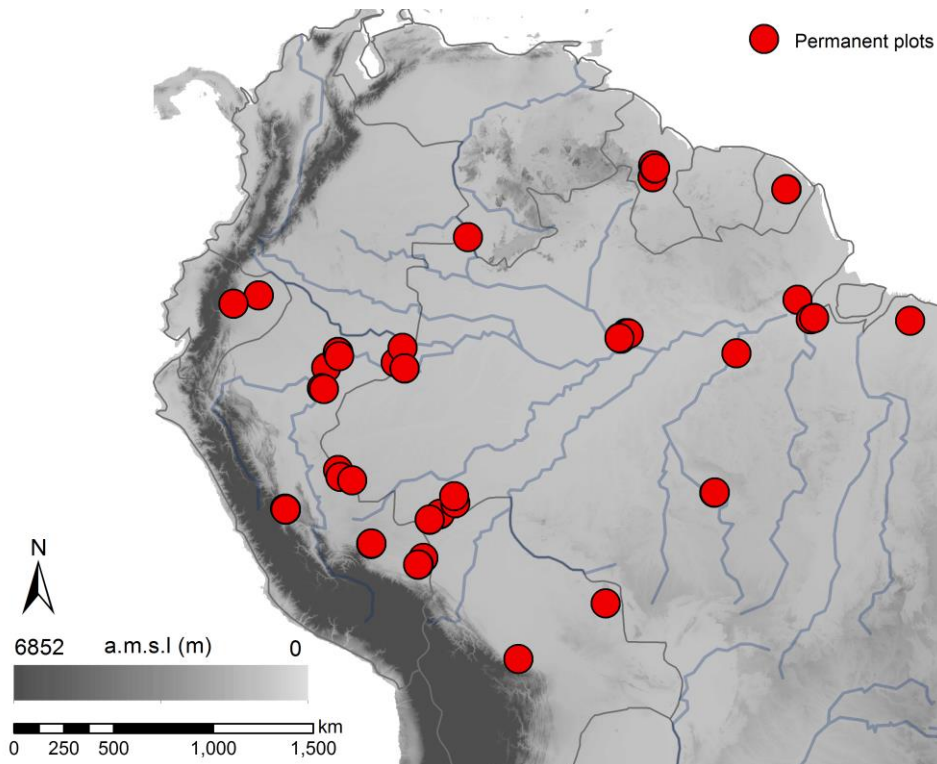
Amazonian forests provide an ideal context for exploring this link between tree diversity and ecosystem functioning. These forests include some of the most species-rich ecosystems on earth (ter Steege *et al.* 2013) and contain a wide variety of angiosperm lineages (Honorio Coronado *et al.* 2015). They also play a

key role in regulating planetary biogeochemical cycles, including by annually fixing as much carbon as the combined global human economy emits (Beer *et al.* 2010), and storing an order of magnitude more (Malhi *et al.* 2004). Here I use a unique, newly constructed pan-Amazon phylogeny and 90 long-term monitoring plots across Amazonia to investigate the relationships between tree diversity and ecosystem function. I investigate the role of taxonomic and evolutionary diversity in promoting aboveground wood productivity (hereafter productivity) and aboveground biomass (hereafter biomass). Because taxonomic and phylogenetic diversity metrics represent different dimensions of biodiversity (Forest *et al.* 2007; Tucker *et al.* 2016), I expect that they will have independent effects on ecosystem function. Evolutionary relatedness amongst tropical tree species tends to reflect their ability to process and store carbon (Coelho de Souza *et al.* 2016), and I therefore hypothesize that evolutionary diversity would have greater predictive power than taxonomic measures of diversity (Cadotte 2013). I expect that communities with greater evolutionary diversity and that encompass disparate evolutionary histories and functional characteristics may be more likely to maximize productivity and carbon storage due to complementarity in resource use. Because environmental factors (Quesada *et al.* 2012; Sullivan *et al.* 2017) and stand structure variables (Fauset *et al.* 2015) are also associated with both productivity and biomass, in all analyses variation in these factors were accounted for using available climate data (Hijmans *et al.* 2005), locally collected soil data (Quesada *et al.* 2010) and stand structural characteristics (Chave *et al.* 2009). Because confounding environmental and structural variables might obscure any underlying effect of diversity on ecosystem function, I compare the effects of taxonomic and evolutionary diversity metrics in relation to null models, defined as the best-performing model of productivity or biomass based on environmental, stand structural variables and residual spatial autocorrelation (see Methods for details).

## 3.2 Methods

### 3.2.1 Tree community data

To investigate the relationship between biodiversity and ecosystem functioning, I estimated diversity, wood productivity and aboveground biomass using data from 90 long-term forest inventory plots in the Amazon and adjacent lowland forests from the RAINFOR (Amazon Forest Inventory) network (Appendix 1; Figure 3.1). Data were extracted from the ForestPlots.net database, which curates tree-by-tree records from RAINFOR and other networks (Lopez-Gonzalez *et al.* 2009; Lopez-Gonzalez *et al.* 2011). Plots were all 1 ha in size (except for two plots of 0.96 ha) and located in structurally intact and old-growth closed-canopy forest. Analyses were restricted to continuous lowland, *terra firme*, Amazonian forests, a coherent biome - excluding montane, swamp, seasonally dry tropical forest, white sand and savanna plots. Restricting the analyses to this single biome, allowed us to limit the effect of ecological factors operating over evolutionary timescales (Dexter *et al.* 2017) (i.e. clades more restricted to areas outside this continuous area may have very different unmeasured traits, such as root-shoot ratio and canopy structure) - which could have an effect on how different metrics of evolutionary diversity relate to ecosystem function. Plots were established between 1975 and 2010 and were all monitored for at least two years, with regular censuses and a mean total monitoring period of 16.1 years. All trees and palms with diameter at breast height (dbh) greater than 10 cm were included in the analyses. In the dataset, all recorded species and genus names were checked and standardized using the Taxonomic Name Resolution Service (Boyle *et al.* 2013). Across all plots 94.9% of stems were identified to the genus level, with a minimum of 70% identified to genus per plot. All individuals not identified to genus-level (5.1%) were excluded from biodiversity metric calculations.



**Figure 3.1** Geographical distribution of 90, one-hectare permanent inventory plots analysed in this study. Plots are all located in lowland moist forests on well-drained soils across the Amazon Basin (please see methods for details).

### 3.2.2 Phylogenetic tree

I constructed the largest pan-Amazon phylogeny to date, including 1122 genera based on two portions of DNA chloroplast gene regions, *rbcL* and *matK*, following protocols developed by (Dexter & Chave 2016). These genes were chosen based on their universality, typical sequence quality, level of species discrimination, sequencing costs and their recommendation as standard DNA barcodes in plants (Kress *et al.* 2010; Kress & Erickson 2012). In total, 214 *rbcL* and 270 *matK* sequences were generated; all other sequences were obtained from Genbank. For 837 genera (74.4%) both *rbcL* and *matK* sequences were available and for 132 (11.7%) and 156 (13.9%) just *rbcL* and *matK* respectively. Sequences that were unavailable for one region were left as missing data. Preliminary phylogenetic analyses and basic local alignment enabled to exclude sequences that were likely to represent taxonomic misidentifications. The details of DNA

extraction, PCR, and DNA sequencing protocols can be found in .Gonzalez *et al.* (2009). A list of sampled genera, their respective family, and Genbank accession numbers are available in Appendix 3.1.

Multiple sequence alignments, separately for each region, were conducted using MAFFT v.6.822 (Kato *et al.* 2002) followed by manual adjustments in Mesquite (Maddison & Maddison 2015). Prior to manual alignments, I removed all sites in which more than 99% genera appear as missing data, reducing alignment issues. Then, all *rbcL* and *matK* sequences were combined to generate a maximum likelihood tree using RAxML v.7.2.7 on the CIPRES Science Gateway (Miller *et al.* 2010). A topological constraint specifying the major relationships among angiosperm orders was imposed based on the Angiosperm Phylogeny (Stevens 2001). A basal angiosperm *Nymphaea alba* (Nymphaeaceae) was specified as an outgroup and the initial tree was made ultrametric implementing the nonparametric rate smoothing method of Sanderson (2002), implemented in the ape (Paradis *et al.* 2004) package in the R Statistical Software (Team 2014). This phylogeny was then used as a starting tree in subsequent analyses to simultaneously estimate tree topology and divergence times of taxa, a Bayesian Markov Chain Monte Carlo (MCMC) approach was conducted using BEAST v.1.8.2 on the CIPRES server. An uncorrelated lognormal (UCLN) relaxed molecular clock was implemented, and the tree prior was under a Birth-Death Incomplete Sampling model of speciation (Stadler 2009). To calibrate the phylogenetic tree, 86 previously compiled fossil-based age constraints were implemented on nodes (Baker *et al.* 2014; Magallon *et al.* 2015) (see Appendix 3.2 for a list of priors and their respective nodes). Nodes were constrained using a log-normal distribution with a mean value equal to the fossil age, a standard deviation of 2 and a hard constraint for a minimum age equal to 80% of the estimated fossil age. No constraints were placed on the root age of the tree. Using the maximum likelihood tree, preliminary runs of  $10^6$  generations were conducted to optimize operator settings before conducting the final runs.

We conducted three independent MCMC runs under the same estimation conditions for  $70.2 \times 10^5$ ,  $58.6 \times 10^5$  and  $80.3 \times 10^5$  generations. In order to ensure stability, a burn-in of  $10 \times 10^5$  and  $20 \times 10^5$  generations for the first two and third

runs respectively were excluded. After excluding the burn-in and combining the three independent runs using LogCombiner, 282 trees spaced evenly through the posterior were sampled to be used to generate a consensus tree using the all-compatible consensus option in the phyutility software (Smith & Dunn 2008). Branch-lengths and divergence times (node heights) were optimised on this tree as the mean values across the posterior distribution of trees in Treeannotator.

The analyses in this chapter included 615 genera where phylogenetic data were available: 90.5% of the total number of genera and 97.95% of all stems identified.

### **3.2.3 Biodiversity metrics**

To represent the different aspects of biodiversity, I calculated ten genus-level diversity metrics, including taxonomic diversity indices and metrics that incorporate the evolutionary history within communities (Appendix 3.3). Because different metrics can reflect similar dimensions of diversity (Appendix 3.4), in the main text, results from five diversity metrics are shown: (1) taxonomic richness, a common and widely used diversity metric, here evaluated as the sum of all identified genera in a given community; (2) Simpson index of diversity, a common diversity metric that incorporate genus abundance, representing the probability that two stems randomly selected from a community belong to different genus; (3) total lineage diversity, the standardized effect size of phylogenetic diversity (sesPD), estimated as the sum of all branch lengths including genera within a community (Faith 1992), while controlling for the effect of genus richness; (4) neighbour lineage diversity, which is quantified by the standardized effect size of mean nearest taxon distance (sesMNTD), also controlling for the effect of genus richness, which is more sensitive to relatedness near to the tips of the phylogeny (Webb 2000; Webb *et al.* 2002) and (5) basal lineage diversity, which is quantified by mean pairwise distance (MPD) and reflects phylogenetic structure at the deepest nodes (Webb 2000; Webb *et al.* 2002) (see Appendix 3.7 for results that include all metrics).

Because the null expectation for the PD and the MNTD of communities necessarily shows strong relationships with the total taxonomic richness of

communities, their standardized values were quantified: the degree to which communities show greater (+) or less (-) PD or MNTD than expected given their genus richness. I calculated the standardised effect sizes, *sesPD* and *sesMNTD*, by first generating a null expectation via randomly shuffling genera tip labels in the phylogeny 999 times. The effect size was then calculated as the difference between the observed and expected values, the latter being the mean across randomizations, and dividing this difference by the standard deviation of values across the randomisations. These standardized metrics essentially represent the residuals from the relationship between each evolutionary diversity metric and genus richness within each plot and allowed to identify areas with high or low evolutionary diversity whilst accounting for the effect of richness. The standardised effect size for MPD was also calculated, but as MPD does not vary systematically with taxonomic richness, its raw value and standardised effect size are strongly correlated. For simplicity, I focus on the results for MPD.

### **3.2.4 Wood productivity and aboveground biomass**

Aboveground wood productivity was estimated as the rate of gain in stem biomass during each census interval. Because longer census intervals increase the proportion of productivity that cannot be directly detected due to trees growing and dying during the census interval (Lewis *et al.* 2004), productivity was corrected for varying census interval lengths. Following the methodology developed by Talbot *et al.* (2014) estimates of annualized productivity per plot were computed as: i) the sum of tree growth alive in the first and in the last censuses, ii) growth of trees that recruited during the census interval, iii) estimates of unobserved growth of trees that died during the census interval and iv) estimates of unobserved trees that both recruited and died between census periods. As plots vary in total monitoring period and census-interval length is expected to affect the estimates of productivity: plots monitored over short total census lengths are more likely to be affected by stochastic changes over time and measurement errors (Lewis *et al.* 2009). Productivity estimates were therefore, weighted by the cubic root of census-interval length (Appendix 3.5).

Aboveground biomass per stem was estimated using a pan-tropical, three parameter equation  $AGB = 0.0673 * (wd D^2 H)^{0.976}$ , from (Chave *et al.* 2014), where *wd* is the stem wood density (in  $g.cm^3$ ) from the Global Wood Density database (Chave *et al.* 2009; Zanne *et al.* 2009), *D* is the tree diameter (in cm) at 1.3 m or above the buttress and *H* tree height (in m). Tree height was estimated based on regional diameter-height Weibull equations (Feldpausch *et al.* 2011). Similar to productivity, in order to reduce the influence of potential stochastic changes and due to variation in census interval within plots, I estimated biomass per plot using a weighted average across multiple censuses (Appendix 3.5).

### 3.2.5 Environmental variables

Because variation in both productivity and biomass in the Amazonian forests is mediated by soil and climate, environmental variables were included as covariates in the models used here. For climate data, to avoid collinearity among explanatory variables, I selected just mean annual temperature (MAT °C), extracted from the WorldClim dataset at 30' ( $\approx 1km$ ) resolution (Hijmans *et al.* 2005) and cumulative water deficit (CWD), a measure of water stress, extracted from a global gridded layer (Chave *et al.* 2014). For soil data, I used values for 0-30 cm depth collated at ForestPlots.net and based on intensive soil sampling from each RAINFOR plot that used standardised field and analytical protocols (Quesada *et al.* 2010; Quesada *et al.* 2011; Quesada *et al.* 2012). Protocols for collecting and analysing soil data have been previously described (Quesada *et al.* 2010; Quesada *et al.* 2011).

Because silt, clay, and sand content are strongly correlated, soil texture was expressed as the first two axes of a principal component analysis (PCA). The first axis was strongly positively related with sand and negatively with silt content, whilst the second axis negatively with clay (Appendix 3.6). Soil fertility was represented by total phosphorus (P  $mg\ kg^{-1}$ ) and the sum of exchangeable bases (TEB  $cmol\ kg^{-1}$ ).



### 3.2.6 Stand structure variables

We also included descriptors of stand structures as covariates in the models, including wood density, potential tree size and number of stems, all of which have been shown to shape productivity and biomass in tropical tree communities (Baker *et al.* 2004b; Fauset *et al.* 2015). Wood density data were extracted from the Global Wood Density database (Chave *et al.* 2009; Zanne *et al.* 2009) selecting data for Mexico, Central America and South America. The data were matched to each stem in the plot data at the species-level, and in cases where this information was unavailable, matched to the average of species values for that genus (Baker *et al.* 2004b). I then calculated the mean wood density value across all stems in a plot. For potential tree size, I used data from chapter 2 spanning 577 single census plots from across Amazonia, to derive the potential size that each genus could achieve and assigned these values to each individual tree based on its identity. I then derived for each plot the mean potential tree size. The number of stems per plot was calculated as the average number of individuals with dbh greater than 10 cm across multiple censuses.

### 3.2.7 Statistical analyses

To investigate the strength of the relationship between each measure of ecosystem functioning (i.e. productivity and biomass) and the set of diversity metrics in each plot, I conducted: (1) bivariate Kendall's  $\tau$  non-parametric correlation tests and (2) generalised least squares modelling (GLS). For bivariate correlations, testing the relationships for the range of biodiversity metrics involved ten tests for each dependent variable P-values were therefore adjusted for multiple comparisons using the false discovery rate (Benjamini & Hochberg 1995) (Appendix 3.7 - Table A.3.7.1).

Environmental variables also influence the diversity of an ecosystem (ter Steege *et al.* 2006; Coronado *et al.* 2009; Honorio Coronado *et al.* 2015) and its ability to process and store carbon (Quesada *et al.* 2012), and may therefore obscure relationships between diversity and ecosystem functioning. To account for the effect of multiple environmental variables I constructed generalised least square

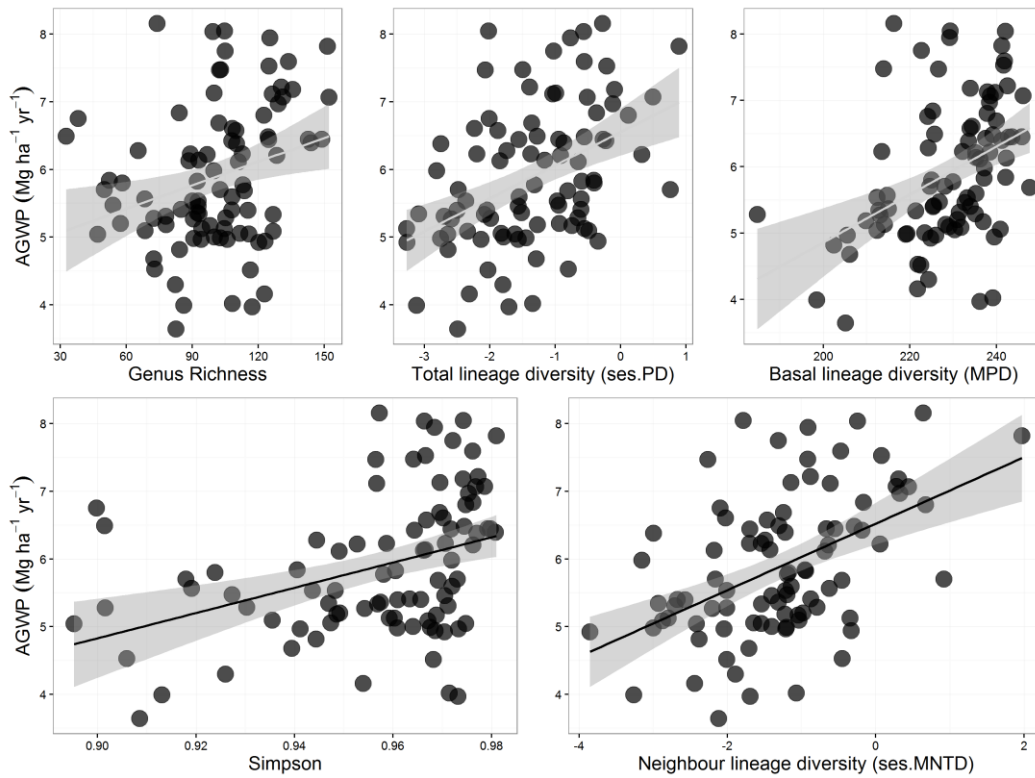
models where ecosystem functioning was modelled as a function of diversity metrics, climatic and edaphic and stand structure variables. To avoid multicollinearity amongst variables in the model, I confirmed that for each explanatory variable variance inflation factors (VIFs) were less than five (Kutner *et al.* 2005). Spatial autocorrelation was accounted for in the GLS analyses by specifying a Gaussian spatial autocorrelation structure, which is consistent with the shape of the semivariograms for these forest properties (Johnson *et al.* 2016). To account for heteroscedasticity and ensure that the residuals were normally distributed, productivity and biomass were log-transformed prior to analyses.

Separate models for each ecosystem functioning property and diversity metric were conducted. For each response variable (productivity and biomass), I generated a global model including all soil, climate and stand structure variables and applying a Gaussian spatial autocorrelation structure. I then generated a set of models including all possible combinations of climate, soil, and stand structure variables. To find the most parsimonious model for each response variable, I selected the best null model using Akaike Information Criterion (AIC). To investigate the relationship between diversity and both productivity and biomass, each single diversity metric was added individually to the best model (i.e. the model including selected climate, soil and stand structure variables for productivity or biomass), hereafter referred to as the null model. The null model was then compared with models including each single diversity metric: models with a difference in AIC greater than 2 when compared to the null model, indicate models with improved support. I further combined two significant diversity metrics (i.e. representing different facets of diversity Appendix 3.4) into a single model to investigate whether a more complex model provides better predictively ability over single diversity metric models. To allow comparisons of the strength of significance of the explanatory variables, they were all normalised to have a mean of zero and a standard deviation of one.

Analyses were performed in the R Statistical software v3.1.1 (Team 2014) using the *vegan* (Oksanen *et al.* 2013), *picante* (Kembel *et al.* 2010), *BiomasaFP* (Lopez Gonzalez *et al.* 2015), *nlme* (Pinheiro *et al.* 2014) and *MuMIn* (Barton 2015) packages.

### 3.3 Results

Both taxonomic and evolutionary measures of diversity showed strong positive, bivariate relationships with productivity (Figure 3.2; Appendix 3.7). Three of these bivariate relationships were significant after accounting for the influence of environmental factors and structural characteristics on productivity; standardised neighbour lineage diversity (sesMNTD;  $R^2 = 0.40$ ;  $\Delta AIC = -2.65$ ; Table 3.1), Simpson's index ( $R^2 = 0.36$ ,  $\Delta AIC = -5.09$ ) and basal lineage diversity (MPD;  $R^2 = 0.34$ ,  $\Delta AIC = -2.88$ ) all improved the fit compared to the null model. In contrast, the number of genera in each community - genus richness - had no effect on productivity after accounting for environmental and structural factors (Table 3.1, full coefficients from the models are shown in Appendix 3.8). The best statistical model of productivity contained a combination of evolutionary and taxonomic measures of diversity. Amongst models containing two significant biodiversity metrics, a model including both sesMNTD and Simpson index provided the greatest predictive power ( $R^2 = 0.41$ ;  $\Delta AIC = -7.13$ ; Figure 3.3), showing that these metrics reflect distinct aspects of diversity that are both important for understanding patterns of productivity (Appendix 3.4).

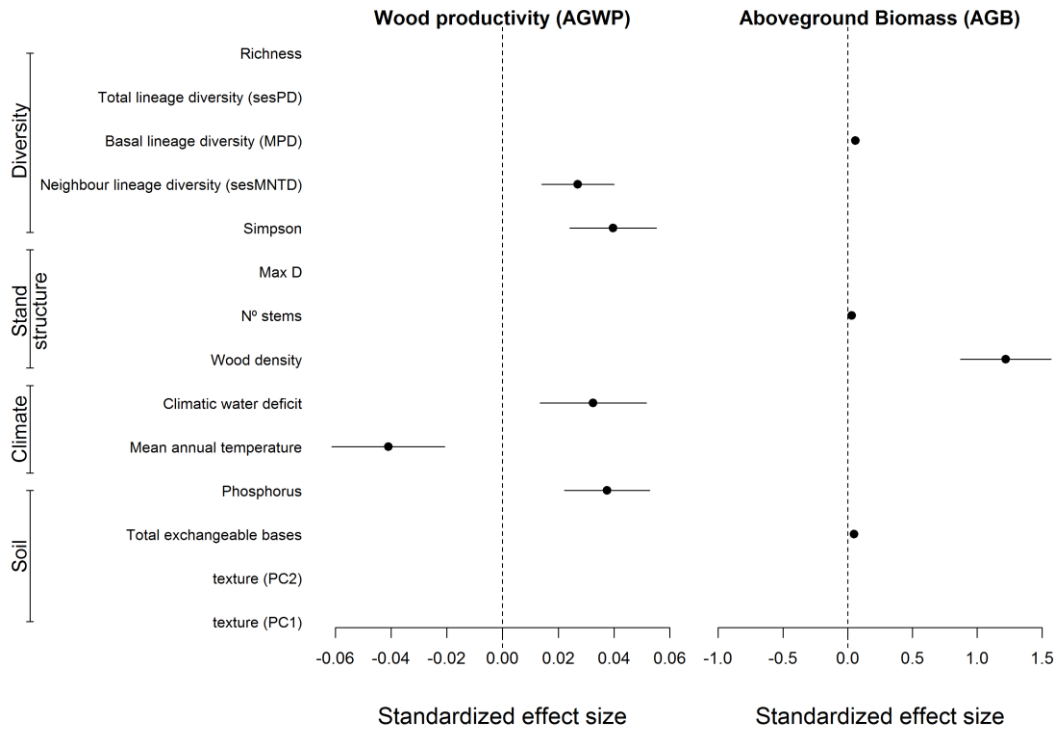


**Figure 3.2** Relationships between aboveground wood productivity (AGWP) and different tree diversity metrics from 90 single hectare plots across Amazonia. Continuous black lines indicate significant relationships after accounting for environmental factors, forest structure, and spatial autocorrelation (Gaussian correlation structure). Dashed grey lines indicate significant bivariate correlations between productivity and diversity metrics (please see Appendix 3.7-table A.3.7.1 for coefficients and significance).

**Table 3.1** Results for generalised least square (GLS) models across 90, one ha plots for aboveground wood productivity (ln AGWP) and aboveground biomass (ln AGB) as a function of diversity metrics, structural attributes, climate, soil variables, and accounting for spatial autocorrelation (Gaussian correlation structure). Best model for both AGWP and AGB are highlighted in bold - full coefficients from the models shown in Appendix 4. Results are shown for the best-fit model, with lowest AIC values, incorporating environmental variables (climate and soil), functional attributes (mean wood density, potential tree size and number of stems), and spatial autocorrelation. \*Indicate significant biodiversity metrics (p-values  $\leq 0.05$ ) in the GLS analyses.

Model	AGWP			AGB		
	R <sup>2</sup>	AIC	$\Delta$ AIC	R <sup>2</sup>	AIC	$\Delta$ AIC
sesMNTD + simpson	<b>0.41*</b>	<b>-116.16</b>	<b>-7.13</b>	-	-	-
sesMNTD	0.40*	-111.68	-2.65	0.67	-65.11	1.83
sesPD	0.38	-105.38	3.65	0.68	-65.12	1.82
simpson	0.36*	-114.12	-5.09	0.67	-65.28	1.66
mpd	0.34*	-111.91	-2.88	<b>0.69*</b>	<b>-69.41</b>	<b>-2.47</b>
richness	0.34	-104.64	4.39	0.68	-66.86	0.08
null	0.34	-109.03	0.00	0.67	-66.94	0.00

Climatological and soil variables were also associated with variation in productivity (Figure 3.3; Figure A.3.7.3). Mean annual temperature, cumulative water deficit and soil total phosphorus were all importantly associated with productivity (Figure 3.3): with higher rates of wood growth more common in areas in the western Amazon with low water deficit and greater nutrient availability. The standardized effect size of biodiversity variables in the best model was similar to the effect sizes of climate and soil variables (Figure 3.3), suggesting a similar importance for biodiversity and environmental factors for determining Amazonian forest productivity.



**Figure 3.3** Regression estimates for the best-fit generalised least square model across plots for both aboveground wood productivity (ln AGWP) and aboveground biomass (ln AGB) as a function of diversity metrics, structural attributes, climate and soil variables selected based on the lowest AIC values and largest proportion of the variance explained ( $R^2$ ). The best model for AGWP includes neighbour lineage diversity ( $p=0.05$ ) and Simpson index ( $p=0.01$ ) as biodiversity metrics, mean annual temperature ( $p=0.05$ ), cumulative water deficit ( $p=0.09$ ), and total phosphorus ( $p=0.02$ ). The best model for AGB includes basal lineage diversity ( $p=0.04$ ), wood density (quadratic  $p<0.001$ ; linear=0.01), total exchangeable bases ( $p=0.04$ ), and number of stems ( $p=0.11$ ). The relationship between AGB and WD is non-linear and in all AGB analyses, WD was specified as linear and quadratic terms, but for clarity, in the graph, effect size is shown only for the quadratic term. For each variable in the model, dots represent the standardized effect size and lines one standard error. In some cases, error lines are unobserved due to very small standard errors. See Appendix 3.7 for detailed bivariate correlations and Appendix 3.8 for all the coefficients of the models.

Bivariate correlations indicated significant negative associations between biomass and nearly all diversity metrics (Figure A.3.7.4; Table A.3.7.1). However, when environmental and structural characteristics were accounted for, biodiversity and biomass were almost completely unrelated, in contrast to the significant biodiversity-productivity relationships (Figure A.3.7.5). Basal lineage diversity

(MPD) did have a significant positive relationship with biomass after accounting for other factors, but it was weak (Figure 3.3) and there was no evident correlation between the residuals from the null model and MPD (Figure A.3.7.5) indicating that it is of limited importance. Instead, biomass was largely determined by wood density and to a lesser extent by stem abundance and the concentration of total exchangeable bases (Figure 3.3; Figure 3.7.6). Biomass was strongly positively related with wood density and marginally with the number of stems per plot. Among the climatological and soil variables, total exchangeable bases was the only variable associated with biomass.

### **3.4 Discussion**

This study demonstrates that there is a significant effect of both taxonomic and evolutionary measures of diversity on wood productivity in tree communities across lowland, *terra firme*, Amazonian forests, after accounting for the influence of environmental factors, stand structural variables, and spatial autocorrelation (Figure 3.2; Figure 3.3; Table 3.1). The strength of these effects was similar to previous studies at small experimental scales in grassland ecosystems (Cadotte *et al.* 2008; Cadotte *et al.* 2009; Cadotte 2013). However, in contrast, aboveground biomass and both taxonomic and evolutionary diversity appear to be largely unrelated (Figure 3.3).

A range of mechanisms may underlie the significant relationships of neighbour lineage diversity (sesMNTD) and Simpson index with productivity (Figure 3.3; Table 3.1). In general, the contribution of sesMNTD to explaining variation in productivity, even after accounting for two major stand structural attributes (wood density and tree size), suggests that among lineages, there are additional functional characteristics that are significantly related to phylogeny and that promote productivity within plots. Since the evolutionary relationships among species tend to reflect their similarity in functional traits (Coelho de Souza *et al.* 2016; Dexter & Chave 2016) and because evolutionary diversity explicitly incorporates species differences, the effect of sesMNTD on productivity is likely to be a result of increased functional complementarity among lineages (Maherali

& Klironomos 2007; Cadotte 2013). If so, communities encompassing more distantly related lineages (greater sesMNTD) will use resources more efficiently and consequently achieve higher productivity (Cadotte *et al.* 2008; Cadotte *et al.* 2009; Srivastava *et al.* 2012; Cadotte *et al.* 2013). Higher Simpson index – a higher proportion of rare genera, and a more even distribution of abundances among different genera - may also increase niche complementarity (Cavanaugh *et al.* 2014; van der Sande *et al.* 2017b).

An increase in functional complementarity and productivity in more diverse communities may be associated with resource partitioning among lineages due to variation in canopy structure. Canopy structure is a key determinant of productivity in temperate forests (Reich 2012) and experiments with young trees (Williams *et al.* 2017) demonstrate that a mixture of species with complementary crown morphologies and branching patterns enables trees to pack their canopy more densely (Pretzsch 2014; Jucker *et al.* 2015; Williams *et al.* 2017). For instance, species with different crown architecture (e.g. height and crown width) distribute their branches and leaves in complementary height layers of the canopy, leading to denser canopies which in turn allow higher light interception and higher productivity (Jucker *et al.* 2015). In Amazonian forests, there is a wide range of canopy architectures among species and complementarity in their crowns may enable trees to utilize canopy space more efficiently. For 2457 trees in Madre de Dios in the Peruvian Amazon (Goodman *et al.* 2013, 2014) crown architecture varied widely among families (Appendix 3.9). Differences in crown architecture among genera from different families may enhance canopy space filling with complementary crown morphologies and branching patterns and promote optimization of resource uptake.

The effect of diversity on productivity may also reflect pathogen dilution in more diverse communities. Host ranges of most tree pests and pathogens show a clear phylogenetic signal, with co-occurring closely related plant lineages being more vulnerable to similar natural enemies than distantly relatives (Parker *et al.* 2015; Gilbert & Parker 2016). A community with greater sesMNTD (i.e. comprising more distantly related lineages) is therefore expected to be less susceptible to disease pressure (Gilbert & Parker 2016), thus needing fewer resources invested



in defence, allowing faster growth rates (Fine *et al.* 2004). Indeed, in tropical regions, where strong conspecific negative density dependence is observed (LaManna *et al.* 2017), individual trees will tend to have lower performance (e.g. growth rates) in less diverse areas when growing near conspecific neighbours. Although at the individual level rare species are more strongly affected by their conspecifics (LaManna *et al.* 2017), at the community level, a single species will have a better performance in more diverse compared to less diverse forests. Thus, it is also likely that communities with a greater proportion of rare species (i.e. higher Simpson's index) are less susceptible to attacks as the probability of an individual tree being vulnerable to a particular species-specific pathogen and herbivore decreases, which may explain the finding that, contrary to my hypothesis, taxonomic and evolutionary diversity contributed similarly to explain variation in productivity.

Diversity had very little effect on aboveground living biomass, similar to a previous pan-tropical study that used an overlapping dataset (Sullivan *et al.* 2017). Not surprisingly, but contrary to the positive effect of diversity on productivity, biomass was strongly determined by functional characteristics (Figure 3.3), with variation in wood density being the most important variable on controlling patterns of biomass in these forests (Cavanaugh *et al.* 2014; Fauset *et al.* 2015; Poorter *et al.* 2015b). To a lesser extent and in agreement with previous findings that have found stem density to partially drive biomass-diversity relationship (Poorter *et al.* 2015b), the number of stems had a marginal and positive effect on biomass (Figure 3.3). These results corroborate a recent meta-analysis in tropical forests, which found that stand structural variables are more important than taxonomic diversity for predicting biomass (van der Sande *et al.* 2017b). Additionally, stem mortality rates exert strong and negative control on biomass, with variation in the numbers and diameters of dead trees playing a major role (Johnson *et al.* 2016). In general, as variation in mortality rates is the most important driver that dominates variation in stand biomass (Johnson *et al.* 2016) and tree death is a highly stochastic process (Chao *et al.* 2008), any positive effect of tree diversity on biomass through increased productivity is likely obscured by variation in stem mortality rates.

Overall, results reported here suggest that multiple facets of diversity affect the present-day functioning of the world's largest tropical forest. In particular, this study provides the first evidence that evolutionary diversity is related to ecosystem functioning at large scales in natural ecosystems. While evolutionary diversity has previously been suggested as a factor to consider in the identification of priority areas for conservation because of its role in enhancing ecosystem function (Srivastava *et al.* 2012; Cadotte 2013), this study provides the first quantitative evidence for this assertion in tropical forests, which in turn is where the planet's terrestrial biodiversity is concentrated. Results found here therefore indicate that there is a synergy between preserving diverse forests that encompass greater evolutionary heritage, and protecting ecosystem function.

## **Chapter 4 : Environmental preferences of tropical trees are strongly shaped by evolution**

### **Abstract**

Understanding the role of evolution for shaping the environmental preferences of different tropical tree lineages is crucial for comprehending the mechanisms underlying species diversity and distributions, and to elucidate how tropical tree species will respond under climatic and anthropogenic change. Across the tropics, variation in temperature, precipitation, and edaphic preferences is related to species turnover across space. However, the evolutionary history of these environmental niches has not been investigated. Here, using a newly developed sequence-based phylogeny and estimates of environmental niches of 510 tropical tree genera from a large network of forest plots in the Neotropics, I investigated how environmental niches correlate with phylogenetic relatedness. I found that evolutionarily closely related genera have more similar temperature, precipitation, and edaphic niches than expected by chance. Overall, across both montane and lowland forests, temperature showed the strongest link to evolution, whereas among lowland forests, edaphic and climatic factors are equally important in constraining occurrence and distribution of tree genera. These results have important implications for understanding the role of historical processes in shaping species diversity patterns and give us a glimpse into how species are likely to adapt to on-going increases in temperature and deforestation. Specifically, shared environmental preferences among closely related species suggest that under predicted climate change, species loss may be biased against certain clades, and have a stronger impact on the tree of life than if there were no phylogenetic signal for environmental niches.

## 4.1 Introduction

The Neotropics is among the most biodiverse regions on earth, harbouring approximately 22 500 tree species (Fine & Ree 2006) with very high turnover across space (Gentry 1982; Tuomisto *et al.* 1995; ter Steege *et al.* 2006). This high diversity and variation in species composition results from the interplay of ecological and evolutionary processes. The role of ecological processes, such as environmental preferences for maintaining species diversity and distributions, is well known. For example, variation in species richness and composition is generally explained by associations with current climate (Gentry 1988a; ter Steege *et al.* 2003; Esquivel-Muelbert *et al.* 2017a), edaphic gradients (Phillips *et al.* 2003; Tuomisto *et al.* 2003; Tuomisto *et al.* 2016), or a combination of both (Clinebell *et al.* 1995; Coronado *et al.* 2009; Moulatlet *et al.* 2017). However, the extent to which historical, evolutionary processes underlie these preferences for species-specific environmental conditions remains poorly explored.

One way to investigate the role of evolution for generating and maintaining species diversity is to examine the evolutionary fingerprint of environmental niche preferences and its similarity among related lineages (Wiens 2004a; Wiens & Donoghue 2004; Losos 2008a; Wiens *et al.* 2010; Cavender-Bares *et al.* 2016). If long-distance dispersal (Dexter *et al.* 2017) or physical barriers (Haffer 1969; Hoorn *et al.* 2010; Antonelli & Sanmartin 2011) have been important for promoting species diversification, I would expect that closely related species will share similar habitat preferences and species associated with environmental extremes would be clustered in the phylogeny (Peterson *et al.* 1999; Wiens 2004a, 2007): they would be represented within few clades that developed physiological tolerances to cope with those extreme conditions.

In contrast, if ecological speciation due to habitat specialization has been more important for the diversification of new species, then I expect a pattern where specific environmental preferences are scattered over the phylogeny and there is high variation within clades (Fine *et al.* 2005; Simon *et al.* 2009; Fine *et al.* 2014; Misiewicz & Fine 2014; Fine & Baraloto 2016). This mechanism might have been

important if contrasting environmental conditions select for different traits and environmentally mediated pressures impose divergent selection among related lineages. Specialization to a variety of different habitats is one way in which this may happen. This pattern of overdispersed niches across the phylogeny would support the gradient hypothesis, which states that under selective disadvantage, species will tend to diverge as a result of parapatric speciation (Endler 1977). Moreover, randomly distributed niches across the phylogeny would also suggest that adaptation to extreme environmental conditions may have evolved repeatedly and independently in many lineages over evolutionary timescales (Fine *et al.* 2005; Simon *et al.* 2009).

The degree to which environmental preferences are associated with phylogenetic relatedness is also important to understand species responses to climate change (Malhi & Wright 2004; Marengo *et al.* 2009) and increasing deforestation (Soares-Filho *et al.* 2006). If environmental niches have evolved little from their ancestral state (i.e. niche conservatism or significant phylogenetic signal), species may struggle to adapt to changing environments and their only possible response may be to change their distributions to track their most suitable environment conditions (Wiens & Donoghue 2004; Wiens *et al.* 2010). However, these shifts in species geographical distributions may not be possible given human impacts on the environment (Feeley *et al.* 2012; Feeley & Rehm 2012) and the difficulty of dispersing across large areas of unsuitable habitat. Local extinction may therefore occur and because vulnerability to climate change may be associated with environmental preferences, species losses may be particularly heavy in certain clades in the tree of life (McKinney 1997; Willis *et al.* 2008). This selectivity would cause disproportionate loss of evolutionary diversity. Conversely, if environmental niches are overdispersed across the phylogeny, this may indicate a more rapid ability of lineages to adapt to climatic change. If so, facing predicted climate change, fewer species would be under risk and species loss would be random, rather than biased against certain clades, which may protect evolutionary diversity from being degraded.

A number of studies have investigated the extent of similarity amongst environmental preferences within tropical trees. However, these studies are either

limited to small spatial scales with incomplete sampling of environmental gradients (Schreeg *et al.* 2010; Zhang *et al.* 2017) or focused on specific clades (Fine *et al.* 2005; Fine *et al.* 2014; Misiewicz & Fine 2014; Fine & Baraloto 2016). For example, for 64 species in a 20-ha plot in a Chinese tropical forest Zhang *et al.* (2017) suggested that environmental niches (in this case a preference for specific topographic positions and soil fertility levels) are highly labile. Nevertheless, estimates of niche preferences across small scales may not reflect patterns across larger scales in tropical forests as they do not encompass complete environmental gradients or have sufficient replication to make accurate inferences. Large spatial scales are important to capture the full distribution of species and the heterogeneity of habitats that they occupy (ter Steege *et al.* 2003; ter Steege *et al.* 2006).

The evolution of preferences for specific environments has also been investigated for certain clades but different studies show contrasting results (Fine *et al.* 2005; Kursar *et al.* 2009; Baldeck *et al.* 2013; Fine *et al.* 2014; Misiewicz & Fine 2014). For example, Fine *et al.* (2005) found that specific soil preferences of 35 species of the Protieae (Burseraceae) were scattered across the Protieae phylogeny, which could suggest that edaphic specialization has been an important driver of ecological speciation in western Amazonia. In addition, within *Cedrela* (Meliaceae) there is high divergence in climatic tolerances between sister-species, providing evidence that recent speciation events may be related with adaptations to different conditions in terms of temperature (Koecke *et al.* 2013). In contrast, Kursar *et al.* (2009) found that co-occurring species of the tree genus *Inga* (Fabaceae: Mimosoideae) in floodplain and terra firme forests in the Peruvian Amazon were more closely related than expected by chance. Analyses at the community level are necessary to understand which pattern is typical across the tropical flora.

Within tropical forests, the three major environmental gradients that are important for determining community assembly and large-scale floristic turnover are precipitation, temperature and soil fertility (Gentry 1988a, b; ter Steege *et al.* 2003; Tuomisto *et al.* 2003; ter Steege *et al.* 2006; Moulatlet *et al.* 2017). The amount of rainfall is an important physiological challenge for species distribution:

water availability imposes strong constraints on species establishment and drier tree communities are generally less diverse than wetter forests (Gentry 1988a; Clinebell *et al.* 1995; ter Steege *et al.* 2003; Esquivel-Muelbert *et al.* 2017a). Variation in temperature is associated with the distribution of many tropical tree species: lowland and montane forests have strong differences in floristic composition (Gentry 1988b; Feeley *et al.* 2011a; Feeley *et al.* 2011b). Niche partitioning along edaphic gradients is also important for structuring tree communities (Fine *et al.* 2005; Coronado *et al.* 2009; Fine *et al.* 2014; Moulatlet *et al.* 2017), both at the community level and for floristic turnover in different plant groups, (e.g. pteridophytes, palms, Zingiberales, and Melastomataceae; Tuomisto *et al.* 2016).

To investigate the legacy of evolution on present day environmental preferences across the Neotropics, I combined a newly developed sequence based phylogeny including 510 angiosperm tree and palm genera with an extensive forest plot dataset. Using local soil (Quesada *et al.* 2010; Quesada *et al.* 2012), precipitation and temperature data (Hijmans *et al.* 2005; Chave *et al.* 2014) to calculate environmental niches, I investigated the fingerprint of evolution on environmental niches by: 1) estimating phylogenetic signal, which represents the extent to which phylogenetic relatedness is associated with environmental preferences (Pagel 1999; Freckleton *et al.* 2002); 2) comparing the fit of different evolutionary models of environmental preferences (Kozak & Wiens 2010b; Wiens *et al.* 2010) and 3) investigating the disparity of environmental preferences through time (Harmon *et al.* 2003).

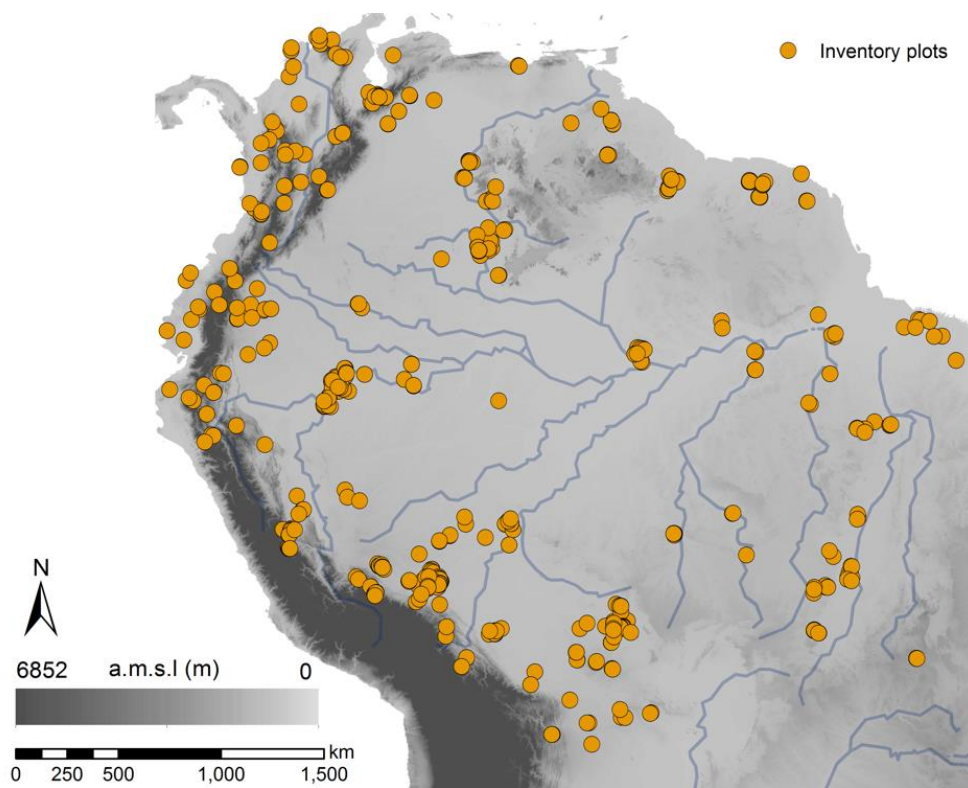
## **4.2 Methods**

### **4.2.1 Tree community data**

This chapter used inventory data from 788 forest plots across the Neotropics, from the RAINFOR forest plot network. All trees and palms with diameter equal or greater 10 cm were included. Data were extracted from ForestPlots.net database which curates tree-by-tree records from RAINFOR and other networks (Lopez-

Gonzalez *et al.* 2009; Lopez-Gonzalez *et al.* 2011). Distinct from the previous chapter that focused in Amazonia and the Guiana Shield, here I also included adjacent biomes in the Neotropics (Figure 4.1). In order to consistently estimate environmental niches, it is necessary to include the full range of environmental conditions associated with species distributions. Thus, because several genera within Amazon also occur in adjacent biomes (i.e. seasonally dry forest, savanna, tropical montane cloud forest) they were also included.

All species and genus names were checked and standardized using the Taxonomic Name Resolution Service (Boyle *et al.* 2013).



**Figure 4.1** Location of 788 inventory plots in the Neotropics over a backcloth of elevation data from the Shuttle Radar Topography Mission (SRTM) (Jarvis *et al.* 2008).

#### 4.2.2 Environmental variables

In order to characterize climatic preferences I used 5 descriptors of temperature and precipitation obtained from the WorldClim dataset (Hijmans *et al.* 2005). The WorldClim database consists of a series of global interpolated climate surfaces with a spatial resolution of 1 km from weather stations, recorded monthly from



1950 to 2000. Additionally, because patterns of species distribution and diversity are strongly associated with climatological water deficit (CWD) (Esquivel-Muelbert *et al.* 2017a) I used CWD as a proxy for water availability (Chave *et al.* 2014). CWD is a metric of seasonal moisture deficit calculated by summing the difference between monthly precipitation and evapotranspiration: more negative CWD values indicate preference for drier environments and CWD of zero represents preference for wetter communities (Chave *et al.* 2014). Thus, the amount of rainfall was represented by both mean annual precipitation and cumulative water deficit. Because floristic variation is associated with minimum, maximum (Feeley & Silman 2010) as well as mean annual temperature (Toledo *et al.* 2011) I used these three variables to describe thermal niches. For edaphic niches I used soil data from 0-30 cm depth for 160 plots for which local soil data is available from ForestPlots.net (Quesada *et al.* 2010; Quesada *et al.* 2012). Soil texture was described by the proportion of clay, sand and silt, whilst soil fertility by concentrations of total phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca) and the sum of total exchangeable bases (i.e. potassium, magnesium, calcium and sodium).

### **4.2.3 Niche preferences**

Here, I use the term ‘*niche preference*’ to describe the environment in terms of climatic and edaphic conditions where the relative abundance of a specific taxa is greatest. This measure therefore reflects the realised niche of these taxa in terms of these environmental conditions (Hutchinson 1957; Rutherford *et al.* 1995; Moscoso *et al.* 2013). I calculated niche preference for each genus as an index that describes the correlation between taxon’s observed distribution and the environmental conditions to which there are associated (Pearman *et al.* 2008; Tingley *et al.* 2014). A similar approach has been previously used to describe the preferred elevation of taxa across an altitudinal gradient in Borneo (Chen *et al.* 2009) and the preferred precipitation levels for genera across Western Amazon (Esquivel-Muelbert *et al.* 2017a; Esquivel-Muelbert *et al.* 2017b). This index has the advantage of including taxon abundance and is based on plot data where all individuals and species within an area are sampled, regardless of commonness or

rarity. For each taxon I calculated the mean niche value where the taxon occurs, weighted by their relative abundance in each community. I first calculated the number of individuals that belonged to a given genera and multiplied by the value of the environmental variable in that specific plot. Then I summed the values for each specific genera and divided by their total abundance:

$$env.niche = \frac{\sum_1^n env \times Ra}{\sum_1^n Ra}$$

Where n = number of plots

env = specific environmental variable (i.e. minimum, mean and maximum temperature, cumulative water deficit, mean annual temperature, proportion of clay, sand and silt, concentrations of total phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca) and the sum of total exchangeable bases

Ra = relative abundance based on the number of individuals. Niches were calculated for all taxa recorded in at least 10 forest plots.

A key requirement of this approach is to include the full range of environmental conditions associated with the distribution of different taxa, and sample these environments in proportion to their coverage (Rutherford *et al.* 1995; Moscoso *et al.* 2013; Soberon & Arroyo-Pena 2017). As a result, in this chapter I included plots from lowland Amazonian rain forest (591 plots; 75% – 422 ha; 79%), tropical montane cloud forest (104 plots; 13.2% – 49 ha; 9.2%) and dry tropical forests and savannas (93 plots; 11.8% – 61.2 ha; 12%). The representation of these plots in the data is similar to the area of these different forest types in the Neotropics. For example, dry tropical forests are estimated to occupy 1,094.831 km<sup>2</sup> (Portillo-Quintero & Sánchez-Azofeifa 2010), ca. 17% of the 6.29 million km<sup>2</sup> estimated size of the Amazon rain forest (ter Steege *et al.* 2013). While, tropical montane forests are estimated to occupy 1,150.588 km<sup>2</sup>, ca 14.8% of all tropical forest in the Americas (Bruijnzeel *et al.* 2011).

#### **4.2.4 Association between niche variables**

To specifically investigate the relationship among different environmental niches (i.e. precipitation, temperature and soil) and show that different environmental

factors affect species distributions independently, I conducted a principal component analyses (PCA) using all environmental preferences for each taxa. Environmental niche values were standardized to a mean of zero and a unit variance to ensure that each variable contributed equally to the PCA.

#### **4.2.5 Phylogenetic data**

I used a sequence based phylogeny including 510 genera based on two chloroplast DNA gene regions: *rbcL* and *matK*. Full details of the temporally calibrated, ultrametric phylogeny construction can be found in Chapter 3.

#### **4.2.6 Niche similarity among related lineages**

To understand the processes that determine large-scale distribution and diversity of clades I quantified niche evolutionary patterns following three different approaches. Firstly, to measure the extent of phylogenetic signal I used Pagel's Lambda (Pagel 1999; Freckleton *et al.* 2002). This choice contrasts with the metric - Blomberg's K - used to estimate the extent of similarity amongst related lineages in Chapter 2 (Blomberg *et al.* 2003). Blomberg's K was used in the previous chapter as it is standardised in relation to the expectation under a null Brownian motion model of evolution, and enabled the comparison of phylogenetic signal estimates amongst the distinct phylogenies used in previously published studies. However, here I chose to use Pagel's lambda due to its better performance on incompletely resolved phylogenies: lambda is strongly robust to both incompletely resolved phylogenies and suboptimal branch-length information (Molina-Venegas & Rodriguez 2017). Lambda is also estimated in a maximum likelihood framework, which allows different models of evolution, with and without phylogenetic signal, to be compared using information criteria.

Lambda quantifies the similarity among sister lineages and normally varies from 0 to 1. Values of 0 show that there is no correlation between taxa relatedness and their niche similarity, and values of 1 indicate that phylogenetic distance amongst taxa is equivalent to their divergence time and perfectly explains niche similarity: the phylogenetic signal expected under a Brownian motion null model of

evolution (Freckleton *et al.* 2002). Significant values between 0 and 1 reflect intermediate levels of phylogenetic signal: close relatives share similarities in their niche preferences but other evolutionary processes, such as selection, may be influencing the observed patterns (Crisp & Cook 2012). To test if phylogenetic signal estimates were greater than that expected by chance, I shuffled niche values randomly among taxa and determined the proportion of 1000 randomizations where lambda was greater than the observed value. Phylogenetic signal was calculated and averaged across 100 trees from the posterior distribution.

In order to detect which clades were driving the strength of phylogenetic signal I compared estimates of the ancestor state at each node with ancestor states reconstructed after tips of the phylogeny were randomised 1000 times *sensu* Dexter and Chave (2016). Ancestor states were estimated through maximum likelihood (Schluter *et al.* 1997). For each node, a reconstructed ancestor state greater than 97.5 % of the randomised values suggest niche values that are greater than expected by chance, whilst values lower than 2.5% were assumed to be significantly lower (Dexter & Chave 2016). Because basal branches contribute disproportionately to the ancestral state reconstruction and uncertainty is larger deeper in the phylogeny, to investigate which clades were driving the extent of phylogenetic signal a clade age threshold of 75 Million years was imposed. Prior to phylogenetic signal analyses I logged niche values to achieve normally distributed values as appropriate.

The second approach to explore niche similarity among related taxa was to compare the fit of four different models of evolution for each niche variable. Model fitting was conducted under White Noise (WN), Brownian motion (BM), Lambda and Ornstein-Uhlenbeck with a single optimum (OU) models of evolution. The White Noise model provides evidence that niches are unrelated to the phylogeny and reflects an absence of phylogenetic signal. In contrast, a better fit of the Brownian motion, Lambda, or Ornstein-Uhlenbeck models indicates that evolution is important for determining niche values and there is a correlation between phylogenetic distance between species and their niche values. The Brownian motion model provides evidence of pure genetic drift whilst a better fit of an Ornstein-Uhlenbeck model suggests stabilizing selection around a single

optimal value. (Kozak & Wiens 2010b; Wiens *et al.* 2010; Pyron *et al.* 2015). Under stabilizing selection, environmental niches remain similar to their ancestors because niche values represent optimal states (Cadotte *et al.* 2017b). The relative fit of the four different models was compared using the Akaike information criterion (AIC).

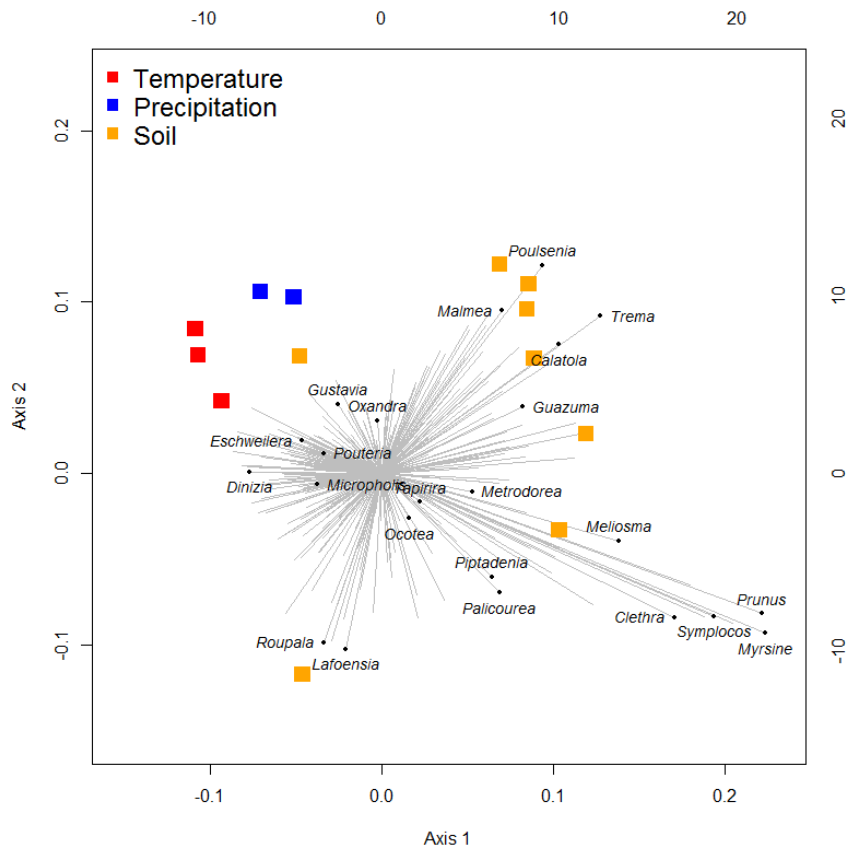
The third approach consisted of investigating the disparity in environmental preferences through time. Analyses of disparity through time avoids estimation of ancestor states and enable to explore how niche variation is partitioned within or among clades (Harmon *et al.* 2003). At every node in the phylogeny disparity is calculated as  $\frac{\sum di}{n-1}$  where  $di$  is the pairwise Euclidian distance and  $n$  is the number of taxa within that clade. At each point in time, the mean relative disparity through time was calculated averaging the value for all existent clades and then normalised by the total disparity of all tips in the phylogeny (Harmon *et al.* 2003; Aristide *et al.* 2015). Values of relative disparity through time  $< 1$  suggest greater variation among rather than within clades, whilst values  $> 1$  greater variation within clades in comparison to all the variation across the phylogeny (Harmon *et al.* 2003; Loza *et al.* 2017). I compared the relative disparity with the expectation under a null Brownian motion model of evolution by simulating evolution of the different niche axes 1000 times across the phylogeny.

Analyses were conducted for two nested datasets: all 788 plots and across 658 solely lowland forest plots (i.e. excluding plots where altitude  $\geq 500$  m a.m.s.l.). All analyses were done at genus-level due to the availability of the phylogeny at this taxonomic scale. Analyses were all conducted in the R Statistical Software (Team 2014) using functions in the phytools (Revell 2012), ape (Paradis *et al.* 2004) and geiger (Harmon *et al.* 2008) packages.

### **4.3 Results**

Precipitation, temperature and edaphic niches represent independent axes of environmental requirements (Figure 4.2 – Appendix 4.1). Principal component analysis (PCA) indicates three main axes of variation associated with

environmental niches. The first axis (PC1) explained 44.6% of the variation and shows strong negative loadings for temperature. PC1 thus represents a continuum from forest communities at high altitudes including genera with low temperature preferences (e.g. *Myrsine*, *Prunus*, *Symplocos*, *Clethra*) to lowland forest communities with higher temperature preferences (e.g. *Eschweilera*, *Dinizia*). In contrast, the second axis (PC2) explains 21.1% of the variation and shows strong positive loadings for soil fertility and negative for soil sand content, reflecting a continuum of edaphic preferences. Additionally, the third axis (PC3) explained 14.6% of the variation and is associated with water availability, representing a continuum from wetter forests (e.g. *Eschweilera*, *Pouteria*, *Dinizia*) to drier areas (e.g. *Piptadenia*, *Guazuma*).



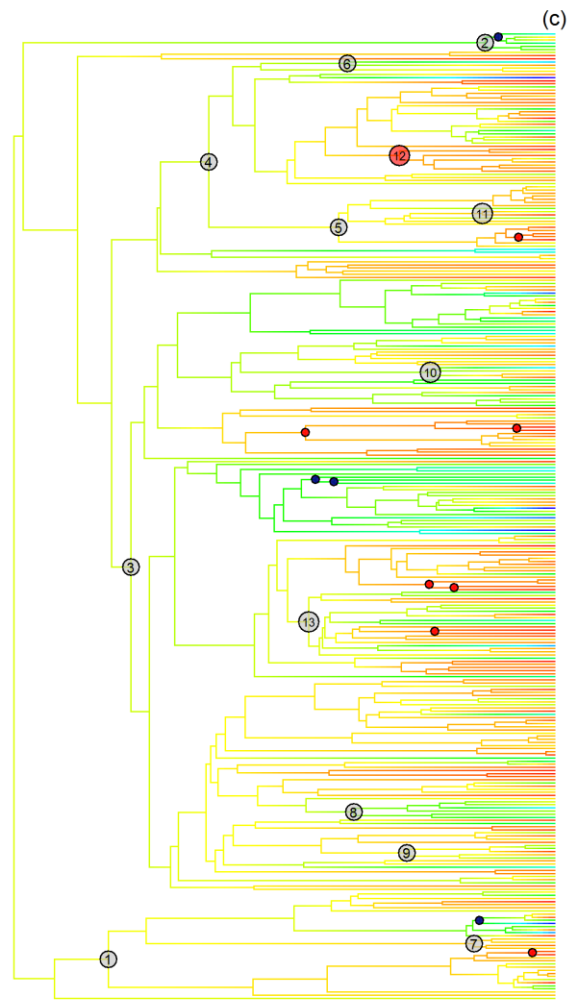
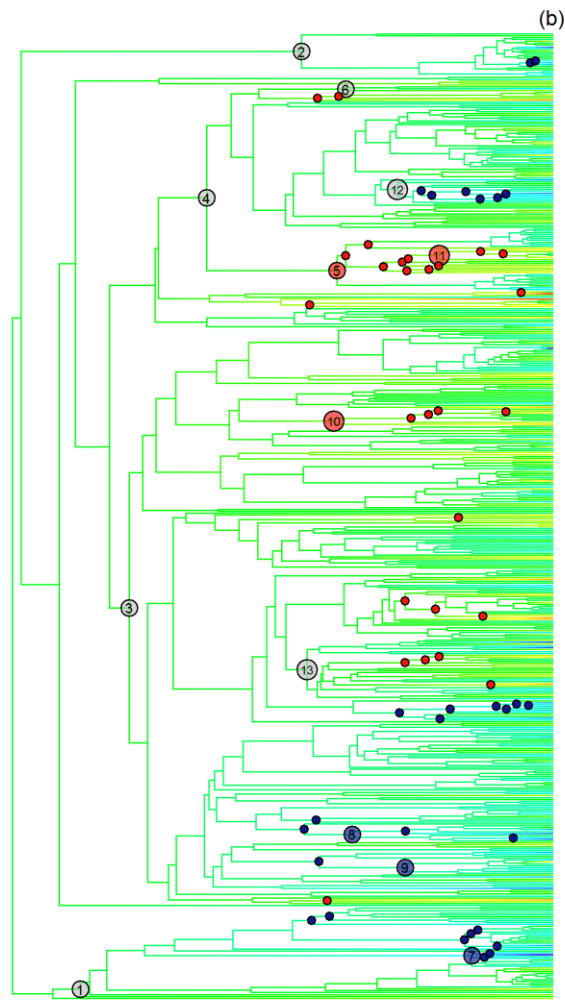
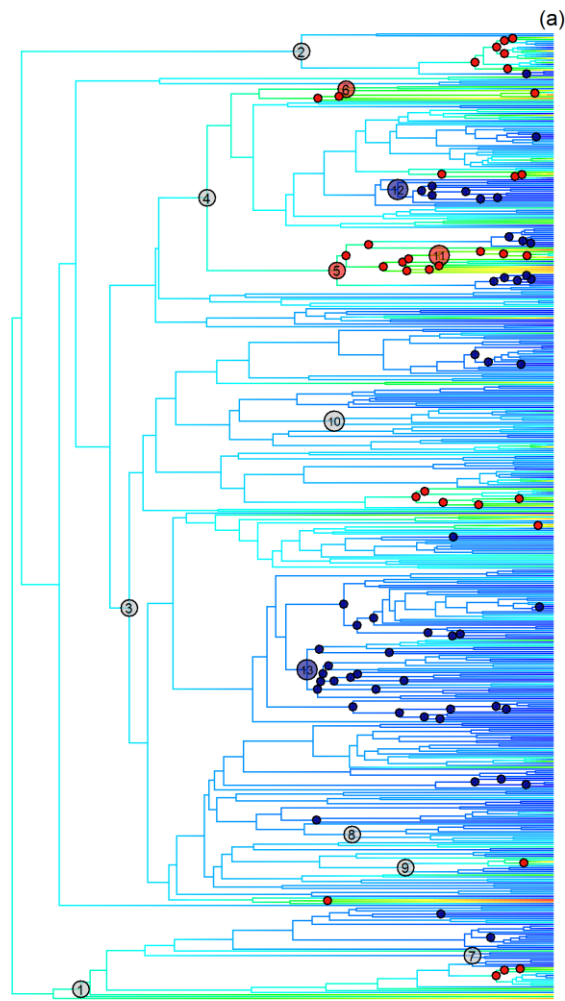
**Figure 4.2** Principal component analyses related to temperature, precipitation, and soil variables using Euclidian distance as a measure of the variation in genus-level environmental niches for 310 Neotropical tree genera. Squares represent the niche variables, and the lines represent the ordination of genera. Key genera are labelled in the graph.

There is significant and moderate levels of phylogenetic signal for nearly all aspects of environmental niche: precipitation, temperature and soil (Table 4.1), showing that closely related genera tend to have more similar environmental preferences than expected by chance (Table 4.1; Figure 4.3). In the full analyses, the strength of the signal varied from 0.23 to 0.60 for temperature, from 0.37 to 0.40 for precipitation and 0.15 to 0.45 for edaphic niches. The only niche variable that did not exhibit significant signal was clay content. All temperature and precipitation variables showed significant phylogenetic signal. These results were consistent across 100 trees from the posterior distribution of the phylogeny (Table 4.1; Figure 4.4). Results and discussion focus on a representative variable for each niche category (mean annual temperature for temperature preferences, annual rainfall for precipitation and total exchangeable bases for edaphic preferences), as the strength of the signal was consistent within each niche group (Figure 4.4).

**Table 4.1** Summary of climate and soil niches estimated for all genera occurring in at least 10 forest plots and their respective phylogenetic signal. Phylogenetic signal for each niche variable was calculated across 100 trees randomly drawn from the post-burn-in fraction of the BEAST analysis. Lambda is the fitted value for lambda, LogL is the log-likelihood, and LogL0 is the log-likelihood for a lambda value equal to zero. Number of genera varied from 510 and 310 for climate and soil variables respectively according to the number of plots available for each variable; see methods for details.

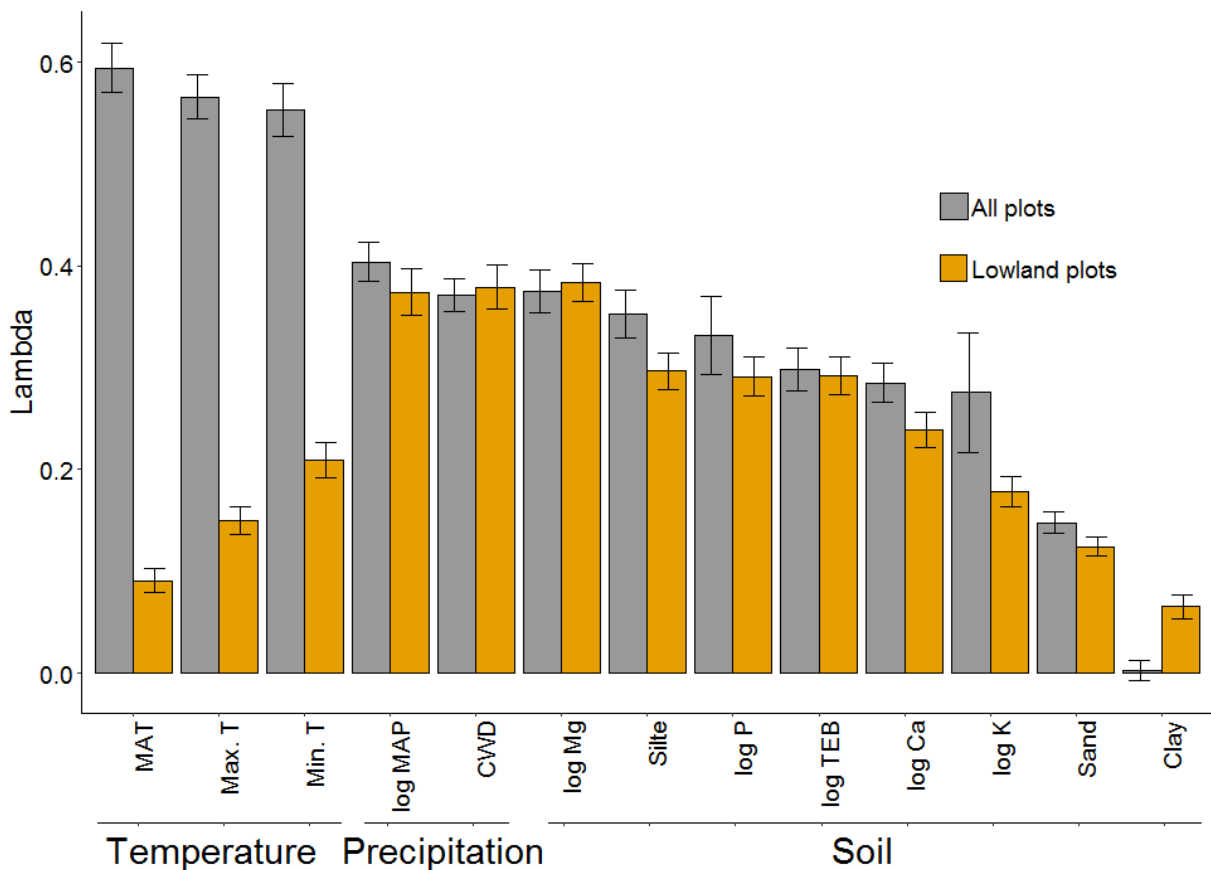
	Niche	Units	Range	Lambda	p value	logL	logL0
Temperature	MAT	°C	14.7 - 27.3	0.59 ± 0.002	<0.001	-2304	-2340.7
	Max. T	°C	22.4 - 34.7	0.57 ± 0.002	<0.001	-2293.2	-2331.9
	Min. T	°C	16 - 22.3	0.55 ± 0.003	<0.001	-2450.6	-2474.6
Precipitation	log MAP	mm	1901 - 3686	0.40 ± 0.002	<0.001	464.5	445.6
	CWD	mm	-1116	0.37 ± 0.002	<0.001	-3257.6	-3278.6
Soil	log Mg	mg.kg	23.1 - 162.9	0.38 ± 0.002	<0.001	-35.5	-43.9
	Silt	%	19.8 - 65.8	0.35 ± 0.002	<0.001	-1196.5	-1203.7
	log P	mg.kg	176.2 - 947.1	0.33 ± 0.004	0.01	24.3	20.5
	log TEB	mg.kg	191.7 - 1376.6	0.30 ± 0.002	<0.001	-61.5	-66.4
	log Ca	mg.kg	95.1 - 1149.8	0.29 ± 0.002	<0.001	-160.8	-165.7
	log K	mg.kg	40.8 - 352.4	0.28 ± 0.006	0.1	50.4	48.7
	Sand	%	33.7 - 88.3	0.15 ± 0.001	0.02	-1217.5	-1220
	Clay	%	23.4 - 60	-	1	-1145.4	-1145.4





**Figure 4.3** Phylogeny of tropical forests tree and palm genera with frequency  $\geq 10$  plots with branches coloured according to niche variables. One niche variable within each niche category: (a) temperature represented by mean annual temperature ( $^{\circ}\text{C}$ ), (b) precipitation, by mean annual precipitation (mm) and (c) soil fertility by total exchangeable bases (mg.kg). Nodes highlighted by red circles indicate clades encompassing lineages with values lower than expected by chance, whilst blue circles indicate clades including lineages showing higher values than expected by chance. Nodes highlighted in grey give a sense of topology. Nodes are numbered as following: 1) Magnoliids 2) Monocots 3) Rosids 4) Asterids 5) Ericales 6) Aquifoliales 7) Myristicaceae 8) Salicaceae 9) Clusiaceae 10) Sapindaceae 11) Primulaceae 12) Apocynaceae 13) Papilionoideae. Phylogenies for each trait with all tips labelled are available in Appendix 4.2.

Although most climatic and edaphic niches tended to be more similar among related lineages, across niche categories, the strength of the signal was up to four-fold stronger for temperature in relation to precipitation and edaphic niche variables (Figure 4.4). Phylogenetic signal for these niche variables was driven by significantly higher or lower values than expected by chance in a range of lineages. Stronger phylogenetic signal for temperature was clearly reflected in the greater number of nodes encompassing lineages with significantly high or low values in comparison to precipitation and edaphic niches (Figure 4.3). For example, Ericales, Aquifoliales, and Primulaceae showed particularly strong links with temperature niches; these lineages had preferences for cooler forest communities with temperature values that are significantly lower than expected by chance. In contrast, Apocynaceae and the subfamily Papilionoideae displayed high temperature niches. Consistent with orthogonal niche axes (Figure 4.2), none of the higher nodes showed consistently high or low values for all environmental niches (Figure 4.3). For instance, within the Arecaceae, whilst most lineages within this group exhibited low temperature niches, with a marked exception for a single clade that includes *Mauritia*, *Mauritiella*, and *Lepidocaryum* (Figure 4.3), no clades showed particular preferences for either specific levels of soil fertility or precipitation.



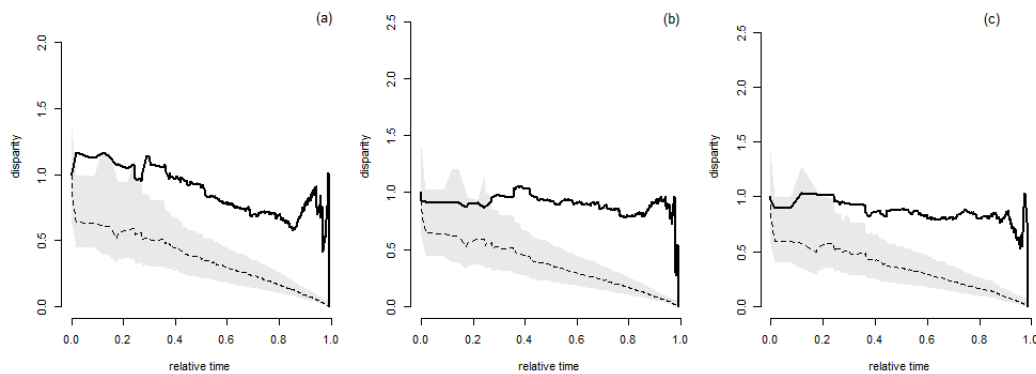
**Figure 4.4** Comparison of the strength of phylogenetic signal among temperature, precipitation, and soil niches across all plots and lowland plots below 500m elevation . Error bars represent standard deviation of estimated phylogenetic signal across 100 trees from the posterior distribution.

Consistent with the analyses of phylogenetic signal, the model selection approach comparing the fit of four different evolutionary models showed that the Lambda model generally provides the best fit for the majority of environmental niche preferences (apart from; Table 4.2). Best-fitting of Lambda suggests significant phylogenetic signal but lower than expected under a pure BM, which may be due to other evolutionary processes such as selection, driving divergence among closely related genera. The WN model of niche evolution provided a slightly better fit for soil clay content, showing that there is no phylogenetic dependence to the observed values of this niche preference. This result corroborates with the lack of phylogenetic signal for clay content (Table 4.1).

**Table 4.2.** Comparison of fit of different models of trait evolution for genus-level temperature, precipitation and soil niches. AIC values are from fitting four evolutionary models: Lambda, Brownian-motion (BM), Ornstein-Uhlenbeck (OU) and White-noise (WN). Values highlighted in bold represent models with better fit.

	Niche	Units	Lambda	BM	OU	WN
Temperature	MAT	°C	<b>4612.9</b>	4802.6	4651.4	4685.5
	Max T	°C	<b>4591.9</b>	4820.7	4647.7	4667.8
	Min T	°C	<b>4906.7</b>	5061.5	4916.3	4953.3
Precipitation	CWD	mm	<b>6521.4</b>	6734.8	6558.4	6561.2
	log MAP	mm	<b>-71.8</b>	145.1	-40.3	-36.4
Soil	Clay	%	2296.9	2486.8	2295.4	<b>2294.9</b>
	Silt	%	<b>2398.9</b>	2511.4	2405.3	2411.4
	Sand	%	<b>2441.0</b>	2600.8	2446.2	2444.1
	log K	mg.kg	<b>422.5</b>	542.9	422.7	423.8
	log Ca	mg.kg	<b>844.8</b>	951.7	853.1	852.5
	log Mg	mg.kg	<b>594.3</b>	696.9	602.3	609.0
	log P	mg.kg	<b>474.9</b>	585.0	475.1	480.1
	log TEB	mg.kg	<b>646.3</b>	748.5	653.0	653.9

Overall, over evolutionary timescales, average disparity through time in environmental niche was consistently greater than expected under the null BM model of evolution and showed a decreasing disparity rate over time (Figure 4.5). This pattern shows that there is a lot of variation within clades in environmental niche, and that therefore, the observed phylogenetic signal for environmental niche is driven mostly by patterns near the tips (i.e. closely related genera do tend to have the similar environmental niches, but deeper in the phylogeny a pattern of phylogenetic autocorrelation does not hold as strongly). These results further confirm that there is a significant phylogenetic signal for climatic and edaphic niches with closely related species having more similar environmental preferences.



**Figure 4.5** Disparity-through-time (DTT) plots for tropical trees and palms for climate and soil niche variables with one niche variable within each niche category: (a) temperature represented by mean annual temperature (°C), (b) precipitation, by annual precipitation (mm) and (c) soil by total exchangeable bases (mg.kg). The solid line indicates the measured relative disparity. Dashed line and light grey area indicate the median and 95% confidence interval across 1000 simulations under the null Brownian motion model of evolution. Time values are relative time as per Harmon et al. (2003), whereby 0.0 represents the root and 1.0 represents the tips.

Although across the whole dataset, temperature niches tended to show stronger phylogenetic signal when compared with both precipitation and soil preferences, its importance is considerably diminished when montane forests are excluded (i.e. forests above 500 a.m.s.l. - Figure 4.4). Marked variation in the importance of temperature among different datasets is explained by the inclusion of plant genera that are more abundant or restricted to high elevation areas, which also show a tendency to be closely related to each other. Specifically, lineages restricted to

montane forests such as *Brunellia* and *Weinmannia* show lower temperature preferences than expected by chance and significantly increase the extent of phylogenetic signal for temperature niches (Figure 4.3). Similarly, lineages from Melastomataceae that occur both in lowland and montane areas, are more abundant in high altitudinal forests, and have lower temperature preferences than expected under the null model. These taxa therefore also increase the strength of phylogenetic signal for this niche axis (Figure 4.3). Once analyses were restricted to lowland forests, results show that precipitation and edaphic variables are equally important for constraining the occurrence and distribution of tree species.

#### **4.4 Discussion**

To the best of my knowledge, this is the first study to directly estimate environmental niches and their evolutionary patterns for tropical trees at such a large phylogenetic and spatial scale. Estimates of phylogenetic signal for different temperature, precipitation, and soil niches show that there is significant correlation between phylogenetic relatedness and environmental niche values for nearly all climate and soil niches (Table 4.1; Figure 4.4). Phylogenetic distances among genera co-vary with their environmental niche preferences. These findings indicate that across tropical trees, sister genera show greater niche similarity than less related ones. Across different niche categories (i.e. temperature, precipitation, and soil), the specific phylogenetic patterns varied substantially (Figure 4.4). Overall, the strong signal found for temperature variables (Table 4.1), show that temperature plays a major role in constraining the occurrence and distribution of lineages among low and high elevation plots. In contrast, analyses restricted to lowland forests show a sharp decrease in the importance of temperature and highlight that edaphic and precipitation preferences are equally important in determining the distribution of genera (Figure 4.4).

High phylogenetic signal (i.e. niche conservatism) would imply strong similarity in habitat use among genera whilst strong selection would imply sister lineages with contrasting environmental preferences. The results found here are between these two extremes: the strength of phylogenetic signal shows that sister lineages

are more similar than expected by chance but there is some extent of divergence, likely via selection promoted by habitat speciation (please see Appendix 4.3 for further discussion). Significant phylogenetic signal for climate and edaphic niches suggest that niche conservatism plays a key role in constraining the occurrence and distribution of both higher and lower-level taxa. The retention of environmental preferences over evolutionary time reported here could have promoted geographical isolation due to species inability to tolerate and adapt to novel environments, and increased the opportunity for allopatric speciation (Wiens 2004a; Kozak & Wiens 2006, 2010b; Wiens *et al.* 2010; Hua & Wiens 2013).

Given the extent of phylogenetic signal (Figure 4.3; Table 4.1) and the fit of Lambda model (Table 4.2), the results found here show that there are preferences of entire clades for certain climatic and edaphic conditions. This finding is consistent with previous studies in a variety of groups and at a range of scales showing that closely related lineages occur in more similar habitats than expected by chance (Kozak & Wiens 2010b; Pei *et al.* 2011; Baldeck *et al.* 2013; Pearman *et al.* 2014; Moriniere *et al.* 2016). In particular, in a subtropical forest analysing topographical preferences across 183 woody species Pei *et al.* (2011) detected non-random habitat associations, showing that closely related species did on average tend to be associated with similar terrain slopes. Partially congruent with the niche conservatism hypotheses, these non-random habitat preferences (Figure 4.3; Figure 4.4; Table 4.1) suggest that niche retention may have been involved in diversification and species turnover. These findings have important implications for the phylogenetic structure of Neotropical tree communities. Previous studies found significant phylogenetic clustering within the Amazon (i.e. co-occurring species are more related than expected) (Kraft & Ackerly 2010; Baraloto *et al.* 2012; Honorio Coronado *et al.* 2015) and results reported here demonstrating that sister lineages share similar habitat preferences helps to explain this pattern. These results are consistent with niche conservatism as one of the drivers in community assembly in tropical forests and also give insights into the possible mechanisms regulating species diversity in the tropics.



Overall, the observed pattern of niche similarity amongst related lineages is more prominent at lower and upper boundaries of the niche spectrum (i.e. lineages with either very high or low niche values are more phylogenetically nested or derived within each clade and restricted to relatively few clades), whilst intermediate niche values are more scattered over the phylogeny (Figure 4.3). These results support previous findings of higher phylogenetic diversity at intermediate levels of precipitation across the Neotropics (Neves *et al.* in review). In particular, because clades at the extremes of climatic gradients belong to a smaller subset of evolutionary related lineages that acquired the ability to persist in these extreme conditions (Zanne *et al.* 2014), areas with intermediate levels of precipitation are a more suitable environment for most plant lineages and may show higher phylogenetic diversity (Neves *et al.* in review).

Although significant phylogenetic signal coupled with the additional support for the Lambda model show that closely related lineages are more similar to each other than expected by chance, results shown here also suggest that selection is also influencing the observed patterns. For example, whilst monocots have generally intermediate precipitation niche values, one single clade (*Iriarte*, *Wettinia* and *Iriatella*) has particularly high values for this variable (Figure 4.3). This niche differentiation amongst sister lineages may reflect either natural selection (e.g. Kozak & Wiens 2006) or evolutionary responses to physiological thresholds imposed by strong environmental pressure - the gradient hypothesis (Endler 1977). Divergent adaptation is expected when sister lineages occupy different habitats. This role of environmental heterogeneity for promoting lineage divergence through habitat specialization has been previously observed across tropical forests (Gentry 1981; Fine *et al.* 2005; Fine *et al.* 2013; Fine *et al.* 2014; Misiewicz & Fine 2014). For instance, investigating soil preferences in the species-rich tropical tree clade Protieae, Fine *et al.* (2005) found that species sharing similar soil niches were often unrelated, suggesting a role for edaphic specialization in plant diversification. The findings reported here at a much broader spatial and phylogenetic scale and across distinct axes of environmental preferences helps to generalise those conclusions on the role of ecological speciation as a driver of diversification within the Neotropics.

Across different niche categories, there is greater phylogenetic signal for temperature variables than the other two aspects of environmental niche: precipitation and edaphic preferences (Figure 4.4). This suggests that over evolutionary scales, temperature preferences may have been more important for constraining species occurrence and distribution. Globally, species and evolutionary diversity are indeed mainly determined by differences in frost tolerance (Zanne *et al.* 2014). However, within the Neotropics, the effect of temperature is only expressed when including high elevation forest plots (Figure 4.4). Forests at high elevation have distinct floristic composition (Gentry 1982, 1988b) and markedly lower temperatures (Grubb 1977) with temperature ultimately setting the upper limits of species distributions (Feeley *et al.* 2011a; Feeley *et al.* 2011b) and leading to major shifts in physiological functioning (Enquist *et al.* 2017). Therefore, stronger phylogenetic signal for temperature niches when including montane forests, indicates that genera with low temperature niches, that are generally restricted to, or more abundant in, mountainous forests, are unevenly distributed across the angiosperm phylogeny, and are concentrated in a few clades.

Interestingly, when excluding high altitudinal forests, precipitation and edaphic variables show moderate and similar extents of phylogenetic signal, highlighting that these are equally important for shaping patterns of tropical tree diversity. These results are broadly consistent with previous findings on the importance of soils (Phillips *et al.* 2003; Tuomisto *et al.* 2003; Coronado *et al.* 2009; Tuomisto *et al.* 2016; Figueiredo *et al.* 2017; Moulatlet *et al.* 2017) and precipitation (ter Steege *et al.* 2003; ter Steege *et al.* 2006; Esquivel-Muelbert *et al.* 2017a) as important predictors of species diversity and turnover across space. However, the results of this study provide an additional evolutionary perspective on these patterns, suggesting more specifically that species distribution is to some extent, controlled by environmental niche conservatism throughout evolutionary history.

Although there is some level of divergence amongst related genera, results found here indicate a prevailing effect of niche retention over time. Given that climate change is likely to consistently increase temperature (Marengo *et al.* 2009) shared temperature preferences amongst related lineages reported here, may have

important consequences for climate-change driven species loss. Predicted increase in temperature suggests that species in montane forests may lose their suitable climate conditions and therefore may be more vulnerable to climate change. Particularly, the finding of significant phylogenetic signal for temperature niches may be useful to identify which lineages may win and which may lose in these montane forests communities: under global warming clades with significantly lower temperature niches may be more vulnerable (i.e. red dots in Figure 4.3a).

The finding that thermal niches are retained over evolutionary timescales suggest that tropical tree species may struggle to adapt to novel environmental conditions and their response may necessarily be to attempt to track their suitable climate. Indeed, shifts in species distribution in response to climate change have been detected already (Feeley *et al.* 2011a; Feeley *et al.* 2011b; Feeley *et al.* 2012). For example, over a short-time scales, increase in temperature have caused non-random shifts (upslope) in the distribution of tropical trees, though rates of changes were significantly slower than the observed rate of rising temperature (Feeley *et al.* 2011b). Such warming-induced changes may have a stronger impact due to shared temperature preferences amongst related lineages: niche retention may prevent species from acclimatizing and adapting to a new environment and their only possible response may be to change their distribution. Thus, to counteract current increases in temperature, the maintenance of landscape corridors that could facilitate species movement will be important in determining the ability of species to migrate and thus the future of the Amazon. Ultimately, results found here may also have important implications for understanding the effect of climate change on the tree of life. Because preferences for certain environmental conditions are clustered rather than overdispersed over the phylogeny, species loss will have a stronger impact on communities' phylogenetic structure, than if niches were scattered across the phylogeny. In this sense, effective conservation strategies to retain different aspects of the tree of life should encompass wide environmental gradients that encompass variation in both climate and soil.



## Chapter 5 : Conclusions

The final chapter concludes and discusses the implications of the results of the thesis. I first give an overview of the whole thesis and a summary of each data chapter, and discuss the overall philosophy of the study: integrating ecology and evolution to understand current patterns. I then provide future research directions, discuss the research implications in an era of anthropogenic and climatic changes, and finally synthesise the main findings.

### 5.1 Overview of findings

This thesis focuses on investigating the legacy of evolution on present-day patterns in tropical forests. My main objectives were: 1) to investigate the relative influence of species' evolutionary heritage versus selection in determining functional traits that directly represent the main axes of life-history variation in tropical forests, and that are also associated with species ability to process and store carbon (Chapter 2), 2) to assess the relationship between taxonomic and evolutionary metrics of diversity and two key measures of ecosystem function: wood productivity, and aboveground biomass (Chapter 3) and 3) to understand how the preferences of certain genera for specific environmental niches have evolved (Chapter 4). To achieve these objectives I combined a long-term inventory dataset (Lopez-Gonzalez *et al.* 2009; Lopez-Gonzalez *et al.* 2011) with recently published phylogenies (Fine *et al.* 2014; Dexter & Chave 2016; Dexter *et al.* 2017) and a new pan-Amazon molecular phylogeny that I constructed (Chapter 3).

Overall, the results presented in this thesis demonstrate that there is a tendency for species to retain their ancestral functional characteristics and environmental preferences, and thus closely related lineages tend to be more similar to each other than expected by chance. However, although there is a tendency of sister taxa to share similar traits and habitats, the strength of similarity cannot be predicted easily. Over evolutionary timescales, selection has also played a role in determining functional traits and environmental preferences: in particular,

divergent selection has also driven close relatives to differ from each other and their ancestors. Thus, rather than being simply assumed, the magnitude of similarity for a particular trait or a specific environmental niche needs to be tested *de novo* for any given dataset.

In addition, I advocate for the use of phylogenetic information as a proxy for species ecological characteristics. More practically, the significant phylogenetic signal found in this thesis suggests that the evolutionary position of species (i.e. the genus or family to which they belong) can provide proxies for the wood density, demographic rates, maximum sizes, climatic and edaphic preferences of tropical trees, overcoming a crucial data limitation for quantifying functional traits. For instance, phylogenetic signal in plant functional trait data (maximum height, seed mass, wood density and leaf size) was used to predict the geographical distribution of functional diversity for North America and European tree species (Swenson *et al.* 2017). Their study for a less diverse temperate flora suggests a possible way to incorporate functional diversity in ecosystem modelling that goes beyond using plant functional types; the results found here support the use of this approach for highly diverse tropical ecosystems. The result of sister taxa sharing a similar ability to process and store carbon also suggests that evolutionary history contributes to understanding ecosystem function in complex and highly diverse tropical forests. Consistent with this finding, by assessing the relationship between evolutionary diversity and ecosystem functioning, I showed that we can still see the legacy of evolution on current patterns of wood productivity today. Taken together, these results highlight that the modern flora and present-day patterns of ecosystem functioning are the result of the interplay between recent ecological and long-term evolutionary processes.

### **5.1.1 Objective 1 - Chapter 2: Investigating the legacy of evolution on Amazon tree ecology**

By investigating the associations among four major traits that represent important functional axes that drive plant form and function (i.e. wood density, potential tree size, growth and mortality rates), I found two main axes of variation, likely to be

associated with adaptations to horizontal and vertical light gradients in tropical forests. Half of the variation was captured by the first axes that shows a trade-off from pioneer to shade tolerant genera, whilst roughly 30% of the variation was captured by the second axis which represents variation in tree size and reflects the continuum from understory to canopy lineages. While a number of studies have previously used readily measured traits as a proxy for ecological strategies relevant to growth and survival (e.g. Diaz *et al.* 2016), here I describe this trade-off using directly calculated demographic data from a large network of forest plots. Additionally, by mapping these functional characteristics on recently published phylogenies (Fine *et al.* 2014; Dexter & Chave 2016; Dexter *et al.* 2017) I show that sister species do indeed tend to resemble each other more than expected by chance. However, phylogenetic signal was lower than expected under a Brownian motion model of evolution, which suggests that divergent selection also played a role and has occurred repeatedly in independent lineages. The strength of similarity amongst these four functional characteristics was similar, suggesting that the main axes of life-history variation among lineages of Amazonian trees represents the result of repeated evolution of a suite of coordinated functional characteristics in relation to adaptations to horizontal and vertical gradients in light. The findings of this study are also important to provide support for using the evolutionary relationships amongst species as proxies for trait values for species where data are not available. This link is potentially of particular importance in tropical forests due to their high tree diversity, where species vary greatly in their functional characteristics and measuring traits of so many species is difficult. Moreover, the intriguing evidence for convergent evolution across distantly related lineages may have promoted the emergence of a range of genera with fast demographic rates that set the scene for the subsequent rapid diversification of these groups (Baker *et al.* 2014) – a suite of events that qualify as a possible ‘synnovation’, or series of key innovations (Donoghue & Sanderson 2015). The emergence of the range of life-history strategies and the subsequent effect of these ecological traits on the diversification of different lineages demonstrate how ecological processes such as habitat specialization in

addition to historical processes may have played a key role in generating the diversity of Amazonian forests.

### **5.1.2 Objective 2, Chapter 3: The legacy of evolution on ecosystem functioning**

Using 615 tree and palm genera and a new large-scale DNA sequence-based genus-level phylogeny, I calculated ten different metrics of both taxonomic and evolutionary diversity and showed that they represent three distinct aspects of diversity associated with 1) common taxonomic diversity metrics; 2) evolutionary relationships close to the tips; and 3) relationships deep in the phylogeny. I show that common diversity metrics are correlated with each other and reflected variation in species number and their respective abundances. In contrast, different aspects of phylogenetic diversity were reflected in the two other dimensions of diversity. These findings support the idea that the relationship between evolutionary diversity and species richness can be decoupled, with phylogenetic diversity metrics representing different facets of diversity (Forest *et al.* 2007; Tucker *et al.* 2016). To investigate the effect of different aspects of biodiversity on both carbon processing and storage, I calculated wood productivity and carbon stocks for 90 lowland forest plots distributed across the Amazon basin and compared the effects of taxonomic and evolutionary diversity on ecosystem function with the effect of environmental drivers and functional characteristics.

By investigating the role of evolutionary relationships among co-occurring genera, in addition to taxonomic metrics of diversity (e.g. genus richness and Simpson index), I show that both taxonomic and evolutionary diversity metrics significantly affect wood productivity in natural communities across the Amazon tropical forest biome. Using appropriate locally collected soil data, climate, and forest structure characteristics, I show that these results hold once I accounted for potential confounding factors that also affect productivity. Because the amount of carbon processed by tropical trees is ultimately largely determined by a complex suite of functional characteristics, I suggest that this additional contribution of evolutionary diversity among lineages to explaining variation in productivity, is a



result of other functional characteristics, besides the ones I quantified here, that promote productivity within plots. Although the effect of biodiversity on wood productivity was not strong, the magnitude of the effect was similar to that observed for environmental variables (Duffy *et al.* 2017).

### **5.1.3 Objective 3, Chapter 4: The role of evolution on shaping environmental preferences in tropical forests**

In this chapter I provide the first large-scale assessment of the relative importance of temperature, precipitation, and edaphic variation for promoting diversification in tropical trees. Overall, across tropical forests, ongoing studies to understand species diversity and spatial turnover typically show that environmental variation (e.g. climate and edaphic regime) is associated with present-day patterns of composition. However, historical processes that underlie these habitat preferences are poorly studied. To understand the role of evolution for shaping present day environmental preferences, I combined the phylogeny constructed in Chapter 3 and a comprehensive database on the distribution of 510 angiosperm tree genera across the Neotropics. I found strong and significant phylogenetic signal for environmental niche preferences (i.e. temperature, precipitation, and edaphic regime), but less than that expected under a null, Brownian motion model of evolution. These results are consistent with a prevalent tendency for evolutionarily related genera to have more similar environmental preferences than expected by chance, but also suggest that divergent habitat specialization has occurred repeatedly and independently in many lineages. The results presented here support other studies at smaller spatial scales and for a restricted number of lineages (e.g. Fine *et al.* 2005).

Comparing the importance of different niche variables, I show that the effect of temperature in constraining lineage diversity and distribution is most evident when including forest plots at high elevations (> 500 a.m.s.l), wherein specific lineages (e.g. Ericales, Aquifoliales and Primulaceae) had preferences for cooler temperatures. In contrast, when analyses focus on lowland plots only, the effect of

temperature is less evident and precipitation and edaphic niches are equally important in constraining species diversity and distribution.

## **5.2 The advantage of integrating ecological and evolutionary approaches**

Ecological and evolutionary processes are usually studied in isolation without taking into account processes operating at multiple temporal scales (Ricklefs 1987). In particular, the role of historical processes has been ignored at the expense of ecological explanations for current patterns of diversity and composition (Ricklefs 2004; Ricklefs & Jenkins 2011). In this context, an overall aim of this thesis was to integrate both macro-ecological and macro-evolutionary approaches into a single framework, to understand the role of historical processes for determining present-day patterns in the distribution and diversity of species, their respective functional characteristics and environmental preferences, and ultimately their effect on ecosystem function. By using a set of different data types (i.e. single census and long-term inventory forest plots, evolutionary relationship among taxa, climatic and edaphic data) it has been possible to explore the legacy of evolution on current patterns of species turnover across space and the contrasting resource acquisition strategies of different species. For instance, this integrated approach allowed me to investigate the role of evolutionary processes such as natural selection for determining key functional characteristics (Chapter 2), and also their role in the spatial distribution and structure of large-scale species assemblages (Chapter 4). These links between evolutionary relationships and both functional characteristics and environmental preferences is particularly useful in tropical forests because of the high tree diversity of these ecosystems (ter Steege *et al.* 2013), which means it is difficult to understand the ecology of all of the many coexisting species.

Likewise, integrating an ecological and evolutionary approach allowed me to investigate the legacy of evolution on carbon stocks and wood productivity (Chapter 3). Although there have been many studies investigating this link over

small spatial scales and with controlled experiments, scaling up these results to scales relevant to conservation planning is an important challenge. To the best of my knowledge, this is the first study combining these approaches to investigate the fingerprint of evolution on current patterns of carbon stocks and wood productivity in such diverse systems and at large spatial scales.

Currently, coupling phylogenies with ecological data is challenging due to the lack of data on evolutionary relationships amongst tropical species: despite the recent emergence of a large number of dated phylogenies, they are generally restricted to specific clades (Simon *et al.* 2009; Couvreur *et al.* 2011; Bardon *et al.* 2013; Fine *et al.* 2014; Misiewicz & Fine 2014; Liu *et al.* 2015; Terra-Araujo *et al.* 2015; Dexter *et al.* 2017). Therefore, an additional contribution of this thesis is a new pan-Amazon phylogeny including 1122 genera, which provides a powerful tool to improve further understanding of historical processes on the distribution and ecology of the modern Amazonian flora.

### 5.3 Future research directions

The results from this thesis provide a number of possible avenues for future research. Firstly, the phylogeny could be further improved. Although the phylogeny constructed in this thesis encompasses the largest number of lineages yet used to investigate the influence of historical processes on extant tropical trees, many genera are still missing at the pertinent phylogenetic scale (i.e. across all angiosperm lineages). Investigating this link between evolutionary relationships and ecological similarity in a complete phylogeny at species level would be indeed the “Holy Grail”. However generating a species-level phylogeny remains a very large-scale project, considering the high diversity of the Amazon and adjacent biomes (Gentry 1982, 1988b; ter Steege *et al.* 2013). A complete phylogeny will indeed increase our understanding on the evolutionary processes underlying current patterns. However, I do not expect that including missing lineages will reduce our estimates of phylogenetic signal for functional characteristics and environmental preferences - and may even increase it. Changes in the magnitude of the effect will largely depend on the prevalence of different types of missing genera (e.g. lianas, clades from temperate zones, understory trees and shrubs, montane taxa). For instance, Malpighiales encompasses 6% of all angiosperm species and are mostly represented by rainforest understory trees (Davis *et al.* 2005), that have much shorter life-cycles than canopy trees. Because small-statured species are generally restricted to a few clades (Dexter & Chave 2016) and share similar growth and survival strategies, I expect that including understory genera (trees  $\leq 10$  cm) would increase the level of phylogenetic signal for the functional traits I studied. Likewise, I expect that including temperate genera may increase phylogenetic signal for environmental preferences, because temperate lineages are clustered within angiosperms (Judd *et al.* 1994), but may not change the extent of the signal for the functional traits I studied because there is substantial variation for these traits within temperate clades. For instance, Fagales, a highly diverse and ecological dominant plant group is generally restricted to temperate areas of the Northern Hemisphere (Cocker 2006; Larson-Johnson 2016). Including genera belonging to this order may therefore increase

the extent of phylogenetic signal for temperature (i.e. few clades with temperature significantly lower than expected by chance). However, within Fagales the trade-off between pioneer and shade tolerant species also exists (e.g. *Betula* versus *Quercus* (Betulaceae/Fagaceae) and reflects similar divergent selection to what I found for traits associated with this trade-off in tropical forests (Chapter 2; e.g. *Inga* versus *Dipteryx/Parkia* in Fabaceae). Thus, I expect that phylogenetic signal for traits associated with growth and survival would be similar once temperate genera are included. In another example, temperature plays a major role constraining genera occurrence and distribution in high elevation plots and lineages restricted to these montane forests are more clustered than expected in the angiosperm phylogeny (e.g. *Saurauia*, *Clethra*, *Styrax*, *Gordonia*). Assuming that additional taxa from montane forest that are not in the phylogeny are largely found within a few families and orders, I would therefore expect that including more taxa from higher elevations will only increase the extent of phylogenetic signal for environmental niches. In sum, I expect that including missing genera that expand the range of trait and environmental preference values (e.g. demographical rates for understory trees or temperature preference for temperate genera) could lead to an increase in the extent of phylogenetic signal. Meanwhile, I expect that including genera that do not affect the overall amplitude of sampled trait variation (e.g. wood density and demographical rates for temperate genera) will not change the extent of phylogenetic signal. However, this may not be the case, and future studies will benefit from a more complete and finely resolved phylogeny.

Studies including additional functional characteristics would also improve our understanding on the mechanisms underlying present-day ecological patterns. Further studies will benefit from both mapping additional traits onto the phylogeny to investigate the extent to which evolutionarily relatedness among species predicts their ecological similarity and also from including other traits as co-variables for predicting ecosystem function. One intriguing possibility would be to compare the extent of phylogenetic signal for “hard” traits (e.g. growth rates, potential tree size) that provide integrated measures of tree performance, versus “soft” traits (e.g. leaf mass per area, leaf nitrogen) that reflect specific aspects of

plant function. I expect that hard traits may show higher levels of phylogenetic signal because they are controlled by a linked set of co-adapted characteristics (Crisp & Cook 2012) and such complex traits may depend on many interacting genes (El-Lithy *et al.* 2004; Conner & Hart 2005). However, hard traits may have lower phylogenetic signal than soft traits simply because they are under greater selective pressure and show higher phenotypic plasticity in response to environmental conditions (Geber & Griffen 2003; Pitchers *et al.* 2014). A third hypothesis would be that hard and soft traits may have similar phylogenetic signal due to coordinated evolution among all traits.

The evolutionary relatedness of taxa can represent a good proxy for overall trait similarity, as phylogeny may integrate more trait information than a limited suite of measured traits and thus provide crucial information on species ecological characteristics. However, a combination of functional traits is ultimately responsible for driving the observed relationship between evolutionary diversity and wood productivity, and if more complete measurements of functional characteristics are made, it will be possible to explore the role of functional diversity for controlling ecosystem function. However, for species-rich plant communities such as tropical forests, obtaining reliable estimates of functional traits is extremely challenging as it requires sampling at least one individual per species in each forest plot (Baraloto *et al.* 2010a). In addition, the high number of rare species in tropical forests (ter Steege *et al.* 2013; Slik *et al.* 2015) that may be associated with a highly distinct set of traits that disproportionately increases community functional diversity, challenges the functional trait approach (Baraloto *et al.* 2010a; Mouillot *et al.* 2013; Umaña *et al.* 2017). For example, within tropical forests, 55% of the species that are more functionally distinct are rare, and on average represented by a single individual per sample (Mouillot *et al.* 2013). Thus, trait sampling in such diverse ecosystem requires considerable effort, but considering the importance of incorporating a combination of key functional characteristics, the investment in complete sampling is worthwhile for at least some traits (Baraloto *et al.* 2010a). For instance, future researchers could focus on measuring crown architecture for different species. Because crown architecture has been shown to be strongly associated with productivity in temperate forests

(Pretzsch 2014; Jucker *et al.* 2015) and experimental studies (Williams *et al.* 2017), measurements of this functional characteristic may be particularly important to understand the biological mechanisms that underlie the diversity-productivity relationship. Thus, despite the difficulty of assessing and quantifying functional characteristics in tropical forests, measuring a number of traits would be essential to genuinely understand the mechanisms that underlie diversity-ecosystem function relationships. Future research should take on the challenging task of measuring these additional traits.

The extent to which the relationship between evolutionary diversity and ecosystem function uncovered here can be generalised to other biomes, such as savannas and seasonally dry tropical forests, also remains to be investigated. The key traits and trait values that influence resource uptake and thus promote ecosystem function may differ widely among biomes with distinct evolutionary histories (Forrestel *et al.* 2017). In fact, clades restricted to seasonally dry tropical forests and savannas have very different characteristics, including high root-shoot ratios and distinct canopy structure, and the majority of biomass may sometimes be allocated belowground. For example, in savannas, root productivity plays a major role in determining total productivity and varies from 4 to 8.3 Mg ha<sup>-1</sup> y<sup>-1</sup> (Pandey & Singh 1992) whilst in tropical forests the contribution of root productivity is generally lower at 1.7 to 7.6 Mg ha<sup>-1</sup> y<sup>-1</sup> (Aragao *et al.* 2009). These differences are an outcome of distinct functional characteristics: savanna woody plants generally show higher root:shoot ratios of 0.6 to 2.9 (Ribeiro *et al.* 2011) in comparison to tropical forest trees ( $0.21 \pm 0.03$  Malhi *et al.* 2009), and these different strategies could have an effect on how different metrics of evolutionary diversity relate to ecosystem function. In particular, because savanna is a disturbance-driven system where ecosystem functions such as wood productivity and biomass will depend on the timing and intensity of the most recent fire (Pellegrini *et al.* 2017), I expect that frequent disturbances may overwrite any effect of evolutionary diversity on ecosystem function. In contrast, seasonally dry tropical forests are less affected by large-scale disturbance events and might show a pattern similar to wet forests. Thus, due to the different ecological and historical context of seasonally dry tropical forests and savannas, it

is likely that within and cross-biome patterns are driven by different historical processes and by a distinct sets of functional traits. For instance, Poorter *et al.* (2017), in assessing the relative importance of biodiversity on ecosystem function across the Neotropics, argued that there is a significant and positive effect of diversity on biomass stocks in cross-biome analyses (i.e. dry and wet forests). However, results within biomes are conflicting, and in a few cases show opposite patterns: there is a positive effect of species richness on carbon stocks within wet forests whilst there is no effect within dry forest communities. Additionally, species richness had a positive effect on biomass growth of surviving trees (i.e. all stems in a plot that survived until the last census) in South America but show a negative effect in Central America (Poorter *et al.* 2017). Thus, interpreting cross-biome patterns is difficult and associations may arise spuriously as it may be driven by the relationship within a single biome rather than consistent patterns across different biomes. I expect that cross-biome effects of diversity may be related to changes in different functional traits and therefore likely to be difficult to interpret. For instance, canopy architecture may be an important driver of productivity in closed canopy forest due to canopy packing, whilst in savannas other functional characteristics may be more important for promoting ecosystem function.

Finally, the most prominent question that emerges for future research concerns assessing species' responses to climate change. Because different species differ in their ability to process and store carbon depending on their life-history strategies and functional characteristics, it is imperative to have a better understanding of which species may 'win' and which may 'lose' and how this may impact on the carbon cycle in tropical forests. Here, I show that lineages tend to retain their ancestral environmental preferences over evolutionary time scales. Thereby under predicted warming, clades with temperature preferences that are lower than expected by chance would be more prone to declines in abundance and/or shifts in their distribution. The results from chapter 4 give us a hint as to which lineages may be 'winners' versus 'losers'. Additionally, analyses coupling the phylogeny constructed here with rates of population change (e.g. Katabuchi *et al.* 2017) may provide a powerful way to potentially predict how species will respond to climatic



changes. Through time, the consequences of climate change on species abundance and geographical distribution is a result of how species respond and whether they can adapt to these changes evolutionarily (Quintero & Wiens 2013). Some taxa are expected to become locally extinct and shift their geographical distribution to remain within their ancestral environment (Parmesan & Yohe 2003). Other taxa may acclimate to rapid changes in climate through phenotypic plasticity in order to survive (Houlton *et al.* 2007) or they may have the evolutionary potential to adapt to environmental changes and persist (Bell & Collins 2008). In contrast, other species may be unable to move or evolve fast enough and may become vulnerable to extinction (Lavergne *et al.* 2013; Quintero & Wiens 2013). One possible way to investigate this link in more detail is to examine the rate of niche evolution among lineages and compare these rates with rates of population change. Species ability to persist in the ecosystem will depend on their adaptive potential which can be evaluated through their past rate of niche evolution. Lineages that have experienced high rates of niche evolution may be more resilient to environmental changes, while those characterized by slow niche evolution may be more susceptible to decline and become extinct (Smith & Beaulieu 2009; Lavergne *et al.* 2013). The constraints on the capacity of species to be rescued from stressful conditions and persist via adaptive evolution will depend on their retention of appropriate genetic variation or a high mutation rate to allow niche shift and adaptation to new climatic conditions (Bell & Collins 2008; Lavergne *et al.* 2013). Genetic diversity may allow different populations to respond to selective pressure by allowing evolutionary changes of species traits, and therefore enhance their potential to adapt (Lavergne *et al.* 2010). The results from chapter 4 of environmental preferences being heritable over evolutionary timescales give us not just an indication of which species may lose and which may win under predicted climatic change, but provides a number of possible avenues for future research, particularly for linking rates of niche evolution with population changes in abundance. However, despite this promising approach to connect estimates of past niche evolution to a present-day ability to cope with climate change, it is important to acknowledge the vastly different timescales involved. On a phylogenetic scale, evolutionary rates are changing over millions

of years (Quintero & Wiens 2013), while the rate which climate is currently changing is much faster; temperature for example is rising at an average rate of  $0.26 \pm 0.05^\circ \text{C}$  per decade across the tropics (Malhi & Wright 2004).

## **5.4 Research implications**

One of the biggest challenges in the conservation realm is to provide decision makers with means to prioritize efforts. Recently there has been an increasing interest of incorporating different aspects of biodiversity in these discussions, which go beyond the number of species, to include other metrics such as functional and evolutionary diversity. In particular, phylogenetic diversity has been widely recommended to be incorporated into conservation strategies (Vanewright *et al.* 1991; Forest *et al.* 2007; Isaac *et al.* 2007; Rolland *et al.* 2012; Honorio Coronado *et al.* 2015; Oliveira *et al.* 2017; Pollock *et al.* 2017). Four key arguments have been suggested to support an evolutionary perspective as an important component of nature conservation: i) phylogenetic diversity as an intrinsic component of biodiversity; ii) as a proxy for functional diversity; iii) because it is related to communities' ability to persist under environmental changes; and iv) because it promotes ecosystem functioning. However, despite the number of arguments repeatedly recommending evolutionary diversity to be relevant for conservation, there seems to have little evidence of the additional value of this approach (Diniz-Filho *et al.* 2013; Winter *et al.* 2013). Here, I discuss how this thesis contributes to each one of these arguments in turn.

### **5.4.1 Phylogenetic diversity as an intrinsic biodiversity component**

There is an intrinsic interest in preserving all the aspects of biodiversity, including protecting the tree of life *per se* (Faith 1992; Forest *et al.* 2007). As species are not all equivalent there are moral and ethical arguments that evolutionary diversity represents a value on its own and the loss of species consequently implies a loss of evolutionary history. In this thesis, I constructed a phylogeny including 1122 Neotropical genera that can be used to show how distinct are those lineages. The evolutionary distinctiveness (ED) of each genus represents the

amount of unique evolutionary history carried by each genus and can be calculated by dividing the total phylogenetic diversity of a clade amongst its members (Vanewright *et al.* 1991; Isaac *et al.* 2007; Jetz *et al.* 2014). For conservation purposes an index of Evolutionary Distinct and Globally Endangered species (EDGE) has recently been suggested for conservation prioritisation (Redding & Mooers 2015). This index gives high values to species that have few close relatives and are under greater risk of extinction, and is calculated by combining the ED and the global extinction (GE) risk from the World Conservation Union Red List Categories (IUCN 2017):

$$EDGE = \ln(ED + 1) + (GE * \ln(2))$$

Where ED represents how much evolutionary ‘information’ would be lost if the taxa dies out and is measured as the distance along the phylogeny from one taxa to its closely relative (i.e. twice the age of their most recent common ancestor). GE reflects the risk of extinction and is attributed based on the IUCN red list: critically endangered (GE = 4), endangered (3); vulnerable (2); near threatened (1) and least concern (0). So far, there are quantifications of EDGE for mammals, amphibians and corals (ZSL 2017) and the phylogeny constructed in this thesis could potentially be used to calculate the EDGE metric for angiosperm genera. The EDGE metric has already been shown to modify conservation initiatives (Isaac *et al.* 2007; Jetz *et al.* 2014; Redding & Mooers 2015). For example, investigating the effectiveness of EDGE as a tool for prioritisation scheme of mammals, Redding and Mooers (2015) showed that ranking species for conservation attention based on EDGE scores captures ‘unique’ species and has the advantage of preserving more of the total evolutionary history and trait diversity compared to conservation prioritisation simply focusing on species that are under greater extinction risk. For angiosperms, the phylogeny produced here therefore offers a powerful tool to support current criteria for identifying target groups. Amongst the 1122 genera in the phylogeny produced here, 320 species belonging to 150 genera had their conservation status accessed in the IUCN red list. I estimated the EDGE index for these genera calculating the evolutionary distinctiveness per genera (ED) and the highest global extinction risk category (GE) within species for that genus. The most distinctive and threatened genera

were: *Duguetia*, *Sorocea*, *Mollinedia*, *Rinorea*, and *Cupania* (complete list with EDGE for the genera accessed in the IUCN red list of threatened species are available in Appendix 5). Interestingly, the genera that I found to deserve higher conservation attention are comprised of small-statured trees that are usually ignored in threat assessments that focus on large iconic timber species. In fact, conservation efforts used to increase awareness about conservation priorities generally rely on iconic and charismatic species while neglecting threatened ones (Barua *et al.* 2011; Bennett *et al.* 2015). Using the EDGE index within conservation schemes may therefore be more effective as conservations funds may be allocated for overlooked threatened species, rather than focusing on iconic and charismatic species that may be not threatened.

#### **5.4.2 Phylogeny as proxy for functional diversity**

Beyond protecting the tree of life *per se* (Isaac *et al.* 2007; Jetz *et al.* 2014), evolutionary diversity is also recommended to be incorporated into conservation strategies for safeguarding the full breadth of functional diversity. Facing the challenge of assessing a suite of functional traits due to budgetary and practical constraints (Baraloto *et al.* 2010a), if closely related species share similar traits, there will be a synergy between protecting phylogenetic and functional diversity. However, the lack of knowledge on species evolutionary relationships (Mace *et al.* 2003) and the little evidence for phylogenetic diversity being a proxy for measured functional diversity (Mouquet *et al.* 2012; Winter *et al.* 2013) have prevented the use of this argument for conservation. In chapter 2, I show that across tropical trees, closely related genera tend to share similar traits that are associated with key aspects of their life-history strategies which strengthens the argument for incorporating an evolutionary perspective into strategies for prioritizing conservation efforts: the results presented here support the idea that conservation of phylogenetically diverse tropical forest tree communities also maximizes the diversity of functional characteristics in these ecosystems.

#### **5.4.3 Species ability to persist under environmental changes**

Another line of argument to promote the use of evolutionary diversity in conservation assessments is that the extent to which environmental niches are retained over evolutionary timescales may be associated with species ability to cope with ongoing climate change. If environmental niches have evolved little from their ancestral state, species may struggle to adapt to changing environments and may need to shift their distribution to track their most suitable environment conditions (Wiens & Donoghue 2004; Wiens *et al.* 2010). By contrast, if environmental niches have diverged from their ancestors, this pattern may suggest that adaptations to novel environments are more likely to occur in the future. In chapter 4, I show that sister lineages tend to share similar environmental preferences. These results may help us to understand and possibly predict the ‘winners’ and ‘losers’ under ongoing climatic and anthropogenic changes. Because the results from chapter 4 show a prevailing tendency for Neotropical trees to maintain the environmental preferences of their ancestors, I expect that facing predicted increase in temperature, lineages with cooler temperature preferences will be more prone to decline in abundance and eventually become locally extinct. Notably, I expect that under global change, species loss may be biased against certain clades, due to the shared environmental niches amongst related lineages, and have a stronger impact on evolutionary diversity than on diversity measures based simply on the number of species. These results from chapter 4 therefore suggest that the protection of evolutionary diversity may benefit from conservation of areas encompassing distinct environmental conditions. Conservation strategies that cover a limited environmental gradient may eventually experience greater losses of evolutionary diversity.

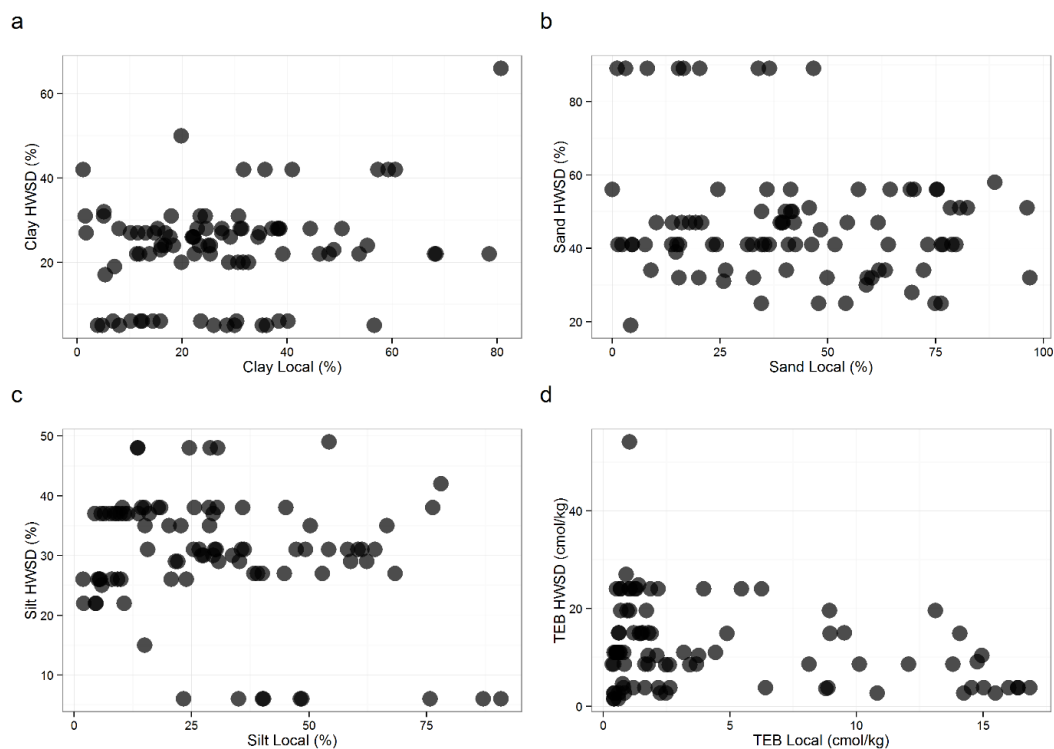
#### **5.4.4 Promote ecosystem functioning**

The strongest argument for incorporating evolutionary diversity into conservation efforts relies on the relationship between diversity and ecosystem function. More evolutionary diverse communities are assumed to increase ecosystem function through complementarity. However, all the evidences supporting this link has come from grassland experiments (Cardinale *et al.* 2007; Cadotte *et al.* 2008; Cadotte *et al.* 2009; Cadotte *et al.* 2013; Cadotte 2013; Cadotte *et al.* 2017b) and

whether more evolutionarily diverse communities maximize function at large scales in natural ecosystems was still lacking (though see Duffy *et al.* 2017). The results from chapter 3 support this argument and for the first time show that evolutionary diversity is positively associated with wood productivity in diverse tropical forests: even after millions of years of evolutionary processes, there is still a legacy of evolution on current patterns of productivity. These results suggest that incorporating evolutionary history into conservation strategies may also maximise ecosystem function. Although the results presented here support the relationship between greater evolutionary diversity and higher productivity it is important to state that this effect is small. Furthermore, in addition to prioritizing areas with greater carbon stocks and productivity, other factors such as belowground carbon should also be considered, particularly in areas of tropical peat swamps (Draper *et al.* 2014).

The amount of carbon processed and stored in aboveground biomass is ultimately determined by variation in local soil and climatic gradients (Malhi *et al.* 2006; Baraloto *et al.* 2011; Quesada *et al.* 2012). Although to my knowledge there are no other studies investigating the legacy of evolution on current patterns of carbon stocks and productivity, recent studies have recommended that biodiversity should be incorporated into conservation strategies that aim to reduce carbon emissions from deforestation and forest degradation (REDD+) (Poorter *et al.* 2015b; van der Sande *et al.* 2017b). These studies found that biodiversity is positively associated with carbon stocks and suggested that biodiversity conservation is not only a goal in itself but also promotes ecosystem functioning. However, we did not find an effect of diversity on carbon stocks, just on wood productivity. Importantly, previous studies that have attempted to account for climatic and edaphic variation have relied on soil properties extracted from digital soil maps from the Harmonised World Soil Database (HWSD) (Nachtergaele *et al.* 2012). In fact, because soil physical and chemical properties vary at local scales and the spatial resolution of HWSD is 1 km, these data fail to capture local soil variation. Here, assessing the association between soil data locally collected across 90 1 ha plots and data from the HWSD, I show that all soil texture metrics and soil fertility represented by total exchangeable bases in the HWSD are completely

uncorrelated with soil properties calculated from locally collected samples (Figure 5.1). Including variables that do not effectively capture local edaphic variation reduces the importance of soil properties and may inflate the effect of biodiversity for promoting ecosystem functioning. Recent studies that showed an effect of biodiversity on aboveground biomass incorporated soil data from digital soil maps (Poorter *et al.* 2015b; Poorter *et al.* 2017). However, considering the limitations of using soil maps to infer local soil properties, these results should be interpreted with caution.



**Figure 5.1** Relationship between soil data collected locally and data from the Harmonized World Soil database (HWSD) across 90 plots: a) Clay content, b) Sand content, c) Silt content and d) Total exchangeable bases.

Recently developed soil grid maps (Hengl *et al.* 2017) improve on the performance of HWSD, and soil properties here are correlated with local soil data (e.g. Sand Kendall's  $\tau = 0.21$   $p=0.04$ ; Silt  $\tau=0.41$   $p<0.001$ ; CEC  $\tau=0.49$   $p<0.001$ ). However, this map does not provide soil data on properties related to fertility (Hengl *et al.* 2014; Hengl *et al.* 2017). For example, CEC extracted from soil grid maps is commonly used as a proxy for soil fertility (e.g. Figueiredo *et al.* 2017; Levis *et al.* 2017), although it represents the level of soil development and quantifies the overall potential of the soil to exchange cations (i.e. calcium, magnesium, potassium, sodium, and aluminium), rather than the amount of nutrients in the soil (Lloyd & Veenendaal 2016). Because CEC includes potentially toxic aluminium, it does not provide an ecologically relevant variable to infer soil fertility in tropical forests. Particularly, in the Neotropics in some highly weathered soils, aluminium can account for up to 99% of the CEC (Quesada *et al.* 2010). Soil variation at small spatial scales, the absence of



relevant soil properties and other issues associated with the use of large scale soil maps, such as georeferencing problems, are discussed in detail elsewhere (Lloyd & Veenendaal 2016; Moulatlet *et al.* 2017).

In short, this thesis provides support for considering the evolutionary dimension of species when making conservation decisions. Each chapter of this thesis provides a distinctive argument for preserving evolutionary diversity in highly diverse tropical forests such as Amazonia.

## **5.5 Final synthesis**

In this thesis, I showed that there is a legacy of evolution on present-day patterns of species turnover across environmental gradients, their respective functional traits and contrasting abilities to process and store carbon. The significant phylogenetic signal for functional traits that represent major axes of plant life-history strategies shows that evolutionary heritage of a lineage can act as a major constraint on the ecological roles that species in the lineage can occupy. Similar levels of phylogenetic signal found across all the four different and correlated traits suggests that the main axes of life-history variation in survival and growth of trees may represent the result of repeated evolution of a suite of coordinated functional characteristics. Analysing the environmental preferences in tropical trees revealed that evolutionarily closely related genera have more similar temperature, precipitation, and edaphic niches than expected by chance. Similar environmental niche preference suggests than under predicted climate change, more phylogenetic diversity may be lost than if environmental preferences were randomly distributed across tree genera. Furthermore, because closely related taxa tend to resemble each other more than expected by chance, I suggest that the evolutionary position of species (i.e. the genus or family to which they belong) can be a useful proxy for the wood density, demographic rates, maximum sizes, climatic and edaphic preferences of tropical trees, overcoming data limitation. This link may be particularly important for incorporating functional diversity in ecosystem modelling to go beyond using a single plant functional type and represent a broader range of vegetation diversity (Swenson *et al.* 2017).

Additionally, investigating the role of historical processes on ecosystem function I showed that Amazonian forest communities that include more evolutionarily distinct lineages and with a higher proportion of rare species, have greater wood productivity. I show that different dimensions of diversity (i.e. taxonomic diversity and evolutionary relationships close to the tips) are more associated with carbon uptake than functional characteristics such as wood density and potential tree size. In essence, these results suggest an additional contribution of unmeasured traits that are significantly related to phylogeny and highlight the importance of phylogeny as a proxy for functional characteristics in hyperdiverse systems where measuring a number of traits remains challenging. The results I presented here advance our understanding of the role evolutionary processes in shaping modern patterns of diversity and ecosystem function and show the need to consider the different dimensions of diversity when prioritizing conservation efforts in tropical forests.

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## Appendices

### Appendix 1 List of plots encompassing the Floristic tree inventories data

List of plots encompassing the Floristic tree inventories for 792 plots compiled from RAINFOR database, with their respective coordinates in Latitude (Lat.) and Longitude (Long.), area in hectare, chapters in which plots were used and data contributors. Chapter in which plots were used are assigned.

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
ACL-01	Venezuela	8.75	-71.5	1			X	Oliver Phillips
ACU-01	Bolivia	-15.25	-61.25	1			X	Jon Lloyd; Luzmila Arroyo, Oliver Phillips, Ted Feldpausch
ACU-02	Bolivia	-15.25	-61.24	1			X	Luzmila Arroyo; Timothy Killeen; Ted Feldpausch
AGJ-01	Peru	-11.89	-71.36	2	X		X	John Terborgh
AGP-01	Colombia	-3.72	-70.31	1	X	X	X	Oliver Phillips; Agustin Rudas; Alvaro Cogollo; Esteban Alvarez; Adriana Prieto;
AGP-02	Colombia	-3.72	-70.3	1	X	X	X	Oliver Phillips; Agustin Rudas; Alvaro Cogollo; Esteban Alvarez; Adriana Prieto;
ALC-01	Brasil	-2.53	-54.91	1			X	Jon Lloyd; Ted Feldpausch
ALC-02	Brasil	-2.49	-54.96	1			X	Jon Lloyd; Ted Feldpausch
ALF-01	Brasil	-9.6	-55.94	1	X	X	X	Ted Feldpausch; Beatriz Marimon; Ben Hur Marimon; Jon Lloyd
ALF-02	Brasil	-9.58	-55.92	1	X	X	X	Ted Feldpausch; Beatriz Marimon; Ben Hur Marimon; Jon Lloyd
ALM-01	Peru	-11.8	-71.47	2	X		X	John Terborgh; Roel Brienens; Nigel Pitman; Fernando Cornejo Abel Monteagudo; Tim Baker; Oliver Phillips; Roel Brienens; Yadvinder Malhi;
ALP-01	Peru	-3.95	-73.43	1	X	X	X	Rodolfo Vasquez
ALP-02	Peru	-3.95	-73.44	1	X	X	X	Abel Monteagudo; Tim Baker; Oliver Phillips ;Roel Brienens
ALP-05	Peru	-3.96	-73.44	0.1	X		X	Oliver Phillips
ALP-06	Peru	-3.95	-73.44	0.1	X		X	Oliver Phillips

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
ALP-10	Peru	-3.95	-73.41	0.1	X		X	Oliver Phillips; Tim Baker; Roel Brien; Rodolfo Vasquez; Abel Monteagudo
ALP-16	Peru	-3.94	-73.43	0.1	X		X	Oliver Phillips; Tim Baker; Roel Brien; Rodolfo Vasquez; Abel Monteagudo
ALP-17	Peru	-3.94	-73.43	0.1	X		X	Oliver Phillips; Tim Baker; Roel Brien; Rodolfo Vasquez; Abel Monteagudo
ALP-18	Peru	-3.95	-73.43	0.1	X		X	Oliver Phillips; Tim Baker; Roel Brien; Rodolfo Vasquez; Abel Monteagudo
ALP-19	Peru	-3.96	-73.44	0.1	X		X	Oliver Phillips; Tim Baker; Roel Brien; Rodolfo Vasquez; Abel Monteagudo
ALP-20	Peru	-3.96	-73.43	0.1	X		X	Oliver Phillips; Tim Baker; Roel Brien; Rodolfo Vasquez; Abel Monteagudo
ALP-23	Peru	-3.95	-73.42	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
ALP-24	Peru	-3.96	-73.43	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
ALP-25	Peru	-3.95	-73.44	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
ALP-26	Peru	-3.95	-73.41	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
ALP-27	Peru	-3.95	-73.44	0.1			X	Oliver Phillips; Rodolfo Vasquez Martinez
ALP-30	Peru	-3.95	-73.43	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brien; Rodolfo Vasquez; Abel Monteagudo
ALP-40	Peru	-3.94	-73.44	1	X		X	Oliver Phillips; Roel Brien;; Abel Monteagudo; Freddy Ramirez
ALV-01	Bolivia	-16.12	-61.89	1			X	Alejandro Araujo-Murakam
ALV-02	Bolivia	-16.08	-61.89	1			X	Alejandro Araujo-Murakam
AMA-02	Colombia	5.58	-77.5	1	X		X	Esteban Álvarez Dávila; Oliver Phillips
AMD-01	Brasil	-1.83	-46.75	1	X		X	Ima Vieira
AMD-02	Brasil	-1.83	-46.75	1	X		X	Ima Vieira
AMI-01	Bolivia	-13.58	-68.76	0.1	X		X	Alwyn Gentry; Percy Núñez Vargas
AMI-02	Bolivia	-13.58	-68.76	0.1	X		X	Alwyn Gentry
AMO-01	Peru	-4.17	-80.58	0.1			X	Alwyn Gentry
AMR-01	Colombia	10.96	-73.98	0.1			X	Alwyn Gentry
ANC-01	Colombia	3.77	-76.87	0.1	X		X	Alwyn Gentry
ANT-01	Colombia	7.26	-75.94	0.1			X	Alwyn Gentry
ARA-01	Brasil	-4.82	-52.52	1			X	William Balee; David G Campbell
ARC-01	Colombia	-0.6	-72.17	6			X	Esteban Álvarez Dávila; Oliver Phillips
ARC-10	Colombia	-0.41	-72.33	0.1	X		X	Alwyn Gentry
ARC-11	Colombia	-0.41	-72.31	0.04	X		X	Alwyn Gentry



Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
ASA-01	Colombia	7.16	-75.9	0.1			X	Alwyn Gentry
ASR-01	Brasil	-4.76	-52.6	1			X	William Balee; David G Campbell
BAC-01	Venezuela	7.46	-71.01	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama ; Geertje van der Heijden; Oliver Phillips
BAC-02	Venezuela	7.46	-71.01	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama ; Geertje van der Heijden; Oliver Phillips
BAC-03	Venezuela	7.46	-71.01	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama ; Geertje van der Heijden; Oliver Phillips
BAC-04	Venezuela	7.46	-71.01	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama ; Geertje van der Heijden; Oliver Phillips
BAC-05	Venezuela	7.47	-71.02	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama ; Geertje van der Heijden; Oliver Phillips
BAC-06	Venezuela	7.47	-71.02	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama ; Geertje van der Heijden; Oliver Phillips
BAR-01	Peru	-11.9	-71.42	1	X		X	Abel Monteagudo; John Terborgh; Oliver Phillips; Percy Núñez Vargas
BBC-01	Bolivia	-14.3	-60.53	1			X	Luzmila Arroyo; Timothy Killeen
BBC-02	Bolivia	-14.3	-60.53	1			X	Luzmila Arroyo; Timothy Killeen
BBS-01	Suriname	4.93	-55.22	1	X		X	Hans ter Steege
BBS-02	Suriname	4.93	-55.19	1	X		X	Hans ter Steege
BBS-03	Suriname	4.95	-55.19	1	X		X	Hans ter Steege
BBS-04	Suriname	4.97	-55.18	1	X		X	Hans ter Steege
BBS-05	Suriname	4.99	-55.2	1	X		X	Hans ter Steege
BBS-06	Suriname	4.94	-55.18	1	X		X	Hans ter Steege
BBS-07	Suriname	4.92	-55.13	1	X		X	Hans ter Steege
BBS-08	Suriname	4.93	-55.14	1	X		X	Hans ter Steege
BBS-09	Suriname	4.95	-55.19	1	X		X	Hans ter Steege
BCA-01	Colombia	3.97	-77.07	0.1	X		X	Emilio Vilanova
BCU-01	Colombia	11.14	-73.47	0.1	X		X	Emilio Vilanova
BDF-01	Brasil	-2.34	-60.1	2	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-03	Brasil	-2.42	-59.85	1	X	X	X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-04	Brasil	-2.43	-59.85	1	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
BDF-05	Brasil	-2.43	-59.85	1	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-06	Brasil	-2.41	-59.86	3	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-07	Brasil	-2.4	-59.9	1	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-08	Brasil	-2.4	-59.9	1	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-09	Brasil	-2.4	-59.85	1	X	X	X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-10	Brasil	-2.39	-59.86	2	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-11	Brasil	-2.38	-59.85	3	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-12	Brasil	-2.39	-59.85	2	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-13	Brasil	-2.4	-59.91	9	X	X	X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BDF-14	Brasil	-2.36	-59.97	1	X		X	William Laurence; Susan Laurance; Ana Andrade; Jose Camargo, Thomas Lovejoy
BEE-01	Bolivia	-16.53	-64.58	1	X		X	Luzmila Arroyo; Alejandro Murakami-Araujo; Oliver Phillips
BEE-05	Bolivia	-16.53	-64.58	1	X		X	Luzmila Arroyo; Alejandro Murakami-Araujo; Oliver Phillips
BES-01	Colombia	10.53	-73.29	1			X	Esteban Álvarez Dávila; Oliver Phillips
BET-01	Colombia	6.92	-73.3	1.035			X	Esteban Álvarez Dávila; Oliver Phillips
BET-02	Colombia	6.92	-73.3	1.035			X	Esteban Álvarez Dávila; Oliver Phillips
BLS-01	Ecuador	0.61	-79.86	0.1	X		X	Alwyn Gentry
BNT-01	Brasil	-2.64	-60.16	1	X	X	X	Niro Higuchi
BNT-02	Brasil	-2.64	-60.15	1	X	X	X	Niro Higuchi
BNT-04	Brasil	-2.63	-60.15	1	X	X	X	Niro Higuchi
BNT-05	Brasil	-2.63	-60.17	1	X		X	Niro Higuchi
BNT-06	Brasil	-2.63	-60.17	1	X		X	Niro Higuchi
BNT-07	Brasil	-2.63	-60.17	1	X		X	Niro Higuchi
BOG-01	Ecuador	-0.7	-76.48	1	X	X	X	Abel Monteagudo; Roel Brienen; Tony DiFiore; Nigel Pitman; Oliver Phillips
BOG-02	Ecuador	-0.7	-76.47	1	X	X	X	Abel Monteagudo; Roel Brienen; Tony DiFiore; Nigel Pitman; Oliver Phillips
BRP-01	Venezuela	2.83	-65.9	0.1	X		X	Gerardo Aymard
BST-01	Peru	-12.38	-72.41	0.5			X	Kyle G. Dexter
BST-02	Peru	-12.48	-72.32	0.5			X	Kyle G. Dexter
BVA-01	Peru	-4.24	-73.2	0.5	X		X	Eurídice Honorio; Tim Baker

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
CAB-01	Bolivia	-14.98	-68.48	0.05			X	Alwyn Gentry
CAC-01	Ecuador	-3.45	-78.36	0.06			X	Alwyn Gentry
CAE-01	Ecuador	-2	-79.96	0.1			X	Alwyn Gentry
CAG-01	Peru	-12.04	-69.11	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-02	Peru	-12.04	-69.1	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-03	Peru	-12.03	-69.1	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-04	Peru	-12.03	-69.1	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-05	Peru	-12.11	-69.14	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-06	Peru	-12.1	-69.18	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-07	Peru	-12.17	-69.14	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-08	Peru	-12.18	-69.13	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-09	Peru	-12.13	-69.11	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-10	Peru	-12.17	-69.05	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAG-11	Peru	-12.18	-69.05	0.1	X		X	Abel Monteagudo; Oliver Phillips; Fernando Valverde
CAI-01	Venezuela	8.7	-70.07	0.25	X		X	Emilio Vilanova; Geertje van der Heijden; Oliver Phillips
CAI-02	Venezuela	8.7	-70.07	0.25	X		X	Emilio Vilanova; Oliver Phillips
CAI-03	Venezuela	8.7	-70.07	0.25			X	Emilio Vilanova; Hirma Ramírez-Angulo
CAI-04	Venezuela	8.7	-70.07	0.25	X		X	Emilio Vilanova; Geertje van der Heijden; Oliver Phillips
CAI-05	Venezuela	8.72	-70.08	0.25			X	Emilio Vilanova; Hirma Ramírez-Angulo
CAI-06	Venezuela	8.72	-70.08	0.25			X	Emilio Vilanova; Hirma Ramírez-Angulo
CAL-01	Peru	-12.8	-71.78	1			X	William Farfan
CAL-02	Peru	-12.81	-71.78	1			X	William Farfan
CAR-01	Brasil	-5.58	-49.72	1			X	Rafael Salomão
CAS-01	Venezuela	2.03	-66.47	1	X		X	Gerardo Aymard
CAS-02	Venezuela	2.32	-66.48	1	X		X	Gerardo Aymard
CAS-03	Venezuela	1.92	-66.62	1	X		X	Gerardo Aymard
CAT-02	Venezuela	8.44	-71.77	0.252	X		X	Jean-Pierre Veillon
CAT-03	Venezuela	8.44	-71.77	0.252	X		X	Jean-Pierre Veillon

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
CAX-01	Brasil	-1.74	-51.46	1	X	X	X	Antonio Lola da Costa da Costa
CAX-02	Brasil	-1.74	-51.46	1	X	X	X	Antonio Lola da Costa
CAX-06	Brasil	-1.72	-51.46	1	X	X	X	Antonio Lola da Costa; Luis Aragao
CAX-08	Brasil	-1.85	-51.47	1	X		X	Antonio Lola da Costa
CAY-01	Peru	-4.66	-79.55	0.1			X	Alwyn Gentry
CBC-01	Venezuela	2.35	-66.55	0.1	X		X	Gerardo Aymard
CBN-01	Venezuela	8.58	-71.42	0.259			X	Jean-Pierre Veillon; Ali D'Jesus; Oliver Phillips
CBN-02	Venezuela	8.58	-71.42	0.259			X	Jean-Pierre Veillon; Ali D'Jesus; Oliver Phillips
CBN-03	Venezuela	8.58	-71.42	0.259			X	Jean-Pierre Veillon; Ali D'Jesus; Oliver Phillips
CBN-04	Venezuela	8.58	-71.42	0.259			X	Jean-Pierre Veillon; Ali D'Jesus; Oliver Phillips
CBN-05	Venezuela	8.58	-71.42	0.259			X	Jean-Pierre Veillon; Ali D'Jesus; Oliver Phillips
CBN-06	Venezuela	8.58	-71.42	0.259			X	Jean-Pierre Veillon; Ali D'Jesus; Oliver Phillips
CBO-10	Venezuela	1.95	-66.98	0.1	X		X	Gerardo Aymard
CBP-01	Peru	-12.39	-69.31	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBP-02	Peru	-12.4	-69.33	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBP-03	Peru	-12.42	-69.28	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBP-04	Peru	-12.41	-69.32	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBP-05	Peru	-12.39	-69.31	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBP-06	Peru	-12.43	-69.28	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBP-07	Peru	-12.42	-69.33	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBP-08	Peru	-12.43	-69.29	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBP-09	Peru	-12.43	-69.29	0.1	X		X	Oliver Phillips; Percy Núñez Vargas
CBR-01	Guyana	4.95	-58.36	1			X	Hans ter Steege
CBR-02	Guyana	4.95	-58.35	1			X	Hans ter Steege
CBR-03	Guyana	4.95	-58.37	1			X	Hans ter Steege
CBR-04	Guyana	4.92	-58.35	1			X	Hans ter Steege
CDK-01	Venezuela	2.92	-66.63	0.1	X		X	Gerardo Aymard
CDM-01	Peru	-10.33	-75.3	1	X		X	Alwyn Gentry

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
CDM-02	Peru	-10.24	-75.21	0.1	X		X	Alwyn Gentry
CDT-01	Venezuela	2.8	-65.95	0.1	X		X	Gerardo Aymard
CED-01	Colombia	4.74	-75.55	0.1			X	Alwyn Gentry
CEN-01	Ecuador	-0.66	-79.29	0.1			X	Alwyn Gentry
CES-01	Colombia	10.38	-72.92	0.1			X	Alwyn Gentry
CHB-01	Peru	-6.16	-78.75	0.04			X	Alwyn Gentry
CHI-01	Peru	-5.25	-78.96	0.1			X	Alwyn Gentry
CHO-01	Bolivia	-14.39	-61.15	1	X		X	Luzmila Arroyo; Timothy Killeen
CHO-02	Bolivia	-14.34	-61.16	1			X	Luzmila Arroyo; Timothy Killeen
CHQ-01	Bolivia	-14.56	-68.46	0.1			X	Alwyn Gentry
CJC-04	Peru	-12.67	-69.11	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CJC-05	Peru	-12.66	-69.08	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CJC-06	Peru	-12.64	-69.1	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CJC-07	Peru	-12.68	-69.11	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CJC-08	Peru	-12.69	-69.12	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CJC-09	Peru	-12.68	-69.18	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CJC-10	Peru	-12.68	-69.18	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLA-03	Venezuela	10.01	-65.32	0.259			X	Emilio Vilanova
CLA-04	Venezuela	10.01	-65.32	0.252			X	Emilio Vilanova
CLO-01	Colombia	9.53	-75.35	0.1	X		X	Alwyn Gentry
CLS-01	Peru	-12.6	-69.02	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLS-02	Peru	-12.6	-69.01	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLS-03	Peru	-12.61	-69.02	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLT-01	Peru	-12.82	-69.35	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLT-02	Peru	-12.8	-69.34	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLT-03	Peru	-12.84	-69.29	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLT-04	Peru	-12.83	-69.27	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLT-05	Peru	-12.82	-69.35	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
CLT-06	Peru	-12.88	-69.28	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLT-07	Peru	-12.85	-69.29	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLT-08	Peru	-12.83	-69.26	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLT-09	Peru	-12.82	-69.3	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CLV-01	Peru	-12.4	-68.82	0.1	X		X	Abel Monteagudo; Oliver Phillips
CLV-02	Peru	-12.39	-68.79	0.1	X		X	Abel Monteagudo; Oliver Phillips
CLV-03	Peru	-12.41	-68.86	0.1	X		X	Abel Monteagudo; Oliver Phillips
CLV-04	Peru	-12.36	-68.8	0.1	X		X	Abel Monteagudo; Oliver Phillips
CLV-05	Peru	-12.43	-68.8	0.1	X		X	Abel Monteagudo; Oliver Phillips
CLV-06	Peru	-12.46	-68.81	0.1	X		X	Abel Monteagudo; Oliver Phillips
CLV-07	Peru	-12.47	-68.8	0.1	X		X	Abel Monteagudo; Oliver Phillips
CLV-08	Peru	-12.45	-68.81	0.1	X		X	Abel Monteagudo; Oliver Phillips
CNG-01	Venezuela	0.83	-66.17	1	X		X	Alwyn Gentry
CNS-01	Peru	-12.56	-68.71	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-02	Peru	-12.56	-68.7	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-03	Peru	-12.56	-68.72	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-04	Peru	-12.59	-68.73	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-05	Peru	-12.6	-68.72	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-06	Peru	-12.61	-68.73	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-07	Peru	-12.6	-68.75	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-08	Peru	-12.59	-68.71	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-09	Peru	-12.63	-68.75	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNS-10	Peru	-12.65	-68.74	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CNT-01	Peru	-12.5	-69.42	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
CNT-02	Peru	-12.49	-69.41	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
CNT-03	Peru	-12.49	-69.41	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
CNT-04	Peru	-12.54	-69.39	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
CNT-05	Peru	-12.5	-69.37	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
CNT-06	Peru	-12.48	-69.39	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
CNT-07	Peru	-12.53	-69.48	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
CNT-08	Peru	-12.53	-69.48	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
CNT-09	Peru	-12.53	-69.48	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
CNT-10	Peru	-12.53	-69.48	0.1	X		X	Abel Monteagudo; Fernando Cornejo; Oliver Phillips; Percy Núñez Vargas
COL-01	Venezuela	2.1	-67.1	0.1	X		X	Gerardo Aymard
CON-01	Peru	-4.12	-72.92	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
CON-02	Peru	-4.12	-72.93	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
CON-03	Peru	-4.12	-72.92	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
CON-11	Peru	-4.25	-72.75	0.1	X		X	Alwyn Gentry
CON-12	Peru	-4.16	-72.96	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
CON-13	Peru	-4.15	-72.96	0.1	X		X	Oliver Phillips; Rodolfo Vasquez
CPA-01	Peru	-12.47	-69.21	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPA-02	Peru	-12.48	-69.2	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPA-03	Peru	-12.47	-69.23	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPA-04	Peru	-12.48	-69.21	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPA-05	Peru	-12.45	-69.2	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPA-06	Peru	-12.46	-69.2	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPA-07	Peru	-12.48	-69.22	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPA-08	Peru	-12.5	-69.22	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPA-09	Peru	-12.48	-69.2	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPN-01	Colombia	4.56	-73.67	0.1			X	Alwyn Gentry
CPN-02	Colombia	4.58	-73.66	0.1			X	Alwyn Gentry
CPO-01	Colombia	11.13	-74.01	0.1			X	Alwyn Gentry
CPP-01	Brasil	-1.84	-47.1	1	X	X	X	Ima Vieira
CPP-02	Brasil	-1.84	-47.1	1	X		X	Ima Vieira
CPR-01	Peru	-12.51	-68.75	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-02	Peru	-12.52	-68.73	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
CPR-03	Peru	-12.5	-68.78	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-04	Peru	-12.5	-68.75	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-05	Peru	-12.55	-68.77	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-06	Peru	-12.49	-68.76	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-07	Peru	-12.5	-68.78	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-08	Peru	-12.52	-68.75	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-09	Peru	-12.53	-68.76	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-10	Peru	-12.53	-68.72	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPR-11	Peru	-12.48	-68.76	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
CPZ-01	Venezuela	2.03	-67.07	0.1	X		X	Gerardo Aymard
CRG-01	Brasil	-5.9	-50.13	1			X	Manoela FF Da Silva; Oliver Phillips
CRP-01	Bolivia	-14.54	-61.5	1	X		X	Abel Monteagudo; Roel Brienen; Alejandro Murakami-Araujo; Luzmila Arroyo; Timothy Killeen
CRP-02	Bolivia	-14.54	-61.5	1	X		X	Abel Monteagudo; Roel Brienen; Alejandro Murakami-Araujo; Luzmila Arroyo; Timothy Killeen
CRZ-01	Venezuela	8.83	-71.86	1	X		X	Jean-Pierre Veillon; Oliver Phillips
CSM-01	Venezuela	2.58	-67.12	1	X		X	Gerardo Aymard
CUA-01	Ecuador	-3.48	-78.23	0.1			X	Alwyn Gentry
CUT-01	Peru	-6.19	-78.67	0.1			X	Alwyn Gentry
CUV-01	Colombia	6.77	-76.22	0.1			X	Alwyn Gentry
CUY-01	Peru	-4.53	-79.73	0.1			X	Alwyn Gentry
CUZ-01	Peru	-12.54	-69.06	1	X	X	X	Abel Monteagudo; Oliver Phillips; Rodolfo Vasquez
CUZ-02	Peru	-12.54	-69.06	1	X	X	X	Abel Monteagudo; Oliver Phillips; Rodolfo Vasquez
CUZ-03	Peru	-12.53	-69.05	1	X	X	X	Abel Monteagudo; Oliver Phillips; Rodolfo Vasquez
CUZ-04	Peru	-12.54	-69.05	1	X	X	X	Abel Monteagudo; Oliver Phillips; Rodolfo Vasquez
CUZ-10	Peru	-12.58	-69.15	0.1	X		X	Alwyn Gentry; Percy Núñez Vargas
CYU-01	Bolivia	-18.76	-62.23	0.1			X	Alwyn Gentry
CYU-02	Bolivia	-18.76	-62.3	0.1			X	Alwyn Gentry
DIV-01	Colombia	7.05	-73.02	1.103			X	Irina Mendoza Polo; Esteban Álvarez Dávila; Oliver Phillips



Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
DOI-01	Brasil	-10.57	-68.32	1	X	X	X	Ted Feldpausch; Marcos Silveira; Tim Baker; Juliana Stropp; Wenderson Castro
DOI-02	Brasil	-10.55	-68.31	1	X	X	X	Ted Feldpausch; Marcos Silveira; Tim Baker; Juliana Stropp; Wenderson Castro
DUR-01	Ecuador	0.25	-76.75	0.04	X		X	Alwyn Gentry
EBB-01	Bolivia	-14.78	-66.34	1	X		X	Gerardo Aymard; James Comiskey
EBB-02	Bolivia	-14.77	-66.35	1	X		X	Gerardo Aymard; James Comiskey
EBB-03	Bolivia	-14.84	-66.34	1.002	X		X	Gerardo Aymard; James Comiskey
EBB-04	Bolivia	-14.87	-66.33	1			X	Jim Comiskey; Rachel Graham
EBB-05	Bolivia	-14.76	-66.34	1	X		X	Gerardo Aymard; James Comiskey
EBB-06	Bolivia	-14.87	-66.33	1			X	Jim Comiskey; Rachel Graham
EBB-07	Bolivia	-14.86	-66.32	1.002	X		X	Gerardo Aymard; James Comiskey
EBB-08	Bolivia	-14.85	-66.34	1.002	X		X	Gerardo Aymard; James Comiskey
EBB-09	Bolivia	-14.73	-66.32	1	X		X	Gerardo Aymard; James Comiskey
EBB-10	Bolivia	-14.89	-66.59	1	X		X	Gerardo Aymard; James Comiskey
EBB-11	Bolivia	-14.85	-66.36	1	X		X	Gerardo Aymard; James Comiskey
EBB-12	Bolivia	-14.64	-66.06	1	X		X	Gerardo Aymard; James Comiskey
EBB-13	Bolivia	-14.74	-66.27	1	X		X	Gerardo Aymard; James Comiskey
EBB-14	Bolivia	-14.74	-66.56	1	X		X	Gerardo Aymard; James Comiskey
ECE-01	Colombia	10.68	-75.27	1			X	Irina Mendoza Polo; Esteban Álvarez Dávila; Oliver Phillips
ECE-02	Colombia	10.68	-75.26	1			X	Irina Mendoza Polo; Esteban Álvarez Dávila; Oliver Phillips
ECM-06	Venezuela	8.67	-71.42	0.25			X	Jean-Pierre Veillon; Oliver Phillips
ELC-01	Ecuador	0.58	-77.72	0.1			X	Alwyn Gentry
ELD-01	Venezuela	6.11	-61.41	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama; Geertje van der Heijden; Oliver Phillips
ELD-02	Venezuela	6.11	-61.41	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama; Geertje van der Heijden; Oliver Phillips
ELD-03	Venezuela	6.09	-61.4	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama; Geertje van der Heijden; Oliver Phillips
ELD-04	Venezuela	6.09	-61.35	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama; Geertje van der Heijden; Oliver Phillips
ELM-01	Colombia	5.57	-77.51	1	X		X	Gloria Galeano

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
EMC-01	Venezuela	8.01	-70.55	1	X		X	Emilio Vilanova
EMC-02	Venezuela	8.01	-70.55	1	X		X	Emilio Vilanova
EMC-03	Venezuela	8.01	-70.55	1	X		X	Emilio Vilanova
EME-01	Ecuador	0.94	-79.66	0.1			X	Alwyn Gentry
ENT-01	Bolivia	-14.63	-60.7	0.1	X		X	Alwyn Gentry
EPA-01	Peru	-6.47	-79.04	0.06			X	Alwyn Gentry
ESM-05	Venezuela	8.68	-71.43	0.25			X	Alwyn Gentry
ESP-01	Peru	-13.18	-71.59	1			X	William Farfan
FAR-01	Colombia	3.5	-76.58	0.1			X	Alwyn Gentry
FEC-01	Brasil	-10.07	-67.62	1	X	X	X	Foster Brown; Marcos Silveira; Oliver Phillips, Plínio Barbosa Camargo; Simone Aparecida Vieira, Ted Feldpausch, Wendeson Castro
FIM-01	Colombia	2.26	-76.2	0.1			X	Alwyn Gentry
FIZ-01	Colombia	3.53	-76.58	0.06			X	Alwyn Gentry
FLO-01	Brasil	-12.81	-51.85	1	X		X	Beatriz Marimon, Ben Hur Marimon Junior; Edmar de Oliveira; Leandro Maracahipes; Ted Feldpausch
FLO-02	Brasil	-12.75	-51.88	1	X		X	Beatriz Marimon, Ben Hur Marimon Junior; Edmar de Oliveira; Leandro Maracahipes; Ted Feldpausch
FMH-01	Guyana	5.17	-58.69	1	X	X	X	Ted Feldpausch; Hans ter Steege; Eric Arets
FMH-02	Guyana	5.17	-58.69	1	X	X	X	Hans ter Steege; James Singh; Roderick Zagt; Oliver Phillips; Roel Brienen; Ted Feldpausch
FMH-03	Guyana	5.18	-58.7	1	X		X	Hans ter Steege; James Singh; Roderick Zagt; Oliver Phillips; Roel Brienen; Ted Feldpausch
FOB-01	Bolivia	-13.57	-61.02	1	X		X	Luzmila Arroyo; Timothy Killeen
FRP-01	Brasil	-11.48	-51.52	1			X	Beatriz Marimon; Ben Hur Marimon Junior
FRP-02	Brasil	-11.24	-51.69	1			X	Beatriz Marimon; Ben Hur Marimon Junior
FZA-01	Ecuador	-3.98	-79.07	1.035			X	David Neill
GAB-01	Venezuela	1.7	-66.98	0.1	X		X	Gerardo Aymard
GAL-01	Venezuela	5.8	-67.33	0.1	X		X	Gerardo Aymard
GAZ-01	Colombia	10.8	-75.25	0.1			X	Alwyn Gentry
GEN-01	Peru	-11.06	-75.4	0.1			X	Alwyn Gentry
GEN-02	Peru	-11.13	-75.37	1			X	Dante Anton; Carlos Reynel

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
GEN-03	Peru	-11.1	-75.34	0.6			X	Sonia Palacios R
GEN-05	Peru	-11.1	-75.35	1			X	Dante Anton; Carlos Reynel
GEN-06	Peru	-11.1	-75.34	1			X	Carlos Vargas; Carlos Reynel
GMT-01	Brasil	-1.11	-47.8	1	X		X	Tim Baker
GUR-05	Venezuela	7.5	-63	0.252			X	Jean-Pierre Veillon
GUR-06	Venezuela	7.5	-63	0.252			X	Jean-Pierre Veillon
HBO-01	Venezuela	8.71	-71.45	0.252			X	Jean-Pierre Veillon
HCC-11	Bolivia	-13.91	-60.82	1			X	Luzmila Arroyo; Timothy Killeen
HCC-12	Bolivia	-13.91	-60.82	1			X	Luzmila Arroyo; Timothy Killeen
HCC-21	Bolivia	-14.53	-60.74	1			X	Alejandro Araujo-Murakami; Jon Lloyd; Luzmila Arroyo; Timothy Killeen; Roel Brien
HCC-22	Bolivia	-14.53	-60.73	1			X	Alejandro Araujo-Murakami; Jon Lloyd; Luzmila Arroyo; Timothy Killeen; Roel Brien
HCC-23	Bolivia	-14.56	-60.75	1			X	Alejandro Araujo-Murakami; Luzmila Arroyo; Timothy Killeen; Roel Brien
HCC-24	Bolivia	-14.57	-60.75	1			X	Alejandro Araujo-Murakami; Luzmila Arroyo; Timothy Killeen; Roel Brien
HCU-01	Venezuela	8.36	-71.69	0.252			X	Jean-Pierre Veillon
HEA-01	Peru	-12.83	-68.83	0.1	X		X	Alwyn Gentry
HHI-01	Colombia	3.63	-76.55	0.04			X	Alwyn Gentry
HSP-01	Venezuela	8.5	-69	1	X		X	Jean-Pierre Veillon
HUA-01	Ecuador	-0.67	-77.54	0.1			X	Alwyn Gentry
HUM-01	Peru	-8.83	-75	0.1	X		X	Alwyn Gentry; Kenneth Young
IBG-01	Brasil	-15.95	-47.87	1			X	Jon Lloyd; Oliver Phillips
IBG-02	Brasil	-15.95	-47.87	1			X	Jon Lloyd; Oliver Phillips
IBG-03	Brasil	-15.93	-47.87	1			X	Jon Lloyd; Oliver Phillips
IBG-04	Brasil	-15.94	-47.86	1			X	Jon Lloyd; Oliver Phillips
ICA-01	Brasil	1.55	-68.68	1			X	Juliana Stropp
ICH-01	Bolivia	-15.91	-67.58	0.1			X	Alwyn Gentry
IMA-01	Venezuela	7.44	-61.17	1	X		X	Gerardo Aymard; Oliver Phillips
IMA-02	Venezuela	7.45	-61.17	1	X		X	Gerardo Aymard; Oliver Phillips

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
IMA-03	Venezuela	7.62	-61.25	1			X	Gerardo A. Aymard C
IMA-04	Venezuela	7.62	-61.25	1			X	Gerardo A. Aymard C
IND-01	Peru	-3.52	-72.85	1	X		X	John Pipoly; Rodolfo Vasquez
IND-10	Peru	-3.51	-73.06	0.1	X		X	Alwyn Gentry
INF-01	Peru	-12.73	-69.7	1.3	X		X	Miguel Alexiades; Oliver Phillips
IPR-01	Colombia	13.35	-81.36	0.1	X			Alwyn Gentry
ISR-01	Colombia	9.92	-75.81	1	X			Esteban Álvarez Dávila
IVC-01	Venezuela	1.92	-67.03	0.1	X		X	Gerardo Aymard
IVC-02	Venezuela	1.92	-67.03	0.1	X		X	Gerardo Aymard
IVC-03	Venezuela	1.92	-67.03	0.1	X		X	Gerardo Aymard
IWO-03	Guyana	4.53	-58.78	1	X		X	Anand Roopsind; Oliver Phillips; Raquel Thomas
IWO-09	Guyana	4.61	-58.73	1	X		X	Anand Roopsind; Oliver Phillips; Raquel Thomas
IWO-11	Guyana	4.62	-58.72	1	X		X	Anand Roopsind; Oliver Phillips; Raquel Thomas
IWO-12	Guyana	4.73	-58.72	1	X		X	Anand Roopsind; Oliver Phillips; Raquel Thomas
IWO-21	Guyana	4.63	-58.74	1	X		X	Anand Roopsind; Oliver Phillips; Raquel Thomas; Roel Brien; Ted Feldpausch
IWO-22	Guyana	4.62	-58.72	1	X	X	X	Anand Roopsind; Oliver Phillips; Raquel Thomas; Roel Brien; Ted Feldpausch
JAC-01	Brasil	-2.61	-60.21	5	X	X	X	Niro Higuchi
JAC-02	Brasil	-2.62	-60.2	5	X	X	X	Niro Higuchi
JAM-01	Brasil	-4.67	-66.17	4	X		X	Antonio S. Lima
JAS-02	Ecuador	-1.07	-77.62	1	X	X	X	Roel Brien; David Neill
JAS-03	Ecuador	-1.08	-77.61	1	X	X	X	Roel Brien; David Neill
JAS-04	Ecuador	-1.07	-77.61	1	X	X	X	Roel Brien; David Neill
JAS-05	Ecuador	-1.06	-77.62	1	X		X	David Neill
JAS-10	Ecuador	-1.06	-77.6	0.1	X		X	Alwyn Gentry; David Neill
JAU-01	Ecuador	-1.1	-79.63	0.1	X		X	Alwyn Gentry; David Neill
JBU-01	Brasil	-1.14	-47.7	1	X		X	Ima Vieira
JEN-01	Peru	-4.91	-73.75	0.1	X		X	Rodolfo Vasquez
JEN-11	Peru	-4.88	-73.63	1	X	X	X	Euridice Honorio

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
JEN-12	Peru	-4.9	-73.63	1	X		X	Euridice Honorio
JEN-13	Peru	-4.92	-73.54	1	X	X	X	Euridice Honorio
JEN-14	Peru	-4.84	-73.83	0.5	X		X	Euridice Honorio
JEN-15	Peru	-4.84	-73.65	0.5	X		X	Euridice Honorio
JFR-01	Brasil	-10.48	-58.47	0.93	X		X	Ted Feldpausch
JFR-02	Brasil	-10.55	-58.49	0.525	X		X	Ted Feldpausch
JFR-03	Brasil	-10.48	-58.52	1.025	X		X	Ted Feldpausch
JFR-04	Brasil	-10.48	-58.48	1	X		X	Ted Feldpausch
JFR-05	Brasil	-10.48	-58.48	1	X		X	Ted Feldpausch
JFR-06	Brasil	-10.47	-58.49	1	X		X	Ted Feldpausch
JFR-07	Brasil	-10.48	-58.5	1.025	X		X	Ted Feldpausch
JFR-08	Brasil	-10.47	-58.5	1	X		X	Ted Feldpausch
JFR-09	Brasil	-10.47	-58.51	0.975	X		X	Ted Feldpausch
JRI-01	Brasil	-0.89	-52.19	1	X	X	X	Natalino Silva
JUY-01	Ecuador	-2.13	-76.2	1	X		X	Kenneth Young; Ophelia Wang
KAL-01	Colombia	11.24	-74.14	1			X	Irina Mendoza Polo; Esteban Álvarez Dávila; Oliver Phillips
KEN-01	Bolivia	-16.02	-62.73	1			X	Yadvinder Malhi; Alejandro Araujo-Murakam
KEN-02	Bolivia	-16.01	-62.74	1			X	Yadvinder Malhi; Alejandro Araujo-Murakam; Ted Feldpausch
KND-01	Colombia	11.11	-74.03	0.1			X	Alwyn Gentry
LAS-01	Peru	-12.55	-70.11	2	X		X	Fernando Valverde; Nigel Pitman
LAS-02	Peru	-12.57	-70.09	1	X		X	Fernando Valverde; Nigel Pitman
LAS-03	Peru	-12.53	-70.08	2	X		X	Fernando Valverde; Nigel Pitman
LCA-13	Bolivia	-15.68	-62.78	1			X	Todd Fredericksen, Marielos Pena-Claros, Marisol Toledo
LCA-16	Bolivia	-15.68	-62.78	1			X	Todd Fredericksen, Marielos Pena-Claros, Marisol Toledo
LCA-29	Bolivia	-15.68	-62.77	1			X	Todd Fredericksen, Marielos Pena-Claros, Marisol Toledo
LCA-30	Bolivia	-15.68	-62.77	1			X	Todd Fredericksen, Marielos Pena-Claros, Marisol Toledo
LCL-01	Colombia	9.96	-75.16	0.1	X		X	Alwyn Gentry
LFA-01	Brasil	-5.85	-50.48	1			X	Manoela FF Da Silva

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
LFB-01	Bolivia	-14.58	-60.83	1	X	X	X	Roel Brien
LFB-02	Bolivia	-14.58	-60.83	1	X	X	X	Roel Brien
LFB-03	Bolivia	-14.6	-60.85	1			X	Alejandro Araujo-Murakami; Ted Feldpausch; Jon Lloyd
LGB-01	Bolivia	-14.8	-60.39	1			X	Luzmila Arroyo; Timothy Killeen
LJV-01	Venezuela	2.07	-67.08	0.1	X		X	Gerardo Aymard
LMS-01	Suriname	4.27	-54.75	1	X		X	Hans ter Steege
LMS-02	Suriname	4.26	-54.74	1	X		X	Hans ter Steege
LMS-03	Suriname	4.27	-54.74	1	X		X	Hans ter Steege
LMS-04	Suriname	4.25	-54.73	1	X		X	Hans ter Steege
LMS-05	Suriname	4.25	-54.73	1.002	X		X	Hans ter Steege
LMS-06	Suriname	4.26	-54.78	1	X		X	Hans ter Steege
LMS-07	Suriname	4.27	-54.78	1	X		X	Hans ter Steege
LMS-08	Suriname	4.27	-54.75	1	X		X	Hans ter Steege
LOR-01	Colombia	-3.06	-69.99	1	X	X	X	Adriana Prieto; Agustin Rudas
LOR-02	Colombia	-3.06	-69.99	0.52	X		X	Adriana Prieto; Agustin Rudas
LOR-03	Colombia	-3.06	-69.99	0.48	X		X	Adriana Prieto; Agustin Rudas
LPL-01	Colombia	1.13	-77.96	0.1			X	Alwyn Gentry
LSL-01	Bolivia	-14.4	-61.14	1	X		X	Alejandro Araujo-Murakami; Jon Lloyd; Luzmila Arroyo; Timothy Killeen; Roel Brien
LSL-02	Bolivia	-14.4	-61.14	1	X		X	Alejandro Araujo-Murakami; Jon Lloyd; Luzmila Arroyo; Timothy Killeen; Roel Brien
LST-01	Colombia	4.91	-74.83	0.1	X		X	Alwyn Gentry
MAC-01	Ecuador	0.11	-78.61	0.1			X	Alwyn Gentry
MAJ-01	Venezuela	1.9	-67.03	0.1	X		X	Gerardo Aymard
MAJ-02	Venezuela	1.9	-67.05	0.1	X		X	Gerardo Aymard
MAN-01	Colombia	10.38	-73.09	0.07			X	Alwyn Gentry
MAS-01	Colombia	7.55	-76.08	0.1	X		X	Alwyn Gentry
MBT-01	Bolivia	-10.07	-65.89	1	X		X	Marisol Toledo; Roel Brien; Guido Pardo; Juan Licona
MBT-02	Bolivia	-10.05	-65.89	1	X		X	Marisol Toledo; Roel Brien; Guido Pardo; Juan Licona

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
MBT-04	Bolivia	-10.31	-65.55	1	X		X	Marisol Toledo; Roel Brienens; Guido Pardo; Juan Licona
MBT-05	Bolivia	-10.03	-65.63	1	X		X	Marisol Toledo; Roel Brienens; Guido Pardo; Juan Licona
MBT-06	Bolivia	-10.04	-65.64	1	X		X	Marisol Toledo; Roel Brienens; Guido Pardo; Juan Licona
MBT-07	Bolivia	-9.91	-65.74	1	X		X	Marisol Toledo; Roel Brienens; Guido Pardo; Juan Licona
MBT-08	Bolivia	-9.94	-65.75	1	X		X	Marisol Toledo; Roel Brienens; Guido Pardo; Juan Licona
MCB-01	Brasil	-1.44	-48.41	2	X		X	Rafael Salomão
MCP-01	Brasil	-5.88	-50.47	1			X	Oliver Phillips; Manoela FF Da Silva
MIA-01	Ecuador	-4.28	-78.64	0.1			X	Oliver Phillips
MIN-01	Brasil	-8.57	-72.9	1	X	X	X	Ted Feldpausch; Marcos Silveira; Jorcely Barroso
MNU-01	Peru	-11.89	-71.41	2.25	X		X	John Terborgh; Roel Brienens; Fernando Valverde
MNU-03	Peru	-11.9	-71.4	2	X	X	X	John Terborgh; Roel Brienens; Fernando Valverde
MNU-04	Peru	-11.9	-71.4	2	X	X	X	John Terborgh; Roel Brienens; Fernando Valverde
MNU-05	Peru	-11.88	-71.41	2.25	X	X	X	John Terborgh; Roel Brienens; Fernando Valverde
MNU-06	Peru	-11.89	-71.4	2.25	X	X	X	John Terborgh; Roel Brienens; Fernando Valverde
MNU-08	Peru	-12	-71.24	2	X		X	John Terborgh; Roel Brienens; Fernando Valverde
MNU-09	Peru	-12.04	-71.21	2	X		X	John Terborgh; Roel Brienens; Fernando Valverde
MNU-10	Peru	-11.85	-71.31	0.1	X		X	John Terborgh; Roel Brienens; Fernando Valverde
MOL-04	Venezuela	8.67	-71.58	0.25			X	Oliver Phillips; Jean-Pierre Veillon
MRB-01	Brasil	-5.73	-49.05	2	X		X	Rafael Salomão
MRB-02	Brasil	-5.72	-49.03	2	X		X	Rafael Salomão
MRB-03	Brasil	-5.7	-49	2	X		X	Rafael Salomão
MSH-01	Peru	-3.78	-73.5	1	X		X	Alwyn Gentry; Oliver Phillips; Rodolfo Vasquez
MSH-10	Peru	-3.78	-73.5	0.1	X		X	Alwyn Gentry
MSH-11	Peru	-3.78	-73.5	0.1	X		X	Alwyn Gentry
MSH-12	Peru	-3.78	-73.5	0.1	X		X	Alwyn Gentry
MTG-01	Bolivia	-19.27	-63.83	0.25			X	Luzmila Arroyo; Jeanneth Villalobos
MTG-02	Bolivia	-19.27	-63.83	0.25			X	Luzmila Arroyo; Jeanneth Villalobos
MTG-03	Bolivia	-19.27	-63.83	0.25			X	Luzmila Arroyo; Jeanneth Villalobos

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
MTG-04	Bolivia	-19.27	-63.83	0.25			X	Luzmila Arroyo; Jeanneth Villalobos
MTG-05	Bolivia	-19.27	-63.84	0.25			X	Luzmila Arroyo; Jeanneth Villalobos
MTG-06	Bolivia	-19.27	-63.84	0.25			X	Luzmila Arroyo; Jeanneth Villalobos
MTG-07	Bolivia	-19.27	-63.84	0.25			X	Luzmila Arroyo; Jeanneth Villalobos
MTG-08	Bolivia	-19.27	-63.85	0.25			X	Luzmila Arroyo; Jeanneth Villalobos
MTH-01	Brasil	-8.88	-72.79	1	X	X	X	Ted Feldpausch; Marcos Silveira; Jose Barroso; Wenderson Castro
MTV-01	Colombia	6.28	-75.51	1			X	Esteban Álvarez Dávila; Zorayda Correa
MUR-01	Colombia	6.61	-76.58	0.1			X	Alwyn Gentry
MVE-01	Bolivia	-15.01	-61.13	1	X		X	Luzmila Arroyo; Timothy Killeen
NAN-01	Ecuador	-4.3	-78.66	0.07			X	Alwyn Gentry
NCR-01	Bolivia	-14.64	-61.16	1	X		X	Luzmila Arroyo; Timothy Killeen
NCR-02	Bolivia	-14.71	-61.15	1	X		X	Luzmila Arroyo; Timothy Killeen
NEB-01	Venezuela	0.83	-66.18	0.1	X		X	Gerardo Aymard
NEB-02	Venezuela	0.83	-66.18	0.1	X		X	Gerardo Aymard
NEN-01	Bolivia	-13.63	-60.89	1			X	Luzmila Arroyo; Timothy Killeen
NEN-02	Bolivia	-13.63	-60.89	1			X	Luzmila Arroyo; Timothy Killeen
NEU-01	Colombia	5.16	-74.05	0.05			X	Alwyn Gentry
NLT-01	Bolivia	-13.65	-60.82	1			X	Luzmila Arroyo; Timothy Killeen
NLT-02	Bolivia	-13.65	-60.83	1			X	Luzmila Arroyo; Timothy Killeen
NLT-03	Bolivia	-13.66	-60.82	1	X		X	Luzmila Arroyo; Timothy Killeen
NMS-01	Suriname	4.78	-54.62	1	X		X	Hans ter Steege
NMS-02	Suriname	4.82	-54.61	0.5	X		X	Hans ter Steege
NMS-03	Suriname	4.82	-54.6	1	X		X	Hans ter Steege
NMS-04	Suriname	4.93	-54.52	1	X		X	Hans ter Steege
NMS-05	Suriname	4.93	-54.52	1	X		X	Hans ter Steege
NMS-06	Suriname	4.83	-54.61	1	X		X	Hans ter Steege
NMU-01	Bolivia	-10.65	-66.76	0.1	X		X	Alwyn Gentry
NOU-01	French Guiana	4.09	-52.67	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto



Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
NOU-02	French Guiana	4.09	-52.67	1	X	X	X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-03	French Guiana	4.09	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-04	French Guiana	4.09	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-05	French Guiana	4.09	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-06	French Guiana	4.09	-52.68	1	X	X	X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-07	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-08	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-09	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-10	French Guiana	4.09	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-11	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-12	French Guiana	4.08	-52.68	1	X	X	X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-13	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-14	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-15	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-16	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-17	French Guiana	4.08	-52.68	1	X	X	X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-18	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-19	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-20	French Guiana	4.08	-52.68	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-21	French Guiana	4.08	-52.68	1	X	X	X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NOU-22	French Guiana	4.08	-52.67	1	X		X	Jerome Chave; Ted Feldpausch; Chris Baraloto
NXV-01	Brasil	-14.71	-52.35	1			X	Beatriz Marimon; Ben Hur Marimon Junior
NXV-03	Brasil	-14.71	-52.35	0.5			X	Beatriz Marimon; Ben Hur Marimon Junior
NXV-05	Brasil	-14.71	-52.35	1			X	Beatriz Marimon; Ben Hur Marimon Junior
NXV-06	Brasil	-14.72	-52.36	0.47			X	Beatriz Marimon; Ben Hur Marimon Junior
NXV-07	Brasil	-14.72	-52.36	0.47			X	Beatriz Marimon; Ben Hur Marimon Junior
NXV-08	Brasil	-14.72	-52.36	0.47			X	Beatriz Marimon; Ben Hur Marimon Junior
NXV-09	Brasil	-14.69	-52.35	0.5			X	Beatriz Marimon; Ben Hur Marimon Junior

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
NXV-10	Brasil	-14.71	-52.35	1			X	Beatriz Marimon; Ben Hur Marimon Junior
ODE-01	Brasil	-3.48	-51.67	3			X	David G Campbell; Douglas C Daly
ODE-02	Brasil	-3.48	-51.67	0.5			X	David G Campbell; Douglas C Daly
OTT-01	Bolivia	-16.39	-61.21	1			X	Jon Lloyd; Ted Feldpausch; Luzmila Arroyo; Oliver Phillips
OTT-02	Bolivia	-16.41	-61.19	1			X	Jon Lloyd; Ted Feldpausch; Luzmila Arroyo; Oliver Phillips
OTT-03	Bolivia	-16.42	-61.19	1			X	Jon Lloyd; Ted Feldpausch; Luzmila Arroyo; Oliver Phillips
PAB-01	French Guiana	5.27	-52.92	6.25	X		X	Bruno Hérault; Chris Baraloto
PAB-02	French Guiana	5.27	-52.92	25	X		X	Bruno Hérault; Chris Baraloto
PAK-01	Peru	-11.94	-71.28	1	X		X	James Comiskey; Oliver Phillips; Patricia Alvarez Loayza
PAK-02	Peru	-11.97	-71.27	1.4	X		X	James Comiskey; Oliver Phillips; Patricia Alvarez Loayza
PAR-20	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-21	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-22	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-23	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-24	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-25	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-26	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-27	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-28	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAR-29	French Guiana	5.28	-52.92	0.49	X		X	Damien Bonal
PAS-01	Ecuador	-0.46	-78.41	0.04			X	Alwyn Gentry
PAY-01	Ecuador	-0.45	-77.03	1	X		X	Carlos Céron; David Neill; Nigel Pitman; Walter Palacios
PBS-01	Peru	-12.65	-68.74	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
PBS-02	Peru	-12.66	-68.75	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
PBS-03	Peru	-12.73	-68.78	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
PBS-04	Peru	-12.72	-68.81	0.1	X		X	Abel Monteagudo; Oliver Phillips; Percy Núñez Vargas
PEA-01	Brasil	-12.15	-50.83	1			X	Beatriz Marimon; Ben Hur Marimon Junior
PEA-02	Brasil	-12.32	-50.74	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
PEA-03	Brasil	-12.38	-50.89	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Eddie Lenza de Oliveira
PEA-04	Brasil	-12.42	-50.71	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Eddie Lenza de Oliveira
PEA-05	Brasil	-11.9	-50.75	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Eddie Lenza de Oliveira
PEA-06	Brasil	-11.92	-50.71	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Eddie Lenza de Oliveira
PEA-07	Brasil	-12.48	-50.9	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Eddie Lenza de Oliveira
PEA-08	Brasil	-12.54	-50.74	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Eddie Lenza de Oliveira
PEM-01	Ecuador	-1.6	-80.7	0.1			X	Alwyn Gentry
PER-01	Bolivia	-14.63	-62.61	0.1			X	Alwyn Gentry
PGP-01	Venezuela	2	-66.63	0.1	X		X	Gerardo Aymard
PIB-05	Guyana	5.02	-58.62	1	X	X	X	Hans ter Steege; James Singh; Peter van de Hout
PIB-06	Guyana	5.01	-58.62	1	X	X	X	Hans ter Steege; James Singh; Peter van de Hout
PIB-12	Guyana	5.03	-58.6	1	X	X	X	Hans ter Steege; James Singh; Peter van de Hout
PNY-01	Peru	-10.38	-75.47	1			X	Abel Monteagudo; Rodolfo Vasquez Martinez
PNY-02	Peru	-10.3	-75.61	1			X	Abel Monteagudo; Rodolfo Vasquez Martinez
PNY-03	Peru	-10.31	-75.29	1		X	X	Abel Monteagudo; Rodolfo Vasquez Martinez
PNY-04	Peru	-10.34	-75.25	1	X	X	X	Abel Monteagudo; Oliver Phillips; Rodolfo Vasquez;
PNY-05	Peru	-10.35	-75.25	1	X	X	X	Abel Monteagudo; Oliver Phillips; Rodolfo Vasquez;
PNY-06	Peru	-10.36	-75.25	1	X	X	X	Abel Monteagudo; Oliver Phillips; Rodolfo Vasquez;
PNY-07	Peru	-10.35	-75.26	1	X	X	X	Abel Monteagudo; Oliver Phillips; Rodolfo Vasquez;
PNY-08	Peru	-10.55	-75.36	1			X	Abel Monteagudo; Rodolfo Vasquez Martinez
PNY-11	Peru	-10.54	-75.36	1			X	Damien Catchpole; Abel Monteagudo; Rodolfo Vasquez
PNY-12	Peru	-10.53	-75.35	1			X	Damien Catchpole; Abel Monteagudo; Rodolfo Vasquez
PNY-13	Peru	-10.53	-75.34	1			X	Damien Catchpole; Abel Monteagudo; Rodolfo Vasquez
POR-01	Brasil	-10.82	-68.77	1	X	X	X	Marcos Silveira; Oliver Phillips; Ted Feldpausch; Tim Baker
POR-02	Brasil	-10.8	-68.77	1	X	X	X	Marcos Silveira; Oliver Phillips; Ted Feldpausch; Tim Baker
PPB-01	Brasil	-1.18	-47.32	1	X		X	Rafael Salomão
PPB-02	Brasil	-1.18	-47.32	1	X		X	Rafael Salomão
PPB-03	Brasil	-1.18	-47.32	1	X		X	Rafael Salomão

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
PTA-01	Venezuela	5.11	-67.74	1	X		X	Gerardo Aymard; Oliver Phillips
PTA-02	Venezuela	5.84	-67.45	1	X		X	Gerardo Aymard; Oliver Phillips
PTA-03	Venezuela	5.11	-67.74	1	X		X	Gerardo Aymard; Oliver Phillips
PTA-04	Venezuela	5.84	-67.49	1			X	Gerardo Aymard
PTA-05	Venezuela	5.84	-67.45	1	X		X	Gerardo Aymard; Oliver Phillips
PTA-06	Venezuela	5.84	-67.45	1	X		X	Gerardo Aymard; Oliver Phillips
PTA-07	Venezuela	5.78	-67.46	1	X		X	Gerardo Aymard; Oliver Phillips
PTA-08	Venezuela	5.78	-67.46	1	X		X	Gerardo Aymard; Oliver Phillips
PTA-11	Venezuela	5.12	-67.67	0.1			X	Gerardo Aymard
PTA-12	Venezuela	5.08	-67.67	0.1	X		X	Gerardo Aymard; Oliver Phillips
PTB-01	Brasil	-1.17	-56.41	1	X		X	Rafael Salomão
PTB-02	Brasil	-1.48	-56.39	1	X		X	Rafael Salomão
PTN-01	Colombia	6.12	-74.67	1	X		X	Esteban Alvarez
QPA-01	Bolivia	-18.33	-59.5	0.1			X	Alwyn Gentry
QUI-01	Peru	-3.83	-73.32	0.5	X		X	Eurídice Honorio; Tim Baker
RAS-01	Colombia	7.05	-73.01	1.035			X	Esteban Álvarez Dávila; Oliver Phillips
RAY-01	Colombia	8.33	-74.91	0.1	X		X	Alwyn Gentry
RBR-01	Brasil	-11	-61.95	1	X			Rafael Salomão
RCA-01	Peru	-13.47	-69.78	0.1			X	Alwyn Gentry
RCS-01	Peru	-9.47	-74.77	1			X	Abel Monteagudo; Rodolfo Vasquez Martinez
RCS-02	Peru	-9.43	-74.74	1			X	Abel Monteagudo; Rodolfo Vasquez Martinez
RCS-03	Peru	-9.42	-74.74	1			X	Abel Monteagudo; Rodolfo Vasquez Martinez
RCS-04	Peru	-9.42	-74.71	1			X	Abel Monteagudo; Rodolfo Vasquez Martinez
RCS-05	Peru	-9.62	-74.93	1	X		X	Abel Monteagudo; Oliver Phillips
REQ-01	Peru	-4.91	-73.82	0.5	X		X	Eurídice Honorio
REQ-04	Peru	-4.88	-73.79	0.5	X		X	Eurídice Honorio
REQ-05	Peru	-4.81	-73.82	0.5	X		X	Eurídice Honorio
REQ-13	Peru	-4.87	-73.65	0.5	X		X	Eurídice Honorio

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
RET-05	Bolivia	-10.97	-65.72	1	X		X	Marisol Toledo;Roel Brienens; Eric Arets; Laurens Poorter; Marielos Pena Claros; Vincent Vos; Rene Boot; Guido Pardo
RET-06	Bolivia	-10.97	-65.72	1	X		X	Marisol Toledo;Roel Brienens; Eric Arets; Laurens Poorter; Marielos Pena Claros; Vincent Vos; Rene Boot; Guido Pardo
RET-08	Bolivia	-10.97	-65.72	1	X		X	Marisol Toledo;Roel Brienens; Eric Arets; Laurens Poorter; Marielos Pena Claros; Vincent Vos; Rene Boot; Guido Pardo
RET-09	Bolivia	-10.97	-65.72	1	X		X	Marisol Toledo;Roel Brienens; Eric Arets; Laurens Poorter; Marielos Pena Claros; Vincent Vos; Rene Boot; Guido Pardo
RFE-34	Peru	-4.01	-73.45	0.04	X		X	Kalle Ruokolainen
RFE-35	Peru	-4.01	-73.45	0.04	X		X	Kalle Ruokolainen
RFE-36	Peru	-4.01	-73.45	0.04	X		X	Kalle Ruokolainen
RFE-37	Peru	-4.01	-73.45	0.04	X		X	Kalle Ruokolainen
RFH-01	Brasil	-9.75	-67.67	1	X	X	X	Foster Brown; Marcos Silveira; Ted Feldpausch; Wendeson Castro
RGE-14	Peru	-3.61	-73.3	0.04			X	Kalle Ruokolainen
RGE-15	Peru	-3.61	-73.3	0.04	X		X	Kalle Ruokolainen
RGE-16	Peru	-3.61	-73.3	0.04	X		X	Kalle Ruokolainen
RGE-17	Peru	-3.61	-73.3	0.04	X		X	Kalle Ruokolainen
RHA-26	Peru	-3.51	-72.04	0.04	X		X	Kalle Ruokolainen
RHA-27	Peru	-3.51	-72.04	0.04	X		X	Kalle Ruokolainen
RHA-28	Peru	-3.51	-72.04	0.04	X		X	Kalle Ruokolainen
RHA-29	Peru	-3.51	-72.04	0.04	X		X	Kalle Ruokolainen
RIA-01	Brasil	-2.9	-46.15	4			X	William Balee
RIO-01	Venezuela	8.11	-61.69	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama ; Geertje van der Heijden; Oliver Phillips
RIO-02	Venezuela	8.11	-61.69	0.25	X		X	Emilio Vilanova; Hirma Ramirez-Angulo; Armando Torres-Lezama ; Geertje van der Heijden; Oliver Phillips
RMA-22	Peru	-3.6	-72.9	0.04	X		X	Kalle Ruokolainen
RMA-23	Peru	-3.6	-72.9	0.04	X		X	Kalle Ruokolainen
RMA-24	Peru	-3.6	-72.9	0.04	X		X	Kalle Ruokolainen
RMA-25	Peru	-3.6	-72.9	0.04	X		X	Kalle Ruokolainen
RMI-05	Peru	-3.89	-73.48	0.0625	X		X	Kalle Ruokolainen

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
RMI-06	Peru	-3.89	-73.48	0.0625	X		X	Kalle Ruokolainen
RMI-07	Peru	-3.89	-73.48	0.0625	X		X	Kalle Ruokolainen
RMI-08	Peru	-3.89	-73.48	0.0625	X		X	Kalle Ruokolainen
RMI-09	Peru	-3.9	-73.48	0.0625	X		X	Kalle Ruokolainen
RMI-10	Peru	-3.9	-73.48	0.0625	X		X	Kalle Ruokolainen
RMI-11	Peru	-3.9	-73.48	0.0625	X		X	Kalle Ruokolainen
RMI-12	Peru	-3.9	-73.48	0.0625	X		X	Kalle Ruokolainen
RMI-13	Peru	-3.9	-73.48	0.0625	X		X	Kalle Ruokolainen
RMO-01	Peru	-3.67	-73.29	0.06251	X		X	Kalle Ruokolainen
RMO-02	Peru	-3.67	-73.29	0.0625	X		X	Kalle Ruokolainen
RMO-03	Peru	-3.66	-73.29	0.0625	X		X	Kalle Ruokolainen
RMO-04	Peru	-3.66	-73.29	0.0625	X		X	Kalle Ruokolainen
RNA-18	Peru	-4.45	-73.59	0.04	X		X	Kalle Ruokolainen
RNA-19	Peru	-4.45	-73.59	0.04	X		X	Kalle Ruokolainen
RNA-20	Peru	-4.45	-73.59	0.04	X		X	Kalle Ruokolainen
RNA-21	Peru	-4.45	-73.59	0.04	X		X	Kalle Ruokolainen
RNE-01	Bolivia	-9.83	-65.66	0.1	X		X	Alwyn Gentry
RPA-01	Peru	-12.39	-69.36	1	X		X	John Terborgh; Percy Núñez Vargas
RPE-38	Peru	-4.07	-73.46	0.04	X		X	Kalle Ruokolainen
RPE-39	Peru	-4.07	-73.46	0.04	X		X	Kalle Ruokolainen
RPE-40	Peru	-4.07	-73.46	0.04	X		X	Kalle Ruokolainen
RPE-41	Peru	-4.07	-73.46	0.04	X		X	Kalle Ruokolainen
RPI-01	Peru	-12.36	-69.23	1	X		X	John Terborgh; Percy Núñez Vargas
RPL-01	Ecuador	-0.56	-79.33	0.1	X		X	Alwyn Gentry
RPL-02	Ecuador	-0.56	-79.33	0.1	X		X	Alwyn Gentry
RPN-30	Peru	-3.88	-73.08	0.04	X		X	Kalle Ruokolainen
RPN-31	Peru	-3.88	-73.08	0.04	X		X	Kalle Ruokolainen
RPN-32	Peru	-3.88	-73.08	0.04	X		X	Kalle Ruokolainen

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
RPN-33	Peru	-3.88	-73.08	0.04			X	Kalle Ruokolainen
RSA-42	Peru	-4.09	-73.12	0.04	X		X	Kalle Ruokolainen
RSA-43	Peru	-4.09	-73.12	0.04	X		X	Kalle Ruokolainen
RSA-44	Peru	-4.09	-73.12	0.04	X		X	Kalle Ruokolainen
RSA-45	Peru	-4.09	-73.12	0.04	X		X	Kalle Ruokolainen
RSN-46	Peru	-4.54	-73.63	0.04	X		X	Kalle Ruokolainen
RSN-47	Peru	-4.54	-73.63	0.04	X		X	Kalle Ruokolainen
RSN-48	Peru	-4.54	-73.63	0.04	X		X	Kalle Ruokolainen
RSN-49	Peru	-4.54	-73.63	0.04	X		X	Kalle Ruokolainen
RST-01	Brasil	-9.04	-72.27	1	X	X	X	Ted Feldpausch; Marcos Silveira; Jose Barroso
RTA-01	Peru	-13.35	-69.66	0.1	X		X	Alwyn Gentry; Percy Núñez Vargas
RTH-01	Peru	-11.37	-69.66	1	X		X	John Terborgh; Percy Núñez Vargas
RTP-50	Peru	-3.78	-73.45	0.04	X		X	Kalle Ruokolainen
RTP-51	Peru	-3.78	-73.45	0.04	X		X	Kalle Ruokolainen
RTP-52	Peru	-3.78	-73.45	0.04	X		X	Kalle Ruokolainen
RTP-53	Peru	-3.78	-73.45	0.04	X		X	Kalle Ruokolainen
SAA-01	Brasil	-9.79	-50.43	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Eder Carvalho das Neves; Fernando Elias
SAA-02	Brasil	-9.64	-50.45	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Eder Carvalho das Neves; Fernando Elias
SAR-02	Venezuela	9.99	-65.28	0.25			X	Jean-Pierre Veillon
SAS-01	Ecuador	-1.6	-80.7	0.1			X	Alwyn Gentry Beatriz Marimon; Ben Hur Marimon Junior; Eder Carvalho das Neves; Fernando Elias
SAT-01	Brasil	-9.84	-50.46	1	X		X	Elias
SAW-01	Ecuador	-2.64	-77.15	1	X		X	Kenneth Young; Ophelia Wang
SCM-01	Bolivia	-16.3	-67.8	0.1			X	Alwyn Gentry
SCN-01	Venezuela	1.92	-67.03	0.1			X	Gerardo Aymard
SCR-04	Venezuela	1.93	-67.04	1	X		X	Gerardo Aymard; Jon Lloyd; Oliver Phillips; Rafael Herrera Fernández
SCR-05	Venezuela	1.93	-67.04	1	X	X	X	Carlos Quesada; Gerardo Aymard; Oliver Phillips
SCT-01	Bolivia	-17.09	-64.77	1	X	X	X	Luzmilla Arroyo; Casimiro Mendoza; Oliver Phillips; Roel Brien

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
SCT-06	Bolivia	-17.09	-64.77	1	X		X	Luzmilla Arroyo; Casimiro Mendoza; Oliver Phillips; Roel Brienen
SCZ-01	Bolivia	-17.76	-63.06	0.1			X	Alwyn Gentry
SDL-04	Venezuela	6.1	-61.4	0.1			X	Lionel Hernandez
SEU-01	Venezuela	8.66	-71.4	0.252			X	Emilio Vilanova; Hirma Ramírez-Angulo
SEU-02	Venezuela	8.62	-71.14	0.252			X	Emilio Vilanova; Hirma Ramírez-Angulo
SEU-03	Venezuela	8.64	-71.41	0.252			X	Emilio Vilanova; Hirma Ramírez-Angulo
SEU-04	Venezuela	8.64	-71.41	0.252			X	Emilio Vilanova; Hirma Ramírez-Angulo
SEU-05	Venezuela	8.64	-71.4	0.25			X	Emilio Vilanova; Hirma Ramírez-Angulo
SEU-06	Venezuela	8.63	-71.4	0.25			X	Emilio Vilanova; Hirma Ramírez-Angulo
SHI-01	Ecuador	-1.02	-76.98	1	X		X	Carlos Céron; Nigel Pitman
SHR-01	Peru	-10.31	-75.11	0.1	X		X	Alwyn Gentry
SIP-01	Brasil	-11.41	-55.32	1	X		X	Marcos Silveira
SJO-01	Peru	-4.06	-73.2	0.5	X		X	Eurídice Honorio
SMT-01	Brasil	-12.82	-51.77	1			X	Beatriz Marimon; Ben Hur Marimon Junior
SMT-02	Brasil	-12.82	-51.77	1			X	Beatriz Marimon; Ben Hur Marimon Junior
SMT-03	Brasil	-12.83	-51.77	1			X	Beatriz Marimon; Ben Hur Marimon Junior
SNP-01	Brasil	-6.04	-50.15	1			X	Rafael Salomão; Manoela FF Da Silva
SPD-01	Peru	-13.05	-71.54	1			X	William Farfan
SRF-01	Colombia	6.27	-75.09	1			X	Esteban Álvarez Dávila; Oliver Phillips
SRL-01	Peru	-11.13	-75.32	1			X	Dante Anton B; Carlos Reynel
SRQ-01	Bolivia	-14.4	-62.3	1			X	Timothy Killeen
SRT-01	Brasil	-1.46	-47.92	1	X		X	Ima Vieira
SRU-01	Colombia	10.47	-70.8	0.1			X	Alwyn Gentry
SSE-01	Colombia	6.1	-75.51	1.103			X	Esteban Álvarez Dávila; Oliver Phillips
STG-01	Bolivia	-18.35	-59.53	0.06			X	Alwyn Gentry
SUC-01	Peru	-3.25	-72.91	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienen; Rodolfo Vasquez; Abel Monteagudo
SUC-02	Peru	-3.25	-72.9	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienen; Rodolfo Vasquez; Abel Monteagudo
SUC-03	Peru	-3.25	-72.92	1	X		X	Oliver Phillips; Tim Baker; Roel Brienen; Rodolfo Vasquez; Abel Monteagudo



Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
SUC-04	Peru	-3.25	-72.89	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
SUC-05	Peru	-3.26	-72.89	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
SUC-10	Peru	-3.25	-72.91	0.08	X		X	Alwyn Gentry; Rodolfo Vasquez
SUM-01	Ecuador	-0.6	-77.63	0.82			X	Timothy Baker
TAM-01	Peru	-12.84	-69.29	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
TAM-02	Peru	-12.83	-69.29	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
TAM-03	Peru	-12.84	-69.28	0.58	X		X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
TAM-04	Peru	-12.84	-69.28	0.42	X		X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
TAM-05	Peru	-12.83	-69.27	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
TAM-06	Peru	-12.84	-69.3	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
TAM-07	Peru	-12.83	-69.26	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
TAM-08	Peru	-12.83	-69.27	1	X		X	Oliver Phillips; Tim Baker; Roel Brienens; Rodolfo Vasquez; Abel Monteagudo
TAM-09	Peru	-12.83	-69.28	1	X	X	X	Oliver Phillips; Yadvinder Malhi
TAM-20	Peru	-12.78	-69.28	0.1	X		X	Alwyn Gentry; Kenneth Young
TAM-21	Peru	-12.84	-69.29	0.1	X		X	Alwyn Gentry
TAM-22	Peru	-12.78	-69.28	0.1	X		X	Alwyn Gentry
TAM-23	Peru	-12.83	-69.27	0.1	X		X	Alwyn Gentry
TAN-02	Brasil	-13.08	-52.38	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Jon Lloyd; Oliver Phillips; Ted Feldpausch
TAN-03	Brasil	-12.83	-52.35	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Jon Lloyd; Oliver Phillips; Ted Feldpausch
TAN-04	Brasil	-12.92	-52.37	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Jon Lloyd; Oliver Phillips; Ted Feldpausch
TAP-50	Brasil	-3.31	-54.94	0.25	X		X	Natalino Silva
TAP-51	Brasil	-3.31	-54.94	0.25	X		X	Natalino Silva
TAP-52	Brasil	-3.31	-54.94	0.25	X		X	Natalino Silva
TAP-53	Brasil	-3.31	-54.94	0.25	X		X	Natalino Silva
TAP-54	Brasil	-3.31	-54.95	0.25	X		X	Natalino Silva
TAP-55	Brasil	-3.31	-54.95	0.25	X		X	Natalino Silva
TAP-56	Brasil	-3.31	-54.95	0.25	X		X	Natalino Silva

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
TAP-57	Brasil	-3.31	-54.95	0.25	X		X	Natalino Silva
TAP-58	Brasil	-3.31	-54.94	0.25	X		X	Natalino Silva
TAP-59	Brasil	-3.31	-54.94	0.25	X		X	Natalino Silva
TAP-60	Brasil	-3.31	-54.94	0.25	X		X	Natalino Silva
TAP-61	Brasil	-3.31	-54.94	0.25	X		X	Natalino Silva
TAR-01	Peru	-6.58	-76.41	0.1			X	Alwyn Gentry
TAY-01	Colombia	11.33	-74.03	0.1	X		X	Alwyn Gentry
TEC-01	Brasil	-1.71	-51.46	1	X	X	X	Leandro Ferreira
TEC-02	Brasil	-1.74	-51.49	1	X	X	X	Leandro Ferreira
TEC-03	Brasil	-1.73	-51.51	1	X	X	X	Leandro Ferreira
TEC-04	Brasil	-1.75	-51.52	1	X	X	X	Leandro Ferreira
TEC-05	Brasil	-1.78	-51.59	1	X	X	X	Leandro Ferreira
TEC-06	Brasil	-1.73	-51.43	1	X	X	X	Leandro Ferreira
TEM-01	Brasil	-2.97	-59.9	1	X		X	I• eda Amaral; Atila Alves
TEM-02	Brasil	-2.93	-59.95	1	X		X	I• eda Amaral; Atila Alves
TEM-03	Brasil	-2.41	-59.9	1	X	X	X	I• eda Amaral; Atila Alves
TEM-04	Brasil	-2.43	-59.79	1	X	X	X	I• eda Amaral; Atila Alves
TEM-05	Brasil	-2.62	-60.21	1	X	X	X	I• eda Amaral; Atila Alves
TEM-06	Brasil	-2.6	-60.11	1	X		X	I• eda Amaral; Atila Alves
TIP-01	Ecuador	-0.66	-76.4	1	X		X	Abel Monteagudo; Nigel Pitman; Roel Brien
TIP-02	Ecuador	-0.63	-76.14	0.8	X		X	Abel Monteagudo,David Neill,Oliver Phillips,Roel Brien
TIP-03	Ecuador	-0.64	-76.15	1	X		X	Abel Monteagudo,David Neill,Oliver Phillips,Roel Brien
TIP-05	Ecuador	-0.64	-76.14	1			X	Nigel Pitman
TMP-01	Peru	-13.13	-69.57	2.25	X		X	John Terborgh; Percy Núñez Vargas
TRU-01	Peru	-13.11	-71.61	1			X	William Farfan
TRU-02	Peru	-13.11	-71.6	1			X	William Farfan
TRU-03	Peru	-13.11	-71.6	1			X	William Farfan
TRU-04	Peru	-13.11	-71.59	1			X	William Farfan

Plot Code	Country	Lat.	Long.	Plot size (ha)	Chapter 2	Chapter 3	Chapter 4	Data contributors
TRU-05	Peru	-13.09	-71.57	1			X	William Farfan
TRU-06	Peru	-13.08	-71.57	1			X	William Farfan
TRU-07	Peru	-13.07	-71.56	1			X	William Farfan
TRU-08	Peru	-13.07	-71.56	1			X	William Farfan
TUC-01	Bolivia	-18.52	-60.81	1			X	Jon Lloyd; Luzmila Arroyo, Oliver Phillips, Ted Feldpausch
TUC-02	Bolivia	-18.53	-60.63	1			X	Jon Lloyd; Luzmila Arroyo, Oliver Phillips, Ted Feldpausch
TUC-03	Bolivia	-18.19	-60.86	1			X	Jon Lloyd; Luzmila Arroyo, Oliver Phillips, Ted Feldpausch
TUT-01	Colombia	5.76	-76.58	0.1	X		X	Alwyn Gentry
UCM-01	Colombia	3.99	-75.56	0.1			X	Alwyn Gentry
VCE-01	Peru	-5.75	-77.66	0.1			X	Alwyn Gentry
VCR-01	Brasil	-14.83	-52.16	0.64	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Ted Feldpausch; Jon Lloyd
VCR-02	Brasil	-14.83	-52.17	1.2	X			Beatriz Marimon; Ben Hur Marimon Junior; Ted Feldpausch; Jon Lloyd
VCR-03	Brasil	-14.83	-52.16	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Ted Feldpausch; Jon Lloyd
VCR-04	Brasil	-14.83	-52.17	1	X		X	Beatriz Marimon; Ben Hur Marimon Junior; Ted Feldpausch; Jon Lloyd
VEN-01	Peru	-4.67	-73.82	0.5	X		X	Eurídice Honorio; Fredy Rodriguez Dávila
VEN-02	Peru	-4.67	-73.82	0.5	X		X	Eurídice Honorio; Fredy Rodriguez Dávila
VTU-01	Venezuela	4.1	-66.63	0.1	X		X	Gerardo Aymard
VTU-02	Venezuela	4.1	-66.65	0.1	X		X	Gerardo Aymard
VTU-03	Venezuela	4.08	-66.62	0.1	X		X	Gerardo Aymard
VTU-04	Venezuela	4.18	-66.52	0.1	X		X	Gerardo Aymard
VTU-05	Venezuela	4.08	-66.72	0.1	X		X	Gerardo Aymard
VTU-06	Venezuela	4.13	-66.47	0.1	X		X	Gerardo Aymard
VTU-07	Venezuela	4.08	-66.43	0.1	X		X	Gerardo Aymard
VTU-08	Venezuela	4.7	-66.3	0.1	X		X	Gerardo Aymard
WAY-01	Peru	-13.19	-71.59	1			X	William Farfan
YAN-01	Peru	-3.43	-72.84	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienen; Rodolfo Vasquez; Abel Monteagudo
YAN-02	Peru	-3.43	-72.84	1	X	X	X	Oliver Phillips; Tim Baker; Roel Brienen; Rodolfo Vasquez; Abel Monteagudo
YAN-11	Peru	-3.43	-72.85	0.1	X		X	Alwyn Gentry; Rodolfo Vasquez

<b>Plot Code</b>	<b>Country</b>	<b>Lat.</b>	<b>Long.</b>	<b>Plot size (ha)</b>	<b>Chapter 2</b>	<b>Chapter 3</b>	<b>Chapter 4</b>	<b>Data contributors</b>
YAN-12	Peru	-3.43	-72.85	0.1	X		X	Alwyn Gentry; Rodolfo Vasquez
YAN-13	Peru	-3.46	-72.83	0.1	X		X	Alwyn Gentry; Rodolfo Vasquez
YNG-01	Bolivia	-19.7	-62.1	0.1			X	Alwyn Gentry
YUT-01	Ecuador	-2.35	-76.43	1	X		X	Kenneth Young; Ophelia Wang
ZAR-01	Colombia	-4.01	-69.91	1	X		X	Eliana Jimenez, Jon Lloyd, Maria Peñuela, Oliver Phillips
ZAR-02	Colombia	-4	-69.9	1	X	X	X	Eliana Jimenez, Jon Lloyd, Maria Peñuela, Oliver Phillips
ZAR-03	Colombia	-3.99	-69.9	1	X	X	X	Eliana Jimenez, Jon Lloyd, Maria Peñuela, Oliver Phillips
ZAR-04	Colombia	-3.99	-69.91	1	X	X	X	Eliana Jimenez, Jon Lloyd, Maria Peñuela, Oliver Phillips

## **Appendix 2 Supplementary information Chapter 2**

### **Appendix 2.1 Methods for calculating trait intrinsic value**

We calculated ‘intrinsic’ trait values for potential tree size, mean and maximum growth rates and mortality rates using a mixed-effects modelling approach to account for the effect of variation in environmental conditions among plots (e.g. in precipitation, elevation and soil fertility) that affect plant traits (Baker *et al.* 2003; Baker *et al.* 2004b; Quesada *et al.* 2010; Quesada *et al.* 2012). I used models based on restricted maximum likelihood (REML), with plot (representing, for example, variation in topography, soil and/or climate) as a random effect and genus or species as the fixed effect in order to calculate genus-level ‘intrinsic’ values (Fyllas *et al.* 2009).

For potential tree size, the mean values for each genus-level fixed effect and their respective standard errors were used to calculate the 95th percentile of diameter, corrected for variation in environmental conditions. Mixed models were constructed separately for angiosperm trees and palms, as trees and palms have very distinctive growth patterns and physiological characteristics, which lead to different size-distribution patterns. Size distributions of palms are approximately normally distributed and therefore untransformed data was used for the mixed model analysis. However, the diameter distributions of trees are highly skewed to the right, and thus prior to the mixed model analysis, all diameter data was log-transformed to increase the normality of model residuals. Following analysis, estimates of maximum size for trees were then back transformed to be on the original scale.

Growth rates were similarly log-transformed prior to mixed model analysis. Due to the higher sampling needed to consistently estimate mortality rates (Rüger *et al.* 2011), plots located in close proximity (with the same three letter code; Appendix 1) were aggregated and treated as having the same level in the random effect term in the mixed models of mortality rates, following Baker *et al.* (2014).

Statistical analyses were performed in the R 3.1.1 (Team 2014) program using lme4 (Bates *et al.* 2015) and lmerBayes (Condit 2012) packages.

## **Appendix 2.2 Comparison between different evolutionary models**

Although continuous traits are typically assumed to evolve under Brownian motion (BM) (Felsenstein 1985), this may not be the most appropriate evolutionary model, and other models may perform better for estimating phylogenetic signal (Münkemüller *et al.* 2012). I compared the fit of the Brownian motion model of evolution with White-Noise and lambda models. Brownian motion represents a random model of evolutionary change along each lineage, which assumes a constant rate of trait evolution through time, where covariance between genus trait values is proportional to the duration of their shared evolutionary history. Under pure BM, phylogenetic signal is equal to one. A white-noise model assumes that trait data come from a single normal distribution and there is no correlation between the ecological similarity and phylogenetic relatedness. A model including Pagel's lambda represents a modification of a Brownian motion model and assesses the extent of phylogenetic signal by multiplying internal branches of the tree by the lambda parameter, which ranges from 0 to 1. When lambda values equal one, this model corresponds to BM.

Different evolutionary models were compared using the Akaike's information criterion AIC. For all traits, the model including Pagel's lambda provided the best fit.

**Table A.2.2.1** Comparison of different evolutionary models considered for the evolution of: wood density, potential tree size, growth rates, and mortality rates. The table shows lambda estimates and model fitting results statistic, with Akaike's Information Criterion (AIC) statistic for the different models: i) Lambda fits the extent to which phylogeny predict trait data; ii) Brownian Motion model of evolution; and iii) White-noise, stasis model with no phylogenetic signal, where phylogeny does not represents a good proxy for trait data

	Trait	lambda $\lambda$	Lambda AIC	Brownian motion AIC	White-noise AIC
Wood density	wd	0.65	-9.07	198.75	173.73
	Max. D	0.49	424.48	582.30	497.29
Potential size	Max. Dwd	0.49	955.17	1112.34	1027.99
	Max. AGB	0.50	1129.23	1306.76	1215.75
	Maxgr. D	0.40	488.48	632.05	520.77
Growth rates	Maxgr. BA	0.42	770.89	888.98	809.07
	Maxgr. AGB	0.52	866.06	969.25	919.77
	Meangr. D	0.34	537.05	688.85	558.39
	Meangr. BA	0.36	754.16	894.83	785.57
	Meangr. AGB	0.44	733.03	858.56	782.41
Mortality	Mortality	0.39	478.60	596.46	491.45

### **Appendix 2.3 Trait data mapped in the phylogeny**

Please see figure supplement 2.3 located in the back cover folder and refer to the electronic material (Appendix 2.3) - Figures of tree and palm traits mapped onto a phylogeny. The number of lineages varied widely according to the selection criterion for each trait. Branches are coloured according to wood density, potential tree size in diameter (Maximum D), maximum tree growth in diameter (Maximum growth D), and mortality rates. Continuous traits were coloured using a continuous colour gradient, colour codes indicate the wide range of trait values, from blue to red, indicating respectively higher and lower trait values.

### **Appendix 2.4 Phylogenetic Principal Components Analysis (PPCA) performed on trait data**

**Table A.2.4.1** Loadings of the first two axes of Phylogenetic Principal Components Analysis (PPCA) performed on wood density, potential tree size in diameter, maximum growth rate, and mortality rate. All genera (n=214) which had complete set of trait data were used for this analysis.

Trait	PPC1	PPC2
Maximum diameter	0.364	0.909
Maximum growth rates	0.926	0.195
Wood density	-0.786	0.123
Mortality	0.711	-0.584
Proportion of variance explained	52.80%	30.50%

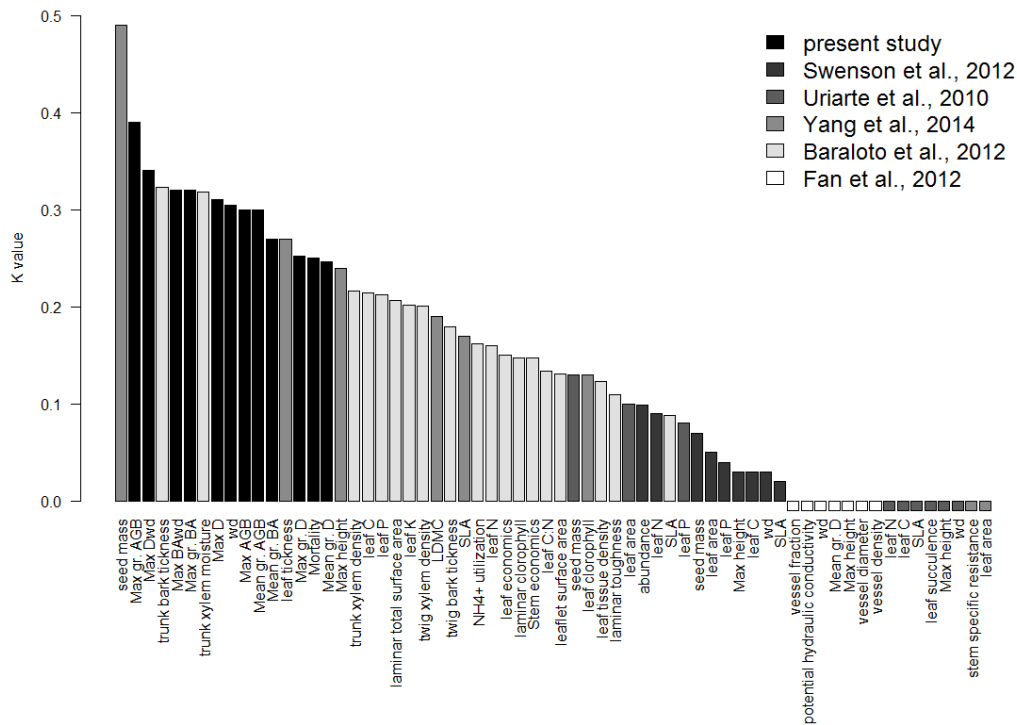


## Appendix 2.5 Sensitivity analysis

**Table A.2.5.1** Summary of trait data calculated across a subset of 26 plots (Manaus region), including number of individuals per genera, number of genera per trait, and number of species. The table also shows the respective phylogenetic signal, for Manaus plots, *Protieae*, *Inga* and restricting the number of lineages to 214 genera that have values for all traits. Phylogenetic signal was measured using Blomberg's *K*. \*\*\* $p < 0.001$ ; \*\* $p < 0.05$ ; \* $p < 0.1$ .

Trait		Manaus			Phylogenetic Signal (K)		Burseraceae		Inga		Restricted number of lineages
		N° ind	N° Genera	N° Species	Intragenetic variation		N° Species	Phylogenetic Signal (K)	N° Species	Phylogenetic Signal (K)	
					No	Yes					
Wood density	wd	-	292	293	0.25***	0.27***	23	0.55	27	0.21	0.24***
	Max. D	33.453	160	364	0.26***	0.40***	37	0.34	40	0.3	0.23**
Potential size	Max. Dwd	33.453	160	364	0.29***	0.44***	37	0.23	40	0.24	0.25***
	Max. BA	33.453	160	364	0.26***	0.40***	37	0.34	40	0.3	0.23***
	Max. AGB	33.453	160	364	0.29***	0.45***	37	0.24	40	0.31	0.24***
	Max. gr. D	27.327	152	315	0.25**	0.41***	31	0.35	29	0.7	0.25**
	Max. gr. BA	27.327	152	315	0.26***	0.37***	31	0.33	29	0.86**	0.2**
Growth rates	Max. gr. AGB	27.327	152	315	0.28***	0.39***	31	0.2	29	0.52	0.22**
	Mean. gr. D	27.327	152	315	0.28***	0.45***	30	0.33	29	0.69	0.26***
	Mean.gr. BA	27.327	152	315	0.28***	0.41***	30	0.38	29	0.76*	0.19*
	Mean.gr.AGB	27.327	152	315	0.30***	0.45***	30	0.16	29	0.4	0.24***
Mortality	Mortality	26.894	67	69	0.32***	0.43***	-	-	-	-	0.24***

## Appendix 2.6 Phylogenetic signal comparison across published studies of tropical forest trees



**Figure A.2.6** Comparison between published values of phylogenetic signal for traits of tropical forest trees measured by Blomberg's K statistic. Bar colour indicates the different studies (Uriarte *et al.* 2010; Baraloto *et al.* 2012; Fan *et al.* 2012; Swenson *et al.* 2012; Yang *et al.* 2014); bars in black are represented by traits calculated in the present study and shades of grey show values for published studies. Bars with negative values represent absence of phylogenetic signal.

## Appendix 3 Supplementary information Chapter 3

### Appendix 3.1 List of 1122 genera used in the phylogenetic reconstructions

List of 1122 angiosperm genera used in the phylogenetic reconstruction, their respective sources of *rbcL* and *matK* sequences and Genbank accession numbers where applicable.

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>	
Acanthaceae	Aphelandra	L01884	Genbank	GQ981937	Genbank	
	Avicennia	AY008830	Genbank	AF531771	Genbank	
	Ruellia	GU135168.1	Genbank	GU135004.1	Genbank	
	Sanchezia	AJ247613	Genbank			
	Suessenguthia			140037105	RBG	
	Trichanthera	GQ981903	Genbank	GQ982116	Genbank	
Achariaceae	Carpotroche			140037111	RBG	
	Kuhlmanniodendron	GU929701	Genbank			
	Lindackeria	GQ981788	Genbank	GQ982034	Genbank	
Achatocarpaceae	Achatocarpus	12-0028245	RBG	120028245	RBG	
Actinidiaceae	Saurauia	AF088852	Genbank	EU310435	Genbank	
Adoxaceae	Sambucus	SBURBCLA	Genbank	HQ593429	Genbank	
	Viburnum	HQ591701	Genbank	HQ591557	Genbank	
Alzateaceae	Alzatea	AVU26316	Genbank	AY151567	Genbank	
Anacardiaceae	Anacardium	JQ626226	Genbank	GQ981932	Genbank	
	Antrocaryon			AY594460	Genbank	
	Apterokarpos	13-0032561	RBG	130032561	RBG	
	Astronium	12-0028223	RBG	120028223	RBG	
	Camptosperma	KJ594639	Genbank	KJ708854	Genbank	
	Cardenasiodendron	GU935419	Genbank			
	Cyrtocarpa	CPU39272	Genbank	AY594464	Genbank	
	Lithraea			AY594470	Genbank	
	Loxopterygium			140037088	RBG	
	Metopium	GU935434.1	Genbank			
	Myracrodruon	13-0032562	RBG	130032562	RBG	
	Ochoterena			130034078	RBG	
	Schinopsis	12-0028234	RBG	120028234	RBG	
	Schinus	12-0028275	RBG	120028275	RBG	
	Spondias	GQ981882	Genbank			
	Tapirira	JQ625925	Genbank	JQ626383	Genbank	
	Thyrsodium	JQ626075	Genbank	JQ626480	Genbank	
	Toxicodendron	U39271	Genbank	AY594491	Genbank	
	Anisophylleaceae	Anisophyllea	AY973480	Genbank	AY973459	Genbank
		Polygonanthus	AY973489	Genbank		
Annonaceae	Anaxagorea	AY743439	Genbank	AY743477	Genbank	
	Annona	JQ625732	Genbank	JQ626342	Genbank	
	Bocageopsis	PER007		120029647	RBG	

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Cardiopetalum			150038112	RBG
	Crematosperma	AY743536	Genbank	AY743559	Genbank
	Cymbopetalum	AY841608	Genbank	DQ125055	Genbank
	Diclinanona	PER023	RBG	DQ125056	Genbank
	Duguetia	AY738171	Genbank	AY740551	Genbank
	Ephedranthus	AY841616	Genbank	AY841396	Genbank
	Fusaea	AY743445	Genbank	AY743483	Genbank
	Guatteria	AY740976	Genbank	AY740927	Genbank
	Hornschuchia	AY841625	Genbank		
	Klarobelia	AY743452	Genbank	AY743490	Genbank
	Malmea	AY743453	Genbank	AY743491	Genbank
	Mosannonna	AY743515	Genbank	AY743508	Genbank
	Onychopetalum	DQ018222	Genbank	DQ018261	Genbank
	Oxandra	AY319066	Genbank	AY518868	Genbank
	Porcelia	AY841649	Genbank		
	Pseudephedranthus	AY841651	Genbank		
	Pseudomalmea	AY841530	Genbank	AY841398	Genbank
	Pseudoxandra	AY319076	Genbank	AY518870	Genbank
	Rollinia			150038517	RBG
	Ruizodendron	AY841657	Genbank	HQ214070	Genbank
	Tetrameranthus	12-0029667	RBG	120029667	RBG
	Trigynaea	AY743449	Genbank	AY743487	Genbank
	Unonopsis	AY743455	Genbank	AY743494	Genbank
	Xylophia	AY238958	Genbank	AY238967	Genbank
Apocynaceae	Allamanda	DQ660626	Genbank	DQ660495	Genbank
	Ambelania	DQ660628	Genbank	DQ660497	Genbank
	Anartia	JQ626134	Genbank		
	Aspidosperma	JQ626066	Genbank	JQ626476	Genbank
	Calotropis	12-0029833	RBG	120029833	RBG
	Couma	DQ660640	Genbank	DQ660512	Genbank
	Forsteronia			130032563	RBG
	Geissospermum	DQ660643	Genbank	DQ660517	Genbank
	Hancornia	DQ660646	Genbank	DQ660519	Genbank
	Himatanthus	JQ625987	Genbank	JQ626428	Genbank
	Lacmellea	JQ626053	Genbank	JQ626466	Genbank
	Laxoplumeria	140037100	RBG	140037100	RBG
	Macoubea	JQ625771	Genbank	JQ626352	Genbank
	Malouetia	JQ625814	Genbank	JQ626356	Genbank
	Molongum	X91765	Genbank	Z70185	Genbank
	Mucoa	12-0029657	RBG	120029657	RBG
	Neocouma			GU973903	Genbank
	Parahancornia	JQ625735	Genbank		
	Plumeria	DQ660661	Genbank	DQ660536	Genbank
	Rauvolfia	DQ660662	Genbank	DQ660537	Genbank
	Rhigospira			GU973904	Genbank
	Spongiosperma			GU973905	Genbank
	Stemmadenia	DQ660666	Genbank	DQ660542	Genbank
	Tabernaemontana	DQ660672	Genbank	DQ660549	Genbank
	Vallesia	AJ419767	Genbank	AM295075	Genbank
Aquifoliaceae	Ilex	12-0028228	RBG	120028228	RBG

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
Araliaceae	Aralia	12-0029800	RBG	120029800	RBG
	Dendropanax	DAU50244	Genbank	DAU58609	Genbank
	Oreopanax	12-0029795	RBG	120029795	RBG
Arecaceae	Schefflera	JQ625964	Genbank	JQ626409	Genbank
	Acrocomia	AM110212	Genbank	AM114639	Genbank
	Aiphanes	AJ404831	Genbank	AM114641	Genbank
	Aphandra	AJ404837	Genbank	AM114612	Genbank
	Archontophoenix	AJ404806	Genbank	AM114660	Genbank
	Astrocaryum	JQ626256	Genbank	JF758213	Genbank
	Attalea	GQ981675	Genbank	GQ981943	Genbank
	Bactris	AM110214	Genbank	AM114642	Genbank
	Butia	JX903252	Genbank	JX903668	Genbank
	Ceroxylon	AJ404781	Genbank	AM114607	Genbank
	Chamaedorea	AJ404787	Genbank	AM114623	Genbank
	Chelyocarpus	AJ404746	Genbank	AM114562	Genbank
	Cocos	AM110211	Genbank	AM114637	Genbank
	Copernicia	AM110199	Genbank	AM114582	Genbank
	Dictyocaryum	AM110204	Genbank	AM114616	Genbank
	Elaeis	AJ404830	Genbank	AM114644	Genbank
	Euterpe	AJ404802	Genbank	AM114647	Genbank
	Geonoma	AJ404834	Genbank	AM114655	Genbank
	Hyospathe	AJ404804	Genbank	AM114646	Genbank
	Iriartea	AJ404793	Genbank	AM114617	Genbank
	Iriartella	AM110203	Genbank	AM114615	Genbank
	Itaya	AJ404748	Genbank	AM114564	Genbank
	Leopoldinia	AJ404798	Genbank	AM114656	Genbank
	Lepidocaryum	AJ829880	Genbank		
	Lytocaryum	AY044633	Genbank		
	Manicaria	AJ404797	Genbank	AM114645	Genbank
	Mauritia	12-0029654	RBG	120029654	RBG
	Mauritiella	12-0029655	RBG	120029655	RBG
	Oenocarpus	12-0029658	RBG	120029658	RBG
	Orbignya	AY012508	Genbank		
	Parajubaea	AJ829891	Genbank		
	Pholidostachys	AM110217	Genbank	AM114651	Genbank
	Phytelephas	AJ404836	Genbank	AM114614	Genbank
	Polyandrococos	AJ829902	Genbank		
	Prestoea	AM110216	Genbank	AM114648	Genbank
	Raphia	AJ829907	Genbank	AM114544	Genbank
	Roystonea	AJ404805	Genbank	AM114630	Genbank
	Scheelea	AY044636	Genbank		
	Socratea	AM110205	Genbank	AM114618	Genbank
	Syagrus	AJ404827	Genbank	AM114638	Genbank
Synechanthus	AJ404786.1	Genbank			
Trithrinax	AJ404745	Genbank	AM114556	Genbank	
Welfia	AJ829917	Genbank	AM114650	Genbank	
Wettinia	AJ404794	Genbank	AM114619	Genbank	
Asparagaceae	Cordyline	HM640529	Genbank	HM640647	Genbank
Asteraceae	Achyrocline	13-0032564	RBG	130032564	RBG
	Ageratina	KJ841084	Genbank	KJ840849	Genbank

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Albizia	12-0027155	RBG	120027155	RBG
	Arnaldoa	EU841098	Genbank	EU841316	Genbank
	Baccharis	12-0028268	RBG	120028268	RBG
	Barnadesia	12-0028293	RBG	120028293	RBG
	Clibadium	AY215095.1	Genbank	AY215775.1	Genbank
	Cnicothamnus	EU384961	Genbank	EU385339	Genbank
	Dasyphyllum	EU841115	Genbank	EU385342	Genbank
	Dendrophorbium	GU817755	Genbank		
	Dinoseris	EU384967	Genbank	EU385346	Genbank
	Eirmocephala	JQ590740	Genbank	JQ586947	Genbank
	Eremanthus	EU384972	Genbank	EU385351	Genbank
	Gochnatia	12-0028274	RBG	120028274	RBG
	Gongylolepis	EU384980	Genbank	EU385359	Genbank
	Kaunia			140037083	RBG
	Koanophyllon			140037092	RBG
	Lychnophora	13-0032565	RBG	130032565	RBG
	Mikania	JF826307	Genbank	JF826294	Genbank
	Morithamnus	13-0032566	RBG	130032566	RBG
	Oyedaea	AY215153	Genbank	AY215835	Genbank
	Paralychnophora			130034081	RBG
	Piptocarpha	PPJCPRBCL	Genbank	150038143	RBG
	Pluchea	EU385011	Genbank	EU385389	Genbank
	Smallanthus	AY215177	Genbank		
	Stenopadus	EU385019	Genbank	EU385398	Genbank
	Stiffitia	EU385020	Genbank	EU385399	Genbank
	Symphyopappus			150038127	RBG
	Tessaria	12-0028258	RBG	120028258	RBG
	Trixis	EU385025	Genbank	EU385405	Genbank
	Verbesina	12-0028251	RBG	120028251	RBG
	Vernonanthura	12-0028278	RBG	120028278	RBG
	Vernonia	12-0028269	RBG	120028269	RBG
	Wunderlichia	EU385028	Genbank	EU385408	Genbank
Begoniaceae	Begonia			130034056	RBG
Berberidaceae	Berberis	AF139878	Genbank	AB069827	Genbank
Betulaceae	Alnus	FJ844584	Genbank	FJ011815	Genbank
Bignoniaceae	Adenocalymma	13-0032567	RBG	130032567	RBG
	Arrabidaea	AF102641	Genbank	130032568	RBG
	Clytostoma	13-0032569	RBG	130032569	RBG
	Crescentia	AF102643	Genbank		
	Cybistax	12-0029819	RBG	120029819	RBG
	Distictella	140037099	RBG	140037099	RBG
	Godmania	13-0032571	RBG	130032571	RBG
	Handroanthus			150038119	RBG
	Jacaranda	JQ626146	Genbank	JQ626519	Genbank
	Lundia	13-0032572	RBG	130032572	RBG
	Macfadyena	AF102649	Genbank	GU134972	Genbank
	Melloa	13-0032573	RBG	130032573	RBG
	Memora			140037123	RBG
	Pleonotoma	KJ594438.1	Genbank	KJ594004.1	Genbank
	Sparattosperma	120028292	RBG	120028292	RBG

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Tabebuia	JQ626096	Genbank	JQ626497	Genbank
	Tecoma	12-0028262	RBG	120028262	RBG
	Xylophragma			140037097	RBG
	Zeyheria	BOLIN034		130034086	RBG
Bixaceae	Bixa	Y15139	Genbank	FM179929	Genbank
	Cochlospermum	AF022129	Genbank	120028291	RBG
Bonnetiaceae	Archytaea	AY380342	Genbank	HQ331545	Genbank
	Bonnetia	HQ332012	Genbank	HQ331549	Genbank
Boraginaceae	Bourreria	AF258345	Genbank	DQ197229	Genbank
	Cordia	JQ626197	Genbank	JQ626469	Genbank
	Heliotropium	HM850048	Genbank	HM850863	Genbank
	Tournefortia	EU599824	Genbank	EU599648	Genbank
	Varronia			140037074	RBG
Brunelliaceae	Brunellia	FJ707536	Genbank	EF135512	Genbank
Burseraceae	Bursera	12-0028241	RBG	120028241	RBG
	Commiphora	FJ466630	Genbank	JF270711	Genbank
	Crepidospermum	150040005	RBG		
	Dacryodes	JQ626006	Genbank	JQ626441	Genbank
	Protium	JQ626194	Genbank	JQ626503	Genbank
	Tetragastris	JQ625986	Genbank	JQ626484	Genbank
	Trattinnickia	JQ626083	Genbank	GQ982114	Genbank
Buxaceae	Buxus	DQ182333.1	Genbank	AF543728.1	Genbank
	Styloceras	AF093733	Genbank		
Cactaceae	Armatocereus			HM041650	Genbank
	Arrojadoa	13-0032574	RBG	130032574	RBG
	Brasilopuntia	AY875234	Genbank	AY875370	Genbank
	Browningia	12-0028248	RBG	120028248	RBG
	Calymmanthium	AY875230	Genbank	AY015291	Genbank
	Cereus	12-0029830	RBG	120029830	RBG
	Cleistocactus			130034067	RBG
	Echinopsis	FR853367	Genbank	FN669743	Genbank
	Espostoa			130034068	RBG
	Espostopsis			HM041694	Genbank
	Harrisia			150038122	RBG
	Hylocereus			AY015310	Genbank
	Melocactus			HM041719	Genbank
	Micranthocereus			AY015314	Genbank
	Neoraimondia			HM041728	Genbank
	Opuntia	AY875233	Genbank	AY875369	Genbank
	Pereskia	AF206805	Genbank	AY875355	Genbank
	Pilosocereus			HM041759	Genbank
	Quiabentia	AY875236	Genbank	AY875372	Genbank
	Rauhocereus			AY015326	Genbank
	Samaipaticereus			140037078	RBG
	Stetsonia			140037084	RBG
	Tacinga			150039161	RBG
	Weberbauerocereus			HM041796	Genbank
Calophyllaceae	Calophyllum	HQ332018	Genbank	HQ331555	Genbank
	Caraipa	HQ332025	Genbank	HQ331564	Genbank
	Clusiella	AY625019	Genbank	HQ331585	Genbank

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Haploclathra	HQ332068	Genbank	HQ331614	Genbank
	Kielmeyera	AY625015	Genbank	HQ331641	Genbank
	Mahurea	AY625018	Genbank	HQ331650	Genbank
	Mammea	AY625029	Genbank	HQ331652	Genbank
	Marila	AY625010	Genbank	HQ331660	Genbank
Canellaceae	Cinnamodendron	EU669512	Genbank	EU669485	Genbank
Cannabaceae	Celtis	12-0028240	RBG	120028240	RBG
	Trema	12-0028244	RBG	120028244	RBG
Capparaceae	Anisocapparis			140037075	RBG
	Atamisquea			140037076	RBG
	Belencita			EU371746	Genbank
	Capparicordis			140037086	RBG
	Capparidastrum	KJ082172	Genbank	KJ012501	Genbank
	Capparis	GQ981684	Genbank	GQ981949	Genbank
	Colicodendron			130034082	RBG
	Crateva	AY483265	Genbank	AY483229	Genbank
	Cynophalla			120029857	RBG
	Morisonia	12-0028282	RBG	120028282	RBG
	Neocalyptrocalyx	JQ625979	Genbank	JQ626425	Genbank
	Preslianthus			120028281	RBG
	Quadrella	KJ082530	Genbank	KJ012740	Genbank
	Sarcotoxicum			140037093	RBG
	Steriphoma	12-0028280	RBG	120028280	RBG
Cardiopteridaceae	Citronella			150038113	RBG
	Dendrobangia	JQ626064	Genbank	JQ626474	Genbank
Caricaceae	Carica	CPACPRBCLA	Genbank	AY483221	Genbank
	Jacaratia	AF405245	Genbank	AY461574	Genbank
	Vasconcellea	12-0029803	RBG	120029803	RBG
Caryocaraceae	Anthodiscus	FJ670162	Genbank	FJ670000	Genbank
	Caryocar	12-0029650	RBG	120029650	RBG
Celastraceae	Anthodon			HM230160	Genbank
	Cheiloclinium	JQ626275	Genbank	JQ626564	Genbank
	Curvea	KJ594207.1	Genbank	KJ593844.1	Genbank
	Elaeodendron	AY380347	Genbank	DQ217541	Genbank
	Fraunhoferia			JF410097	Genbank
	Gymnosporia	AY380352	Genbank	EU328974	Genbank
	Hippocratea	13-0032576	RBG	130032576	RBG
	Hylенаea	KJ594297.1	Genbank	KJ593908.1	Genbank
	Maytenus	JQ626259	Genbank	JQ626557	Genbank
	Peritassa			FJ705544	Genbank
	Plenckia			JF410098	Genbank
	Prionostemma	KJ594446	Genbank	KJ594009	Genbank
	Salacia	AJ402998	Genbank	FJ705557	Genbank
	Schaefferia			130034070	RBG
	Tontelea			FJ705562	Genbank
	Zinowiewia	AY935741	Genbank	AY935922	Genbank
Chloranthaceae	Hedyosmum	HDYCPRBCLA	Genbank	DQ401339	Genbank
Chrysobalanaceae	Acioa	GQ424473	Genbank		
	Chrysobalanus	L11178	Genbank	EF135519	Genbank
	Couepia	JQ625980	Genbank	JQ626426	Genbank



Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Exellodendron	JQ625744	Genbank		
	Hirtella	JQ625956	Genbank	JQ626404	Genbank
	Licania	AB233846	Genbank	GQ982032	Genbank
	Parinari	AB233847	Genbank	AB233743	Genbank
Clethraceae	Clethra	CTFCPRBCLA	Genbank	AJ429281	Genbank
	Purdiaea	AY082698	Genbank		
Clusiaceae	Chrysochlamys	HQ332031	Genbank	HQ331570	Genbank
	Clusia	JQ626019	Genbank	JQ626447	Genbank
	Dystovomita	HQ332051	Genbank	HQ331594	Genbank
	Garcinia	JQ626234	Genbank	JQ626543	Genbank
	Lorostemon	AF518401	Genbank	HQ331648	Genbank
	Moronobea	JQ626143	Genbank	HQ331665	Genbank
	Platonia	JQ626227	Genbank	HQ331670	Genbank
	Symphonia			HQ331680	Genbank
	Tovomita	HQ332120	Genbank	HQ331684	Genbank
	Tovomitopsis	HQ332123	Genbank	HQ331687	Genbank
Columelliaceae	Columellia	130034079	RBG	130034079	RBG
Combretaceae	Buchenavia	FJ381805	Genbank	HM446660	Genbank
	Combretum	EU338147	Genbank	FM179938	Genbank
	Conocarpus	FJ381822	Genbank		
	Laguncularia	FJ381825	Genbank		
	Terminalia	FJ381811	Genbank	GU135057	Genbank
Connaraceae	Connarus	CNFRBCL	Genbank	EU002174	Genbank
	Rourea	FJ707537	Genbank	EF135591	Genbank
Convolvulaceae	Dicranostyles	AY101043	Genbank		
	Ipomoea	AY100962	Genbank	AJ429355	Genbank
	Jacquemontia	AY101039	Genbank	EU330286	Genbank
	Maripa	JQ591163	Genbank	JQ587303	Genbank
Cornaceae	Cornus	EU002276	Genbank	EU002175	Genbank
Cunoniaceae	Lamanonia	13-0032577	RBG	130032577	RBG
	Weinmannia	AF291915	Genbank	GQ248213	Genbank
Cyrtillaceae	Cyrtilla	CYQCPRBCL	Genbank	AJ429282	Genbank
Dichapetalaceae	Dichapetalum	GQ424469	Genbank		
	Stephanopodium	13-0032578	RBG		
	Tapura	12-0029846	RBG	FJ670009	Genbank
Dilleniaceae	Curatella	FJ860341.1	Genbank	120028224	RBG
	Davilla	FJ860342.1	Genbank	FJ514769	Genbank
	Doliocarpus	FJ860360.1	Genbank	130034083	RBG
	Hibbertia	FJ860367.1	Genbank	HQ896421	Genbank
	Tetracera	FJ860393.1	Genbank	AY042665	Genbank
Dipentodontaceae	Perrottetia	AY935736	Genbank	AY935915	Genbank
Ebenaceae	Diospyros	EU980663	Genbank	DQ924003	Genbank
	Lissocarpa	EU980794	Genbank	DQ924078	Genbank
Elaeocarpaceae	Crinodendron	AF291940	Genbank	AY935929	Genbank
	Sloanea	JQ626032	Genbank	JQ626451	Genbank
	Vallea	AJ403035	Genbank		
Ericaceae	Agarista	12-0029835	RBG	120029835	RBG
	Bejaria	GU176639	Genbank	AF440412	Genbank
	Cavendishia			AF382747	Genbank
	Gaultheria	GAHCPRBCLA	Genbank	GEU61317	Genbank

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Thibaudia			AF382790	Genbank
Erythroxylaceae	Erythroxylum	PER028		GQ981987	Genbank
Escalloniaceae	Escallonia	12-0028277	RBG	120028277	RBG
Euphorbiaceae	Acalypha	12-0028252	RBG	120028252	RBG
	Acidoton	AB267913	Genbank	AB268017	Genbank
	Actinostemon	AB233883	Genbank	AB233779	Genbank
	Adelia	12-0029848	RBG	120029848	RBG
	Adenophaedra	AY794930	Genbank		
	Alchornea	HM446755	Genbank	HM641813	Genbank
	Alchorneopsis	AY794962	Genbank	HM446655	Genbank
	Anomalocalyx			140037126	RBG
	Aparisthmium	AY794955	Genbank	GQ981929	Genbank
	Bernardia	12-0029849	RBG	120029849	RBG
	Brasiliocroton	AY794907	Genbank		
	Caryodendron	AB233857	Genbank	AB233753	Genbank
	Chaetocarpus	JQ626189	Genbank	JQ626531	Genbank
	Cleidion	AY794936	Genbank		
	Cnidoscolus	12-0029808	RBG	120029808	RBG
	Conceveiba	AY788170	Genbank	FJ670011	Genbank
	Croton	12-0028261	RBG	HM446680	Genbank
	Ditaxis	AB233865	Genbank	AB233761	Genbank
	Dodecastigma	AY794885	Genbank	150038518	RBG
	Euphorbia	AY794827	Genbank	EF135539	Genbank
	Glycydendron	AB267942	Genbank	AB268046	Genbank
	Gymnanthes	AY794851	Genbank	140037102	RBG
	Hevea	AB267943	Genbank	AB268047	Genbank
	Hura	AB233886	Genbank	AB233782	Genbank
	Jatropha	12-0029805	RBG	120029805	RBG
	Joannesia	AJ418808	Genbank		
	Mabea	JQ625917	Genbank	JQ626381	Genbank
	Manihot	AB233880	Genbank	AB233776	Genbank
	Maprounea	AJ418810	Genbank	150038519	RBG
	Micrandra	AB267945	Genbank	AB268049	Genbank
	Micrandropsis	AB267946	Genbank	AB268050	Genbank
	Nealchornea	AY794865	Genbank	140037129	RBG
	Ophthalmoblapton	AY794848	Genbank		
	Pachystroma	AY794847	Genbank		
	Pausandra	AY794887	Genbank	140037116	RBG
	Pera	AY380355	Genbank	EF135578	Genbank
	Philyra	AB267927	Genbank	AB268031	Genbank
	Pogonophora	AY788185	Genbank	EF135585	Genbank
	Pseudosenefeldera	AY794862	Genbank		
	Rhodothyrus	140037119	RBG	140037119	RBG
	Ricinus	AY788188	Genbank	EF135590	Genbank
	Sagotia	AY794903	Genbank	150038125	RBG
	Sandwithia	AY794904.1	Genbank	140037135	RBG
	Sapium	12-0028301	RBG	GQ982089	Genbank
	Sebastiania	AY794850	Genbank	140037090	RBG
	Senefeldera			150038126	RBG
	Stillingia	AY794843	Genbank	140037089	RBG

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
Fabaceae	Tacarcuna	AY663623	Genbank		
	Tetrorchidium	AB267952	Genbank	AB268056	Genbank
	Euphronia			AB233741	Genbank
	Abarema	12-0027154	RBG	GQ981925	Genbank
	Acaciella			HM020733	Genbank
	Acosmium	12-0027096	RBG	120027096	RBG
	Adesmia	U74254	Genbank	AF142690	Genbank
	Aeschynomene	AB045784	Genbank	AF272086	Genbank
	Aldina	U74252	Genbank		
	Alexa	JQ625719	Genbank	JQ626338	Genbank
	Amburana	12-0027097	RBG	AY553712	Genbank
	Amicia			AF203583	Genbank
	Amphiodon	JQ625776	Genbank		
	Anadenanthera	12-0027156	RBG	EU812064	Genbank
	Andira	12-0027098	RBG	120027098	RBG
	Apuleia	U74249	Genbank	EU361858	Genbank
	Apurimacia	12-0027169	RBG	120027169	RBG
	Arapatiella	AY904376	Genbank	EU361859	Genbank
	Ateleia	12-0027099	RBG	GU220020	Genbank
	Balizia			140035558	RBG
	Barnebydendron			EU361868	Genbank
	Batesia	AY904375	Genbank		
	Bauhinia	12-0027176	RBG	120027176	RBG
	Blanchetiodendron	13-00322580	RBG	130032580	RBG
	Bocoa	JQ626179	Genbank	JQ626415	Genbank
	Bowdichia	12-0027101	RBG	AY386937	Genbank
	Brodriguesia	130032581	RBG	EU361890	Genbank
	Brownea	Z70159	Genbank	EU361891	Genbank
	Browneopsis	AM234233	Genbank	EU361894	Genbank
	Caesalpinia	KP094413	Genbank	KP093492	Genbank
	Calliandra	AM234252	Genbank	HM020736	Genbank
	Campsiandra			EU361908	Genbank
	Candolleodendron	EF466154	Genbank	JX295890	Genbank
	Cascaronia			AF272072	Genbank
	Cassia	AM234244	Genbank	EU361909	Genbank
	Cedrelinga	12-0027105	RBG		
	Cenostigma	13-0032582	RBG	130032582	RBG
	Centrolobium	BOLIN021			
	Chamaecrista	AM234248	Genbank	EU361914	Genbank
	Chloroleucon			AY386921	Genbank
	Clathrotropis			JX295951	Genbank
	Clitoria	12-0027107	RBG	120027107	RBG
	Cojoba	GQ981709	Genbank	GQ981971	Genbank
	Cologania	AF181932	Genbank	GQ246140	Genbank
	Copaifera	12-0029861	RBG	EU361918	Genbank
	Coursetia	12-0027109	RBG	AF547188	Genbank
	Crotalaria	Z70134	Genbank	GQ246141	Genbank
Crudia	AM234230	Genbank	EU361922	Genbank	
Cyathostegia			HM347480	Genbank	
Cyclolobium	BOLLC377	Genbank	GQ246151	Genbank	

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Cynometra	AY289677	Genbank	EU361925	Genbank
	Dahlstedtia			130034051	RBG
	Dalbergia	12-0027161	RBG	HQ427296	Genbank
	Dalea			AY386860	Genbank
	Deguelia	12-0027170	RBG	140035565	RBG
	Derris	U74234	Genbank	AF142715	Genbank
	Desmanthus			AF521820	Genbank
	Desmodium	EU717279	Genbank	EU717420	Genbank
	Dialium	12-0027113	RBG	EU361930	Genbank
	Dicorynia	JQ626129	Genbank	EU361931	Genbank
	Dicymbe	PER024		EU361932	Genbank
	Dimorphandra	12-0027114	RBG	EU361934	Genbank
	Dinizia	13-0032584	RBG	EU361951	Genbank
	Dioclea			130033193	RBG
	Diplotropis	12-0027115	RBG	120027116	RBG
	Dipteryx	12-0027119	RBG		
	Diptychandra	13-0032585	RBG	EU361935	Genbank
	Dussia	JQ625757	Genbank	AY386903	Genbank
	Elizabetha	140037127	RBG	EU361940	Genbank
	Enterolobium	JQ626149	Genbank	GQ981984	Genbank
	Eperua	JQ626198	Genbank	JQ626458	Genbank
	Eriosema	AM235007	Genbank		
	Erythrina	12-0027120	RBG	120027120	RBG
	Erythrostemon	JN796934	Genbank	AY386845	Genbank
	Etaballia			AF272073S2	Genbank
	Exostyles	13-0032586	RBG	150038555	RBG
	Fissicalyx			AF272063	Genbank
	Galactia	EU717287	Genbank	EU717428	Genbank
	Geoffroea	12-0027121	RBG	AF270880	Genbank
	Gleditsia	Z70129	Genbank	AY386849	Genbank
	Gliricidia	JF738386	Genbank	AF547197	Genbank
	Goniorrhachis	AM234232	Genbank	EU361959	Genbank
	Grazielodendron			AF270862	Genbank
	Guianodendron			JX124403	Genbank
	Guibourtia	BOLXX004		EU361962	Genbank
	Guilandina			EU361900	Genbank
	Harleyodendron	13-0032587	RBG	130032587	RBG
	Heterostemon			EU361968	Genbank
	Hoffmannseggia	AY308531	Genbank	EU361969	Genbank
	Holocalyx	U74244	Genbank	AY553714	Genbank
	Hydrochorea			130033195	RBG
	Hymenaea	JQ625969	Genbank	JQ626412	Genbank
	Hymenolobium	PER038		AY386934	Genbank
	Indigofera	U74214	Genbank	AF142697	Genbank
	Inga	12-0029860	RBG	JQ626408	Genbank
	Jacqueshuberia	AY904391	Genbank	EU361984	Genbank
	Krameria	Y15032	Genbank	FJ670058	Genbank
	Lathyrus	HM029364	Genbank	AF522085	Genbank
	Lecointea	AM234260	Genbank	EU361990	Genbank
	Leptolobium	U74255	Genbank		

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Leucaena	GU135204	Genbank	GU135042	Genbank
	Leucochloron	14-0035232	RBG	140035232	RBG
	Libidibia			EU361901	Genbank
	Lonchocarpus	HM446818	Genbank	HM446705	Genbank
	Luetzelburgia	U74185	Genbank	AY553716	Genbank
	Lupinus	HM850145	Genbank	HM851129	Genbank
	Machaerium	12-0027129	RBG	130033200	RBG
	Macrobium	JQ625745	Genbank	EU361996	Genbank
	Macrosamanea			140035543	RBG
	Maraniona	JN083774	Genbank	AY247263	Genbank
	Martiodendron	13-0032589	RBG	EU361999	Genbank
	Melanoxylon	AY904388	Genbank	EU362000	Genbank
	Microlobius	140037104	RBG	AF521842	Genbank
	Millettia	AF308714	Genbank	AF142726	Genbank
	Mimosa	12-0027180	RBG	GU135076	Genbank
	Mimozyanthus	140037085	RBG	AY944556	Genbank
	Moldenhawera	AY904390	Genbank	EU362004	Genbank
	Monopteryx			KP177917	Genbank
	Mora			EU362005	Genbank
	Mucuna	EU717281	Genbank	EU717422	Genbank
	Muelleria	AB045813	Genbank		
	Myrocarpus	13-0032590	RBG	AY386925	Genbank
	Myroxylon	12-0027131	RBG	120029860	RBG
	Newtonia			AF521847	Genbank
	Ormosia	12-0027132	RBG	120027132	RBG
	Paloue			EU362014	Genbank
	Panurea			JX295947	Genbank
	Paramachaerium			AF272062	Genbank
	Parapiptadenia	13-0032591	RBG	AF521849	Genbank
	Parkia	JQ625940	Genbank	JQ626393	Genbank
	Parkinsonia	AY904403	Genbank	AY386917	Genbank
	Peltogyne	AF308718	Genbank	EU362021	Genbank
	Peltophorum	AY904400	Genbank	AY386846	Genbank
	Pentaclethra	AM234250	Genbank	AY386904	Genbank
	Petaladenium			KP177896	Genbank
	Phanera	13-0032592	RBG	130032592	RBG
	Piptadenia	BOLIN205COR		AF521855	Genbank
	Piscidia	AB045816	Genbank	AF142710	Genbank
	Pithecellobium	GQ436357	Genbank	HM020740	Genbank
	Pityrocarpa			130034053	RBG
	Plathymentia	13-0034064	RBG	AF521858	Genbank
	Platycyamus	AB045817	Genbank	AF142709	Genbank
	Platymiscium	JQ626063	Genbank	JQ626473	Genbank
	Platyopodium	GQ981836	Genbank	GQ982065	Genbank
	Poecilanthus	13-0032594	RBG	130032594	RBG
	Poeppigia	AY904370	Genbank	EU362026	Genbank
	Poincianella	12-0027104	RBG	EU361904	Genbank
	Prosopis	12-0027165	RBG	AY944562	Genbank
	Pseudopiptadenia	JQ625948	Genbank	JQ626397	Genbank
	Pseudosamanea	JQ591565	Genbank		

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Pterocarpus	12-0027175	RBG	120027175	RBG
	Pterodon	12-0027139	RBG		
	Pterogyne	AY904377	Genbank	EU362031	Genbank
	Recordoxylon	JQ626133	Genbank		
	Rhynchosia	AB045823	Genbank		
	Riedeliella	13-0032595	RBG	AF272090S1	Genbank
	Samanea	13-0032596	RBG		
	Savia	AY663619	Genbank	AY552449	Genbank
	Schizolobium	AY904398	Genbank	EU362036	Genbank
	Sclerolobium	AM234242	Genbank		
	Senegalia	12-0027181	RBG	HM020731	Genbank
	Senna	GU135268	Genbank	GU135008	Genbank
	Spirotropis			JX295950.1	Genbank
	Stryphnodendron	JQ626052	Genbank	JQ626465	Genbank
	Stylosanthes			AF203595	Genbank
	Swartzia	AM234259	Genbank	EU362053	Genbank
	Sweetia	12-0027150	RBG	AY386911	Genbank
	Tabaroa	130032597	RBG	130032597	RBG
	Tachigali	JQ626001	Genbank	EU362040	Genbank
	Tara	12-0027184	RBG	120027184	RBG
	Taralea	PER085	Genbank		
	Tephrosia	U74211	Genbank	AF142712	Genbank
	Tipuana	JN083777	Genbank	AF270882	Genbank
	Trischidium	13-0032598	RBG	130032598	RBG
	Uleanthus	13-0032599	RBG		
	Ulex	HM850431	Genbank	HM851132	Genbank
	Uribea			AY553719.1	Genbank
	Vachellia	HM850439	Genbank	HM850602	Genbank
	Vatairea	JQ625866	Genbank		
	Vataireopsis	JQ626110	Genbank	AF142680	Genbank
	Vouacapoua	JQ626170	Genbank	JQ626385	Genbank
	Zapoteca	12-0027166	RBG	EU362064	Genbank
	Zollernia	13-0032600	RBG	140035578	RBG
	Zygia	JQ625977	Genbank	JQ626423	Genbank
Gentianaceae	Macrocarpaea			AJ010523	Genbank
	Potalia	AJ235816	Genbank		
Gesneriaceae	Sanango	AJ001763	Genbank		
Goupiaceae	Goupia	JQ626141	Genbank	EF135544	Genbank
Griselinaceae	Griselinia	AF307916	Genbank	AJ429372	Genbank
Hernandiaceae	Gyrocarpus	GYRCPRBCLA	Genbank	DQ401370	Genbank
	Hernandia	HRNCPRBCLA	Genbank	AJ966799	Genbank
	Sparattanthelium	AF052197	Genbank	AJ627931	Genbank
Humiriaceae	Duckesia			140037109	RBG
	Endopleura			140037112	RBG
	Humiria	AB233889	Genbank	AB233785	Genbank
	Humiriastrum	JQ626167	Genbank	JQ626522	Genbank
	Sacoglottis	JQ625910	Genbank	JQ626378	Genbank
	Schistostemon	JX664071	Genbank	JX661963	Genbank
	Vantanea	JQ625882	Genbank	JQ626370	Genbank
Hypericaceae	Vismia	JQ626022	Genbank	HQ331694	Genbank

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>	
Icacinaceae	Calatola	JQ592254	Genbank	JQ588040	Genbank	
	Emmotum	JQ626244	Genbank	JQ626549	Genbank	
	Poraqueiba	JQ626039	Genbank	JQ626457	Genbank	
Ixonanthaceae	Cyriilopsis	FJ670170	Genbank	FJ670024	Genbank	
	Ochthocosmus	FJ707535	Genbank	EF135573	Genbank	
Juglandaceae	Juglans	AF206785	Genbank	U92851	Genbank	
Koeberliniaceae	Koeberlinia	KBECPRBCL	Genbank	AY483222	Genbank	
Lacistemataceae	Lacistema	AB233894	Genbank	AB233790	Genbank	
	Lozania	AJ418804	Genbank	FJ670026	Genbank	
Lamiaceae	Aegiphila	GQ981656	Genbank	GQ981928	Genbank	
	Callicarpa	JQ594368	Genbank	JQ589422	Genbank	
	Cornutia	JQ592281	Genbank	JQ588061	Genbank	
	Hyptidendron			120029809	RBG	
	Lepechinia	AY570387	Genbank			
Lauraceae	Vitex	12-0028287	RBG	AB284182	Genbank	
	Aiouea	JQ625982	Genbank	AJ247143	Genbank	
	Anaueria	PER001		120029645	RBG	
	Aniba	JQ626084	Genbank	JQ626487	Genbank	
	Beilschmiedia			EU153825	Genbank	
	Caryodaphnopsis			EU153828	Genbank	
	Chlorocardium	12-0029651	RBG	120029651	RBG	
	Cinnamomum	CNMCPRBCLA	Genbank	AJ966800	Genbank	
	Cryptocarya	GQ248578	Genbank	AJ247158	Genbank	
	Dicypellium			AJ247161	Genbank	
	Endiandra	JF738632	Genbank	AJ247162	Genbank	
	Endlicheria	JQ625787	Genbank	JQ626354	Genbank	
	Licaria	JQ625945	Genbank	JQ626395	Genbank	
	Mezilaurus			120029656	RBG	
	Nectandra	GQ981812	Genbank	GQ982050	Genbank	
	Ocotea	JQ626098	Genbank	JQ626566	Genbank	
	Paraia			140037133	RBG	
	Persea	12-0028270	RBG	120028270	RBG	
	Pleurothyrium	150040009	RBG	150040009	RBG	
	Rhodostemonodaphne	JQ626255	Genbank	JQ626554	Genbank	
	Sextonia	JQ626173	Genbank	JQ626456	Genbank	
	Urbanodendron			AJ247191	Genbank	
	Williamodendron			AJ247192	Genbank	
	Lecythidaceae	Allantoma	AF077657	Genbank	140037120	RBG
		Asteranthos	Z80198	Genbank		
		Bertholletia	Z80178	Genbank		
		Cariniana	Z80179	Genbank	120028310	RBG
Corythophora		AF077653	Genbank	140037115	RBG	
Couratari		JQ626050	Genbank	JQ626511	Genbank	
Couroupita		Z80181	Genbank			
Eschweilera		JQ625971	Genbank	JQ626416	Genbank	
Grias		AF077652	Genbank			
Gustavia		JQ626207	Genbank	GQ982005	Genbank	
Lecythis		JQ626036	Genbank	JQ626453	Genbank	
Lepidobotryaceae	Ruptiliocarpon	AJ402997	Genbank	AY935918	Genbank	
Linaceae	Hebepetalum	HM544047	Genbank	HM544082	Genbank	

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Roucheria	FJ169603	Genbank	HM544121	Genbank
Loasaceae	Mentzelia	JF308670	Genbank	AF503308	Genbank
Loganiaceae	Antonia	JQ625999	Genbank	150038109	RBG
	Bonyunia	AJ235818	Genbank		
	Strychnos	JQ626240	Genbank	FJ514680	Genbank
Loranthaceae	Gaiadendron	GIDRBCL	Genbank	DQ787445	Genbank
Lythraceae	Adenaria	12-0028257	RBG	120028257	RBG
	Lafoensia	AY905411	Genbank	GQ982030	Genbank
	Physocalymma	120029829	RBG		
Magnoliaceae	Magnolia	12-0029855	RBG	AY008996	Genbank
	Talauma	L12666	Genbank	AF548642	Genbank
Malpighiaceae	Acmanthera	AF344454	Genbank	AF344524	Genbank
	Banisteriopsis	HQ247439	Genbank	HQ247199	Genbank
	Barnebya	AJ402924	Genbank	AF344531	Genbank
	Blepharandra	AF344461	Genbank	AF344532	Genbank
	Bunchosia	HQ247454	Genbank	HQ247225	Genbank
	Burdachia	AF344462	Genbank	AF344534	Genbank
	Byrsonima	AB233898	Genbank	AB233794	Genbank
	Dicella	HQ247479	Genbank	HQ247260	Genbank
	Diplopterys	AF344460	Genbank	AF344530	Genbank
	Glandonia	AF344478	Genbank	AF344548	Genbank
	Heteropterys	HQ247495	Genbank	HQ247284	Genbank
	Lophanthera	AF344491	Genbank	AF344559	Genbank
	Malpighia	HQ247542	Genbank	HQ247334	Genbank
	Mascagnia	AF344500	Genbank	HQ247347	Genbank
	Niedenzuella	HQ247566	Genbank	HQ247369	Genbank
	Pterandra	AF344506	Genbank	AF344573	Genbank
	Ptilochaeta	HQ247570	Genbank	HQ247376	Genbank
	Spachea	HQ247575	Genbank	HQ247380	Genbank
	Stigmaphyllon	AF344514	Genbank	HQ247393	Genbank
	Tetrapteryx	HQ247590	Genbank	HQ247398	Genbank
Malvaceae	Abutilon	12-0028266	RBG	120028266	RBG
	Apeiba	JQ625941	Genbank	JQ626394	Genbank
	Ayenia			130032602	RBG
	Bastardiopsis	KJ082134	Genbank	KJ012469	Genbank
	Bombax	AF022118	Genbank	AY321171	Genbank
	Byttneria	AF022123	Genbank	AY321196	Genbank
	Catostemma	JQ626285	Genbank	AY589069	Genbank
	Cavanillesia	GQ981691	Genbank	HQ696686	Genbank
	Ceiba	12-0029806	RBG	HQ696702	Genbank
	Christiana	AJ233149	Genbank		
	Eriotheca	12-0028226	RBG	120028226	RBG
	Gaya			FJ204706	Genbank
	Goethalsia	AJ233151.1	Genbank		
	Guazuma	GQ981753	Genbank	GQ982003	Genbank
	Helicteres	AJ233127	Genbank	AY321186	Genbank
	Heliocarpus	12-0029818	RBG	120029818	RBG
	Herrania	GQ981762	Genbank	GQ982011	Genbank
	Hibiscus	AY328174	Genbank	AF345329	Genbank
	Huberodendron	13-0032603	RBG	130032603	RBG



Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Luehea	BOLL121		120028254	RBG
	Lueheopsis	JQ626279	Genbank	140037124	RBG
	Malvaviscus	JQ592519	Genbank	JQ588237	Genbank
	Matisia	12-0028305	RBG	120028305	RBG
	Mollia			120029842	RBG
	Ochroma	AF022122	Genbank	AY321172	Genbank
	Pachira	AJ233119	Genbank	AY321170	Genbank
	Patinoa			AY589074	Genbank
	Pavonia	AJ233123	Genbank	AY589056	Genbank
	Pentaplaris	AJ233157	Genbank	AY321163	Genbank
	Phragmotheca			AY589068	Genbank
	Pseudobombax	GQ981847	Genbank	GQ982072	Genbank
	Quararibea	JQ626033	Genbank	JQ626452	Genbank
	Scleronema	12-0029665	RBG	120029665	RBG
	Septotheca			AY589073	Genbank
	Spirotheca			HQ696691	Genbank
	Sterculia	JQ626037	Genbank	JQ626455	Genbank
	Talipariti	AY289678	Genbank	AB233275	Genbank
	Tetrasida			150038128	RBG
	Theobroma	JQ626171	Genbank	FJ514692	Genbank
	Trichospermum	JQ594275	Genbank		
	Triumfetta	JF265638	Genbank	JF270979	Genbank
Marcgraviaceae	Marcgravia	Z83148	Genbank	AJ429289	Genbank
	Norantea	JQ625952	Genbank	JQ626401	Genbank
	Sarcopera	AF303124	Genbank		
	Schwartzia	AF303127	Genbank		
	Souroubea	AF303125	Genbank		
Melastomataceae	Adelobotrys	AF215530	Genbank		
	Behuria	JQ899085	Genbank		
	Bellucia	EU711385	Genbank		
	Blakea	EU711386	Genbank		
	Brachyotum			140037082	RBG
	Conostegia	EU711388	Genbank		
	Graffenrieda	AF215532	Genbank		
	Henriettea	HM446810	Genbank	HM446698	Genbank
	Henriettella	JQ626220	Genbank	150038121	RBG
	Huberia	JQ899092	Genbank		
	Leandra	GQ981785	Genbank	GQ982031	Genbank
	Loreya	JQ626318	Genbank	140037118	RBG
	Macairea	EU711394	Genbank		
	Meriania	EU711395	Genbank		
	Merianthera	JQ899101	Genbank		
	Miconia	JQ626214	Genbank	JQ626538	Genbank
	Mouriri	JQ626296	Genbank	JQ626576	Genbank
	Ossaea	13-0032605	RBG	130032605	RBG
	Tibouchina	150040010	RBG	150040010	RBG
	Tococa	AF215539	Genbank		
	Topobea	JQ899107	Genbank		
	Trembleya			130032606	RBG
	Wurdastom	KF407948	Genbank		

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
Meliaceae	Cabralea	DQ238055	Genbank		
	Carapa	AY128219	Genbank	AY128181	Genbank
	Cedrela	AY128220	Genbank	AY128182	Genbank
	Guarea	AY128229	Genbank	AY128188	Genbank
	Ruagea	DQ238057	Genbank	AY128198	Genbank
	Schmardaea			130034072	RBG
	Swietenia	AY128241	Genbank	AY128200	Genbank
	Trichilia	JQ626046	Genbank	JQ626491	Genbank
Menispermaceae	Abuta	JQ626102	Genbank	JQ626504	Genbank
Metteniusaceae	Metteniusa	AM421128	Genbank		
Monimiaceae	Hennecartia	AF022950	Genbank		
	Macropheplus	12-0029854	RBG		
	Macrotorus			150039162	RBG
	Mollinedia	AF050218	Genbank	GQ429060	Genbank
Moraceae	Bagassa	JQ625997	Genbank	JQ626434	Genbank
	Batocarpus	12-0029793	RBG	120029793	RBG
	Brosimum	JQ625739	Genbank	JQ626346	Genbank
	Castilla	JQ592803	Genbank	JQ588396	Genbank
	Castilla	JQ592803	Genbank	JQ588396	Genbank
	Castilla	JQ592803	Genbank	JQ588396	Genbank
	Castilla	JQ592803	Genbank	JQ588396	Genbank
	Clarisia	12-0029826	RBG	120029826	RBG
	Ficus	JQ626312	Genbank	JQ626578	Genbank
	Helianthostylis			140037106	RBG
	Helicostylis	JQ626081	Genbank	JQ626485	Genbank
	Maclura	12-0028256	RBG	120028256	RBG
	Maquira	JQ626014	Genbank	JQ626443	Genbank
	Morus			AF400590	Genbank
	Naucleopsis	JQ626013.1	RBG		
	Perebea	12-0029664	RBG	120029664	RBG
	Poulsenia	GQ981838	Genbank		
	Pseudolmedia	HM446858.1	Genbank	HM446734.1	Genbank
	Sorocea	12-0028296	RBG	120028306	RBG
	Trophis	KJ082625.1	Genbank	KJ012814.1	Genbank
Trymatococcus	JQ626260	Genbank	JQ626558	Genbank	
Muntingiaceae	Muntingia	Y15146	Genbank	FM179930	Genbank
Myricaceae	Morella			U92857	Genbank
	Myrica	AJ626757	Genbank	AY191715	Genbank
Myristicaceae	Compsonaura	EU090509	Genbank	EU090470	Genbank
	Iryanthera	JQ625975	Genbank	JQ626420	Genbank
	Osteophloeum	JQ625884	Genbank	JQ626371	Genbank
	Virola	JQ626059	Genbank	JQ626468	Genbank
Myrtaceae	Acca	150038523	RBG	150038523	RBG
	Amomyrtella			150038108	RBG
	Blepharocalyx			AY521531	Genbank
	Calycolpus	13-0032607	RBG	130032607	RBG
	Calyptranthes	12-0029828	RBG	120029828	RBG
	Campomanesia	12-0028308	RBG	120028308	RBG
	Eugenia	JQ625914	Genbank	JQ626380	Genbank
	Luma			AM489995	Genbank

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Marlierea	130032608	RBG	130032608	RBG
	Myrceugenia			AM490000	Genbank
	Myrcia	JQ626253	Genbank	JQ626553	Genbank
	Myrcianthes	MFU26328	Genbank	140037079	RBG
	Myrciaria	JQ626319	Genbank	140037136	RBG
	Neomitranthes	KF981266	Genbank	KF981344	Genbank
	Pimenta			AM490013	Genbank
	Plinia	JQ626311	Genbank	AM490007	Genbank
	Psidium	HM850290	Genbank	HM851054	Genbank
	Siphoneugena	12-0029816	RBG	120029816	RBG
	Syzygium	FJ976173	Genbank	GQ248207	Genbank
Nyctaginaceae	Bougainvillea	12-0028246	RBG	120028246	RBG
	Guapira	12-0028249	RBG	120028249	RBG
	Mirabilis	HM850179	Genbank	HM850884	Genbank
	Neea	JQ626040	Genbank	JQ626464	Genbank
	Pisonia	HM446854	Genbank	HM446731	Genbank
	Reichenbachia			140037094	RBG
Nymphaeaceae	Nymphaea	AB917059.1	Genbank	HQ592332.1	Genbank
Ochnaceae	Adenarake	KF263345	Genbank	KF263231	Genbank
	Blastemanthus	KF263343	Genbank	KF263229	Genbank
	Cespedesia	AJ420168	Genbank	EF135518	Genbank
	Elvasia	FJ670171	Genbank	FJ670028	Genbank
	Froesia	FJ670173	Genbank	FJ670036	Genbank
	Godoya	KF263352	Genbank	KF263236	Genbank
	Lacunaria	JQ626113	Genbank	140037117	RBG
	Luxemburgia	Z75685	Genbank		
	Ouratea	JQ625759	Genbank		
	Philacra	KF263408	Genbank	KF263286	Genbank
	Poecilandra	KF263357	Genbank		
	Quiina	AF206815	Genbank	EF135589	Genbank
	Touroulia	Z75690	Genbank	FJ670037	Genbank
	Tyleria	KF263344	Genbank	KF263230	Genbank
	Wallacea	KF263363	Genbank		
Olacaceae	Aptandra	DQ790141	Genbank	DQ790178	Genbank
	Cathedra	JQ625808	Genbank	DQ790182	Genbank
	Chaunochiton	DQ790142	Genbank	DQ790179	Genbank
	Curupira	DQ790150	Genbank	DQ790187	Genbank
	Dulacia	DQ790137	Genbank	DQ790174	Genbank
	Heisteria	DQ790160	Genbank	DQ790196	Genbank
	Maburea	DQ790165	Genbank	DQ790201	Genbank
	Minquartia	FJ038137	Genbank	DQ790185	Genbank
	Ptychopetalum	JQ626003	Genbank	JQ626439	Genbank
	Tetrastylidium	DQ790154	Genbank	DQ790190	Genbank
Oleaceae	Chionanthus	DQ673309	Genbank	HM751206	Genbank
	Priogymnanthus			140037095	RBG
Onagraceae	Fuchsia	HM850012	Genbank	HM851003	Genbank
	Ludwigia	LUDRBLX	Genbank	GU134991	Genbank
Opiliaceae	Agonandra	JQ625908	Genbank	JQ626377	Genbank
Papaveraceae	Bocconia			130034073	RBG
Pentaphragaceae	Ternstroemia	AF380065	Genbank	AF380110	Genbank

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
Peridiscaceae	Peridiscus	AY380356	Genbank	DQ411570	Genbank
Phyllanthaceae	Amanoa	AY663562	Genbank	AY830258	Genbank
	Astrocasia	AY663569	Genbank	AY830261	Genbank
	Didymocistus	AY663581	Genbank		
	Discocarpus	AY663582	Genbank	AY830267	Genbank
	Gonatogyne	AJ418815	Genbank	AY552429	Genbank
	Hieronyma	AY830387	Genbank	AY830268	Genbank
	Jablonskia	AY663590	Genbank		
	Margaritaria	GQ981795	Genbank	GQ982040	Genbank
	Phyllanthus	12-0029817	RBG	120029817	RBG
	Richeria	AY663616	Genbank	AY830281	Genbank
Phytolaccaceae	Gallesia	12-0028302	RBG	AY042590	Genbank
	Phytolacca	12-0028260	RBG	120028260	RBG
	Seguieria	12-0028250	RBG	120028250	RBG
Picramniaceae	Alvaradoa	AF123277	Genbank		
	Picramnia	AF127025	Genbank		
Picrodendraceae	Piranhea	12-0029847	RBG		
	Podocalyx	AY663647	Genbank	EF135583	Genbank
Piperaceae	Piper	AY572252	Genbank	DQ882201	Genbank
Poaceae	Guadua	12-0028311	RBG	120028311	RBG
Polemoniaceae	Cantua	AY725864	Genbank	L48566	Genbank
Polygalaceae	Acanthocladus	AM234190	Genbank		
	Bredemeyera	EU644699	Genbank	EU596520	Genbank
	Moutabea	JQ625841	Genbank	JQ626362	Genbank
	Securidaca	EU644681	Genbank	EU604029	Genbank
Polygonaceae	Coccoloba	JQ626225	Genbank	JQ626541	Genbank
	Ruprechtia	12-0028233	RBG	120028233	RBG
	Symmeria	GQ206235	Genbank	GQ206209	Genbank
	Triplaris	Y16910	Genbank	AY042668	Genbank
Primulaceae	Ardisia			GU134982	Genbank
	Bonellia	12-0029856	RBG	120029856	RBG
	Clavija	CLJCPRBCLA	Genbank	120028286	RBG
	Cybianthus			120029827	RBG
	Embelia	JF738675	Genbank		
	Geissanthus	AF213810	Genbank		
	Jacquinia	AF213816	Genbank	12-0029856	RBG
	Myrsine	12-0029815	RBG	120029815	RBG
	Parathesis	AF213814	Genbank		
	Stylogyne	12-0029827	RBG	120029827	RBG
Proteaceae	Euplassa	PER029	Genbank	EU642689	Genbank
	Oreocallis	130034080	RBG	130034080	RBG
	Panopsis	DQ875850	Genbank	EU642708	Genbank
	Roupala	12-0028232	RBG	120028232	RBG
Putranjivaceae	Drypetes	12-0028225	RBG	120028225	RBG
Quillajaceae	Quillaja	U06822	Genbank	AY386843	Genbank
Rhabdodendraceae	Rhabdodendron	JQ625835	Genbank	JQ626361	Genbank
Rhamnaceae	Ampelozizyphus	AJ390037.1	Genbank		
	Colletia	CUU59819	Genbank		
	Colubrina	AJ390047	Genbank	GU135023	Genbank
	Condalia	12-0028242	RBG	120028242	RBG

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Rhamnidium	12-0028297	RBG	120028297	RBG
	Rhamnus	KJ082543.1	Genbank	KJ012751.1	Genbank
	Sageretia	AJ225785	Genbank	130034074	RBG
	Scutia	AJ390033	Genbank	140037081	RBG
	Ziziphus	AJ390052	Genbank	AF049848	Genbank
Rhizophoraceae	Cassipourea	JQ625770	Genbank	HM446665	Genbank
	Paradrypetes	FJ670175	Genbank	FJ670039	Genbank
	Rhizophora	AF127687	Genbank	AF329465	Genbank
	Sterigmapetalum	AF127671	Genbank	120029666	RBG
Rosaceae	Kageneckia	KAU06808	Genbank	DQ860447	Genbank
	Prunus	12-0029792	RBG	120029792	RBG
Rubiaceae	Alibertia	Z68843	Genbank	GQ981930	Genbank
	Alseis	Y18709	Genbank	FJ905331	Genbank
	Amaioua	JQ626322	Genbank	GQ981931	Genbank
	Arachnothryx	JQ594657	Genbank	JQ589669	Genbank
	Bathysa	AM117206	Genbank	FJ905336	Genbank
	Bertiera	AJ224845	Genbank	HM119515	Genbank
	Borojoa	AJ286694	Genbank	GQ981946	Genbank
	Bothriospora			FJ905339	Genbank
	Botryarrhena	PER008	Genbank	120029648	RBG
	Calycophyllum	12-0028303	RBG	120028303	RBG
	Capirona	JQ626324	Genbank	120029649	RBG
	Carapichea	AJ002184	Genbank		
	Chimarrhis	JQ626106	Genbank	JQ626508	Genbank
	Chiococca	CCWCPRBCL	Genbank	AY538378	Genbank
	Chione	AM117215	Genbank		
	Chomelia	GQ852316	Genbank	140037128	RBG
	Cinchona	AY538478	Genbank	AY538379	Genbank
	Cinchonopsis	AY538482	Genbank	AY538383	Genbank
	Coccocypselum	FJ209066	Genbank		
	Condaminea	HM164161	Genbank	FJ905347	Genbank
	Cordia	150038163	RBG	150038163	RBG
	Cosmibuena	AY538483	Genbank	AY538385	Genbank
	Coussarea	12-0029824	RBG	120029824	RBG
	Coutarea	AM117221	Genbank	GQ981975	Genbank
	Dendrosipanea	HM164162	Genbank	FJ905324	Genbank
	Dialypetalanthus	AJ251366	Genbank	FJ905348	Genbank
	Dolichodelphys			FJ905350	Genbank
	Duroia	JQ626024	Genbank	JQ626449	Genbank
	Elaeagia			FJ905355	Genbank
	Erithalis	X83635	Genbank		
	Exostema	12-0029810	RBG	120029810	RBG
	Faramea	GQ981734	Genbank	GQ981990	Genbank
	Ferdinandusa	JQ625906	Genbank	JQ626376	Genbank
	Genipa	Z68839	Genbank	AY538388	Genbank
	Gonzalagunia	HM446803	Genbank	HM446693	Genbank
	Guettarda	GQ981754	Genbank	GQ982004	Genbank
	Hamelia	GQ981757	Genbank	GQ982006	Genbank
	Henriquezia	140037121	RBG		
	Hillia	AM117233	Genbank		

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Hippotis	HM164165	Genbank	FJ905365	Genbank
	Isertia	AY538489	Genbank	AY538393	Genbank
	Ixora	EU817422	Genbank	HM119545	Genbank
	Joosia	AY538492	Genbank	AY538396	Genbank
	Kerianthera	AY538493	Genbank	AY538397	Genbank
	Kutchubaea	AM117235	Genbank	140037113	RBG
	Ladenbergia	AY538494	Genbank	AY538398	Genbank
	Macbrideina			FJ905366	Genbank
	Machaonia	GQ852339	Genbank	150038129	RBG
	Macrocnemum	12-0028309	RBG	120028309	RBG
	Malanea	AM117245	Genbank		
	Margaritopsis	AM117247	Genbank	140037114	RBG
	Melanopsidium			130032611	RBG
	Molopanthera	HM164172	Genbank		
	Morinda	AJ318448	Genbank	JF954629	Genbank
	Oxyanthus	Z68836	Genbank	HM119554	Genbank
	Pagamea	PER064			
	Palicourea	JQ625897	Genbank	GQ982058	Genbank
	Parachimarrhis			150038526	RBG
	Pentagonia	X83658	Genbank	FJ905374	Genbank
	Pogonopus	12-0028290	RBG	120028290	RBG
	Posoqueria	Z68850	Genbank	AY538412	Genbank
	Psychotria	JQ625868	Genbank	JQ626366	Genbank
	Randia	Z68832	Genbank	HM119563	Genbank
	Remijia	AY538505	Genbank	AY538416	Genbank
	Retiniphyllum	AF331654	Genbank		
	Rondeletia	AM117265	Genbank	HM446741	Genbank
	Rosenbergiodendron	HM164177	Genbank	HM119566	Genbank
	Rudgea	Z68821	Genbank	130034075	RBG
	Rustia	Y18716	Genbank	FJ905380	Genbank
	Salzmannia	13-0032612	RBG		
	Semaphyllanthe			FJ905387	Genbank
	Simira	HM164179	Genbank	FJ905388	Genbank
	Sommeria	AM117278.1	Genbank	FJ905394.1	Genbank
	Sphinctanthus	12-0029834	RBG	120029834	RBG
	Stachyarrhena	JQ625826	Genbank	JQ626359	Genbank
	Stilpnophyllum	AY538510	Genbank	AY538422	Genbank
	Tocoyena	HM164181	Genbank	HM119571	Genbank
	Uncaria	AJ347007	Genbank		
	Warszewiczia	Y18722	Genbank	FJ905398	Genbank
	Wittmackanthus			FJ905399	Genbank
Rutaceae	Adiscanthus			140037125	RBG
	Amyris	KJ082118	Genbank	KJ012461	Genbank
	Angostura	JQ593927	Genbank	JQ589080	Genbank
	Balfourodendron			FJ716747	Genbank
	Casimiroa	EU042975	Genbank	EU042837	Genbank
	Citrus	AB505950	Genbank	FJ716730	Genbank
	Conchocarpus			130032615	RBG
	Dictyoloma	12-0029813	RBG		
	Erythrochiton	12-0028294	RBG		

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Esenbeckia	12-0028271	RBG	120028271	RBG
	Euxylophora			150038117	RBG
	Galipea	150040015	RBG	150040015	RBG
	Helietta			140037103	RBG
	Hortia	JQ625842	Genbank	130034084	RBG
	Metrodorea			130032616	RBG
	Pilocarpus	AF066809	Genbank		
	Raputia			140037134	RBG
	Rauia			130034076	RBG
	Ravenia			FJ716746	Genbank
	Spathelia	AF066798	Genbank	FJ716739	Genbank
	Toxosiphon	JQ593943.1	Genbank	JQ589090.1	Genbank
	Zanthoxylum	12-0028237	RBG	120028237	RBG
Sabiaceae	Meliosma	HM446826	Genbank	HM446712	Genbank
	Ophiocaryon	PER059			
Salicaceae	Abatia	AF206726	Genbank	EF135498	Genbank
	Azara	AJ418820	Genbank		
	Banara	12-0028307	RBG	120028307	RBG
	Casearia	JQ626018	Genbank	JQ626446	Genbank
	Flacourtia	AF206768	Genbank	EF135541	Genbank
	Hasseltia	12-0028227	RBG	12-0028227	RBG
	Homalium	AJ418822	Genbank	HM446700	Genbank
	Laetia	JQ625734	Genbank	JQ626344	Genbank
	Lunania	AB233936	Genbank	AB233832	Genbank
	Pleuranthodendron	AJ418832	Genbank		
	Prockia	AJ418831	Genbank	EF135588	Genbank
	Ryania			150038124	RBG
	Salix	12-0028276	RBG	120028276	RBG
	Tetrathylacium			GQ982110	Genbank
	Xylosma	JQ625911	Genbank	JQ626379	Genbank
	Zuelania	GQ981924	Genbank		
Santalaceae	Acanthosyris	DQ329172	Genbank	DQ329183	Genbank
	Jodina			150038120	RBG
Sapindaceae	Allophylus	JQ626023	Genbank	EU720665	Genbank
	Athyana			140037087	RBG
	Averrhoidium			150038110	RBG
	Cupania	12-0029794	RBG	120029794	RBG
	Diatenopteryx	AJ402943	Genbank	EU720682	Genbank
	Dilodendron	12-0029821	RBG	120029821	RBG
	Diplokeleba	12-0029843	RBG	120029843	RBG
	Dodonaea	AM235129	Genbank	EU720567	Genbank
	Magonia			140037096	RBG
	Matayba	JQ625852	Genbank	EU720676	Genbank
	Melicoccus	JQ626266	Genbank	EU720610	Genbank
	Porocystis			150038123	RBG
	Pseudima			140037110	RBG
	Sapindus	AY724366	Genbank	AY724324	Genbank
	Scyphonychium			EU720672	Genbank
	Serjania	AJ403001	Genbank	EU720640	Genbank
	Talisia	AJ403008	Genbank	EU720643	Genbank

Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
	Vouarana	JQ626103	Genbank	EU720673	Genbank
Sapotaceae	Chromolucuma	EF558591	Genbank		
	Chrysophyllum	JQ626243	Genbank	JQ626548	Genbank
	Diploon	JQ626045	Genbank	JQ626461	Genbank
	Ecclinusa	JQ626076	Genbank	150038116	RBG
	Elaeoluma	JQ626242	Genbank	JQ626547	Genbank
	Manilkara	JQ625936	Genbank	JQ626390	Genbank
	Micropholis	JQ625973	Genbank	JQ626417	Genbank
	Planchonella	GQ248683	Genbank	GQ248187	Genbank
	Pouteria	JQ625955	Genbank	JQ626403	Genbank
	Pradosia	JQ626027	Genbank	JQ626386	Genbank
	Sarcaulus	DQ377537	Genbank	150040018	RBG
	Sideroxylon	Z83136	Genbank	GQ429074	Genbank
Schoepfiaceae	Schoepfia	SHOCPRBCL	Genbank	AY957454	Genbank
Scrophulariaceae	Buddleja	AJ001758	Genbank	AJ429346	Genbank
	Peltanthera	AJ001762	Genbank	AJ429330	Genbank
Simaroubaceae	Castela	EU042989	Genbank	EU042851	Genbank
	Picrasma	EU043010	Genbank	EU042872	Genbank
	Picrolemma	EU043013	Genbank		
	Quassia	EU043017	Genbank	EU042879	Genbank
	Simaba	EU043024	Genbank	EU042886	Genbank
	Simarouba	EU043036	Genbank	EU042898	Genbank
Siparunaceae	Siparuna	JQ626097	Genbank	JQ626498	Genbank
Solanaceae	Acnistus	12-0028239	RBG	120028239	RBG
	Aureliana			EF537319	Genbank
	Brugmansia	HM849829	Genbank	HM851090	Genbank
	Brunfelsia	HM446761	Genbank	HM446659	Genbank
	Capsicum	12-0029804	RBG	120029804	RBG
	Cestrum	12-0028238	RBG	120028238	RBG
	Duckeodendron	Y14760	Genbank	140037108	RBG
	Dunalia			EF438836	Genbank
	Grabowskia	HQ216120	Genbank	140037077	RBG
	Lycianthes	12-0028243	RBG	120028243	RBG
	Lycium	HQ216128	Genbank	AB036627	Genbank
	Metternichia	AF022182	Genbank		
	Nicotiana	12-0029799	RBG	120029799	RBG
	Solanum	HM850361	Genbank	HM851097	Genbank
	Vassobia	12-0028236	RBG	120028236	RBG
Staphyleaceae	Turpinia	BOLLC394		GQ982121	Genbank
Stemonuraceae	Discophora	JQ625904	Genbank	JQ626375	Genbank
Strelitziaceae	Phenakospermum	AF243845	Genbank	AF478911	Genbank
Styracaceae	Styrax	JQ626303	Genbank	JQ626577	Genbank
Symplocaceae	Symplocos	JQ625921	Genbank	AY630657	Genbank
Tamaricaceae	Myricaria	AY099907	Genbank		
Tapisciaceae	Huerteia	AY646109	Genbank	FM179926	Genbank
Tetrameristaceae	Pentamerista	AY725860	Genbank		
Theaceae	Gordonia	AF380042	Genbank	AF380085	Genbank
	Laplacea	AF380045	Genbank	AF380088	Genbank
Thymelaeaceae	Daphnopsis	HM446790	Genbank	HM446682	Genbank
Ticodendraceae	Ticodendron	AB015455.1	Genbank	U92855.1	Genbank



Family	Genus	<i>rbcL</i>	source <i>rbcL</i>	<i>matK</i>	source <i>matK</i>
Trigoniaceae	Trigonia	AB233848	Genbank	AB233744	Genbank
Ulmaceae	Ampelocera	12-0029820	RBG	12-0029820	RBG
	Phyllostylon	BOLXX091		140037091	RBG
Urticaceae	Boehmeria	12-0029802	RBG	120029802	RBG
	Cecropia	JQ626251	Genbank	JQ626552	Genbank
	Coussapoa	12-0029822	RBG	120029822	RBG
	Myriocarpa	KF138193.1	Genbank	KF138021.1	Genbank
	Pourouma	JQ626107	Genbank	JQ626509	Genbank
	Pouzolzia	JF265556	Genbank	JF270899	Genbank
	Urera	12-0028247	RBG	120028247	RBG
	Urtica	FJ432249	Genbank	EU002192	Genbank
Velloziaceae	Vellozia	VELCPRBCL	Genbank	130034065	RBG
Verbenaceae	Aloysia	12-0028259	RBG	120028259	RBG
	Citharexylum	HM853911	Genbank	HM853879	Genbank
	Duranta	12-0028267	RBG	120028267	RBG
	Lantana	HM850104	Genbank	HM850972	Genbank
	Lippia	HM853891	Genbank	HM853858	Genbank
	Recordia	HM853919	Genbank	HM853888	Genbank
	Stachytarpheta	GU135267	Genbank		
Violaceae	Amphirrhox	AB354404	Genbank	AB354476	Genbank
	Fusispermum	AB354410	Genbank	AB354482	Genbank
	Gloeospermum	AB354413	Genbank	AB354485	Genbank
	Leonia	JQ626288	Genbank	JQ626572	Genbank
	Orthion	AB233941.1	Genbank	AB233837.1	Genbank
	Paypayrola	AB354429	Genbank	AB354501	Genbank
	Rinorea	AB354430	Genbank	AB354502	Genbank
	Rinoreocarpus	AB354435	Genbank	AB354507	Genbank
Vochysiaceae	Callisthene			130032617	RBG
	Erisma	JQ626108	Genbank	JQ626510	Genbank
	Qualea	JQ626047	Genbank	JQ626462	Genbank
	Ruizterania	JQ626202	Genbank	JQ626501	Genbank
	Salvertia			130032618	RBG
	Vochysia	JQ625791	Genbank	JQ626355	Genbank
Winteraceae	Drimys	EU669518	Genbank	EU669474	Genbank
Ximeniaceae	Ximenia	DQ790149	Genbank	DQ790186	Genbank
Zygophyllaceae	Bulnesia	EU002275	Genbank	EU002172	Genbank
	Larrea	AF200471	Genbank	AF542602	Genbank
	Porlieria	12-0029807	RBG	12-0029807	RBG

## Appendix 3.2 List of fossil-derived calibrations

**Table A.3.2.1** List of angiosperm clades (nodes) used to date the phylogeny via fossil-derived calibrations, taxa assigned as a reference for fossil placement, minimum age used as offset, mean age of the clades, and their respective sources. Ages in Ma.

Clade	Taxa 1	Taxa 2	Minimum age	Mean age	Source
Winteraceae	Drimys	Cinnamodendron	100	125	Magallon et al.,2015
Magnoliales	Magnolia	Diclinanona	86.4	108	Magallon et al.,2015
Arecaceae	Guadua	Mauritia	66.8	83.5	Magallon et al.,2015
Eudicotyledoneae	Abuta	Acalypha	100	125	Magallon et al.,2015
Ranunculales	Bocconia	Abuta	89.6	112	Magallon et al.,2015
Pentapetalae	Davilla	Matisia	79.68	99.6	Magallon et al.,2015
Dilleniales	Tetracera	Curatella	38.88	48.6	Magallon et al.,2015
Santalales	Jodina	Pouteria	56.48	70.6	Magallon et al.,2015
Loranthaceae	Gaiadendron	Schoepfia	52.4	65.5	Magallon et al.,2015
Phytolaccaceae <sup>''</sup>	Guapira	Seguieria	56.48	70.6	Magallon et al.,2015
Nyssaceae	Cornus	Mentzelia	70	87.5	Magallon et al.,2015
Ebenaceae	Diospyros	Cybianthus	27.12	33.9	Magallon et al.,2015
Ericaceae	Agarista	Saurauia	71.44	89.3	Magallon et al.,2015
Solanaceae	Solanum	Ipomoea	27.12	33.9	Magallon et al.,2015
Rubiaceae	Cinchonopsis	Psychotria	29.76	37.2	Magallon et al.,2015
Apocynaceae	Potalia	Geissospermum	29.76	37.2	Magallon et al.,2015
Bignoniaceae	Jacaranda	Tecoma	31.04	38.8	Magallon et al.,2015
Acanthaceae	Avicennia	Ruellia	22.72	28.4	Magallon et al.,2015
Lamiaceae	Callicarpa	Vitex	22.72	28.4	Magallon et al.,2015
Asteraceae	Lychnophora	Columellia	38.08	47.6	Magallon et al.,2015
Araliaceae	Schefflera	Dendropanax	29.76	37.2	Magallon et al.,2015
Combretaceae	Fuchsia	Terminalia	70	87.5	Magallon et al.,2015
Lythraceae	Lafoensia	Physocalymma	56.48	70.6	Magallon et al.,2015

Clade	Taxa 1	Taxa 2	Minimum age	Mean age	Source
Myrtaceae	Vochysia	Calypttranthes	66.8	83.5	Magallon et al.,2015
Burseraceae	Bursera	Protium	38.88	48.6	Magallon et al.,2015
Meliaceae	Swietenia	Trichilia	38.88	48.6	Magallon et al.,2015
Rutaceae	Spathelia	Zanthoxylum	52.4	65.5	Magallon et al.,2015
Malvaceae	Bixa	Theobroma	44.64	55.8	Magallon et al.,2015
Brassicales	Capparis	Eriotheca	71.44	89.3	Magallon et al.,2015
Mimosoideae	Diptychandra	Inga	38.88	48.6	Magallon et al.,2015
Papilionoideae	Dicorynia	Swartzia	44.64	55.8	Magallon et al.,2015
Rhamnaceae	Colletia	Ziziphus	38.88	48.6	Magallon et al.,2015
Ulmaceae	Ampelocera	Maquira	44.64	55.8	Magallon et al.,2015
Fagales	Anisophyllea	Juglans	70	87.5	Magallon et al.,2015
Betulaceae	Ticodendron	Alnus	66.8	83.5	Magallon et al.,2015
Celastraceae	Zinowiewia	Plenckia	29.76	37.2	Magallon et al.,2015
Cunoniaceae	Weinmannia	Sloanea	63.36	79.2	Magallon et al.,2015
Elaeocarpaceae	Sloanea	Crinodendron	49.36	61.7	Magallon et al.,2015
Clusiaceae	Garcinia	Bonnetia	71.44	89.3	Magallon et al.,2015
Tetrapterys	Tetrapterys	Malpighia	22.72	28.4	Magallon et al.,2015
Euphorbioideae	Hevea	Acalypha	29.76	37.2	Magallon et al.,2015
Anaxagorea	Anaxagorea	-	72.352	90.44	Baker et al., 2014
Bocageopsis	Bocageopsis	-	4.784	5.98	Baker et al., 2014
Duguetia	Duguetia	-	24.512	30.64	Baker et al., 2014
Fusaea	Fusaea	-	24.512	30.64	Baker et al., 2014
Guatteria	Guatteria	-	44.664	55.83	Baker et al., 2014
Malmea	Malmea	-	15.992	19.99	Baker et al., 2014
Pseudoxandra	Pseudoxandra	-	12.072	15.09	Baker et al., 2014
Unonopsis	Unonopsis	-	6.352	7.94	Baker et al., 2014
Xylophia	Xylophia	-	39.984	49.98	Baker et al., 2014
Dacryodes	Dacryodes	-	30.4	38	Baker et al., 2014
Protium	Protium	-	42	52.5	Baker et al., 2014

Clade	Taxa 1	Taxa 2	Minimum age	Mean age	Source
Andira	Andira	-	14.008	17.51	Baker et al., 2014
Cynometra	Cynometra	-	10.344	12.93	Baker et al., 2014
Dialium	Dialium	-	8.72	10.9	Baker et al., 2014
Dicorynia	Dicorynia	-	8.72	10.9	Baker et al., 2014
Dicymbe	Dicymbe	-	9.6	12	Baker et al., 2014
Diplotropis	Diplotropis	-	16.216	20.27	Baker et al., 2014
Dipteryx	Dipteryx	-	21.152	26.44	Baker et al., 2014
Eperua	Eperua	-	9.856	12.32	Baker et al., 2014
Hymenaea	Hymenaea	-	19.736	24.67	Baker et al., 2014
Inga	Inga	-	8	10	Baker et al., 2014
Lonchocarpus	Lonchocarpus	-	12.056	15.07	Baker et al., 2014
Macrobium	Macrobium	-	25.6	32	Baker et al., 2014
Ormosia	Ormosia	-	32.496	40.62	Baker et al., 2014
Parkia	Parkia	-	36.4	45.5	Baker et al., 2014
Peltogyne	Peltogyne	-	23.04	28.8	Baker et al., 2014
Poecilanthe	Poecilanthe	-	32.792	40.99	Baker et al., 2014
Pterocarpus	Pterocarpus	-	13.328	16.66	Baker et al., 2014
Swartzia	Swartzia	-	36.768	45.96	Baker et al., 2014
Tachigali	Tachigali	-	3.72	4.65	Baker et al., 2014
Vouacapoua	Vouacapoua	-	38.952	48.69	Baker et al., 2014
Zygia	Zygia	-	14.256	17.82	Baker et al., 2014
Carapa	Carapa	-	23.6	29.5	Baker et al., 2014
Guarea	Guarea	-	11.84	14.8	Baker et al., 2014
Brosimum	Brosimum	-	38.4	48	Baker et al., 2014
Castilla	Castilla	-	17.6	22	Baker et al., 2014
Clarisia	Clarisia	-	52	65	Baker et al., 2014
Helicostylis	Helicostylis	-	22.4	28	Baker et al., 2014
Poulsenia	Poulsenia	-	17.6	22	Baker et al., 2014
Pseudolmedia	Pseudolmedia	-	28.8	36	Baker et al., 2014

Clade	Taxa 1	Taxa 2	Minimum age	Mean age	Source
Sorocea	Sorocea	-	47.2	59	Baker et al., 2014
Iryanthera	Iryanthera	-	15.2	19	Baker et al., 2014
Virola	Virola	-	13.6	17	Baker et al., 2014
Cecropia	Cecropia	-	35.2	44	Baker et al., 2014
Pourouma	Pourouma	-	35.2	44	Baker et al., 2014

### Appendix 3.3 Biodiversity metrics

**Table A.3.3. 1** Biodiversity metrics, their respective abbreviations, formulas, and descriptions.

Diversity metric	Code	Formula	Description
Genus richness	GR	$GR = \sum_{i=1}^n G_i$ , where $i$ is each individual genus	The total number of genera in a community – richness
Shannon	H'	$H' = \sum p_i \ln p_i$ , where $p_i$ is the proportion of stems of genus $i$ in the plot	Diversity index including both genus richness and abundance
Simpson index of diversity	S	$\lambda = 1 - \sum p_i^2$	Probability that two individuals randomly selected from a community belong to different genera
Fisher's $\alpha$	$\alpha$	$G = \alpha \ln(1 + N/\alpha)$ , where $G$ is the number of genera per plot, $N$ is the number of stems	Fisher's $\alpha$ : a constant derived from the log series distribution of taxa abundance

Diversity metric	Code	Formula	Description
Phylogenetic diversity	PD	$PD_{ss} = \sum_i^B L_i$ , where $L_i$ is the branch length, $B$ is the number of branches in a tree	Total branch lengths of the phylogeny representing all genera in a given community
Mean pairwise taxon distance	MPD	$mpd = \frac{\sum_i^n \sum_j^n d_{ij}}{n}$ , where $d_{ij}$ is the pd between genus $i$ and $j$ and $n$ is total number of genera	Mean of all distances connecting the genera in a specific community
Mean nearest taxon distance	MNTD	$mntd = \frac{\sum_i^n \min d_{ij}}{n}$	Mean phylogenetic distance between each species and its closest relative per plot
Standardized phylogenetic diversity	ses.PD	Deviation of $PD_{ss}$ from a null expectation	Standardized effect size of phylogenetic diversity in communities
Standardized mean pairwise taxon distance	ses.MPD	Deviation of $mpd$ from a null expectation	Standardized effect size of mean pairwise distances in communities

Diversity metric	Code	Formula	Description
Standardized mean nearest taxon distance	ses.MNTD	Deviation of <i>mntd</i> from a null expectation	Standardized effect size of mean nearest taxon distances in communities

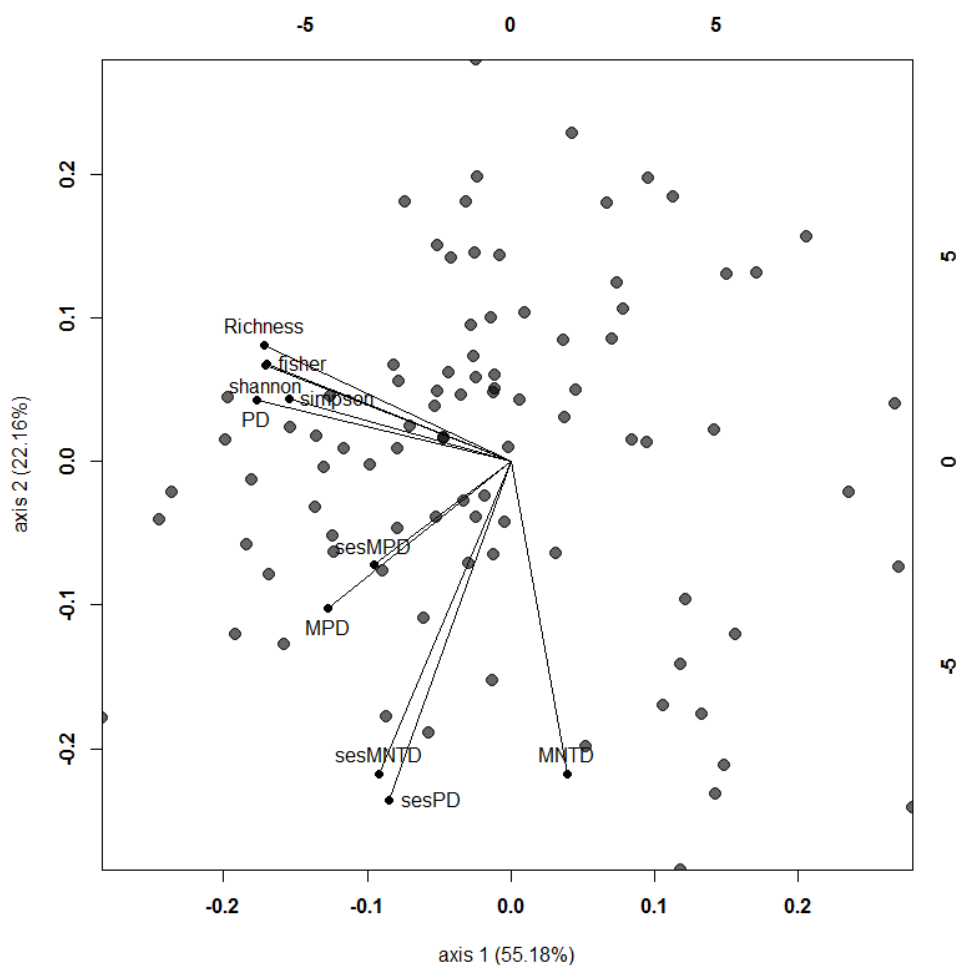


### Appendix 3.4 Association between biodiversity metrics

Traditional and phylogenetic diversity metrics represent different aspects of biodiversity, reflected by three main axis of variation (Table A.3.4.1; Figure A.3.4.1). Common diversity metrics (i.e. richness, Shannon, Simpson and Fisher's Alpha) vary in similar ways reflecting variation in species number and their respective abundances. Raw phylogenetic diversity (or PDss) correlates strongly with this axis. In contrast, other aspects of phylogenetic diversity are reflected in two other dimensions of diversity (Tucker *et al.* 2016). The second axis detected the overall tree topology (ses.PD) and relatedness among lineages closer to the tips (MNTD and ses.MNTD) and a third axis of variation showed patterns at deep phylogenetic nodes (MPD and ses.MPD).

**Table A.3.4.1** Results of Principal Component analyses of 10 diversity metrics in 90 plots across Amazonia.

Diversity metric	PC1	PC2	PC3
Genus richness	-0.40	0.19	-0.01
Shannon	-0.40	0.16	-0.20
Simpson index	-0.36	0.10	-0.27
Fisher's alpha	-0.39	0.16	-0.11
PD	-0.41	0.10	-0.03
Total lineage diversity	-0.20	-0.55	-0.10
MNTD	0.09	-0.51	-0.27
Neighbour lineage diversity	-0.21	-0.51	-0.19
Basal lineage diversity	-0.30	-0.24	0.32
sesMPD	-0.22	-0.17	0.81
% Variance explained	55.18	22.16	9.40



**Figure A.3.4.1** Two first axis of Principal Component Analyses (PCA) of ten diversity metrics, including four traditional measurements: Genus richness, Fisher’s Alpha, Shannon and Simpson indexes, and also six phylogenetic diversity metrics: Phylogenetic diversity stricto sensu (PD), total lineage diversity (sesPD), Mean pairwise taxon distance (MPD), basal lineage diversity (sesMPD), Mean Nearest taxon distance (MNTD) and Neighbour lineage diversity (sesMNTD).

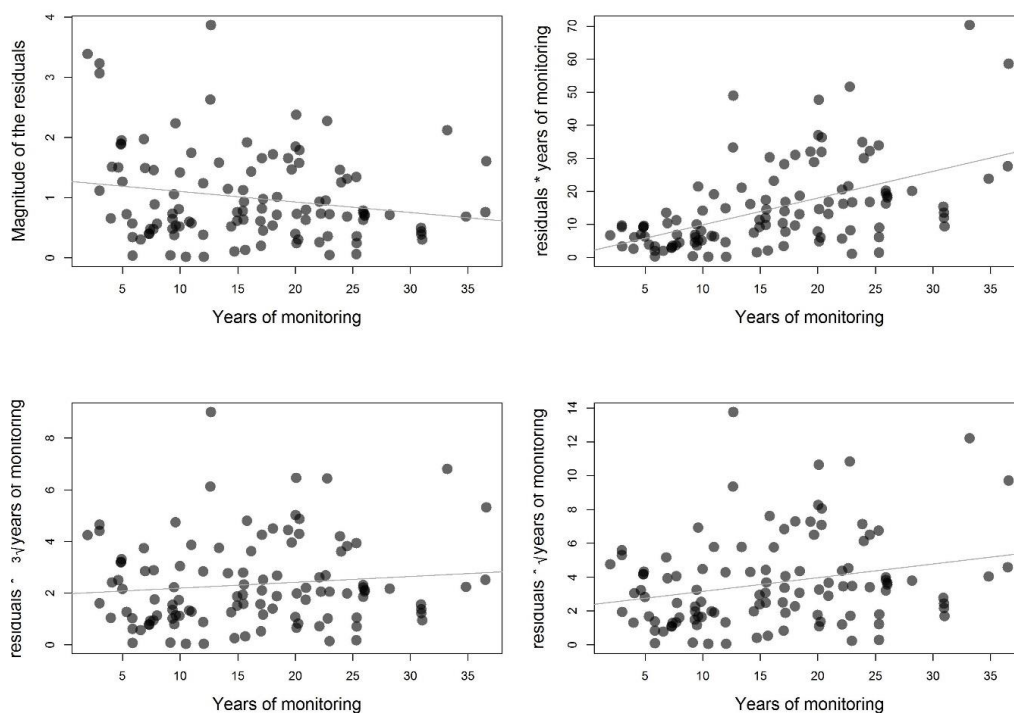
### Appendix 3.5 Weighting of wood productivity and aboveground biomass

Total census length is expected to affect estimates of aboveground wood productivity (AGWP) and aboveground biomass (AGB), with plots monitored over short total census length being more likely to be affected due to stochastic changes over time and measurement errors. Overall, variance of the residuals was greater among plots monitored over shorter total census length and smaller for longer total census length (Figure A.3.5.1). In order to reduce the influence of potential stochastic changes I explicitly tested for the effect of total monitoring

period on wood productivity estimates, using a procedure developed by Lewis *et al.* (2009). Here I found that the cube root of total census length best removed patterns from the residuals (Figure A.3.5.1), and so, to control for the observed variance in the residuals, I weighted AGWP by the cube root of the total census length. Aboveground biomass estimates were calculated by averaging values across multiple censuses. Because census interval varied within plots, mean values were weighted according to each census interval using a trapezoidal rule numerical integration. This method is simply a weighted average that allows more precise estimation of mean values when intervals are unequally spaced:

$$\int_a^b f(x)dx \approx \frac{1}{2} \frac{1}{b-a} \sum_{i=1}^{N-1} (AGB_{i+1} + AGB_i)(Yr_{i+1} - Yr_i)$$

where  $N$  is the number of census interval,  $a$  is the year of the first census and  $b$  the year when the plot was last monitored,  $AGB_i$  is the value of aboveground biomass at year  $i$ ,  $Yr_i$  is the year of census monitoring.



**Figure A.3.5.1** Standardised residuals from wood productivity (AGWP) versus years of monitoring with different weights to remove patterns from the residuals, for 90 permanent inventory plots located in lowland moist forest across the Amazon Basin. Weights all plots: a) equally ( $\text{adj}R^2 = 0.02$   $p = 0.04$ ); b) by years of monitoring ( $\text{adj}R^2 = 0.26$   $p < 0.001$ ); c) by the cube root of years of monitoring ( $\text{adj}R^2 = 0.003$   $p = 0.24$ ) and d) by the square root of the years of monitoring ( $\text{adj}R^2 = 0.05$   $p = 0.008$ ).

### Appendix 3.6 Principal component analyses for soil texture

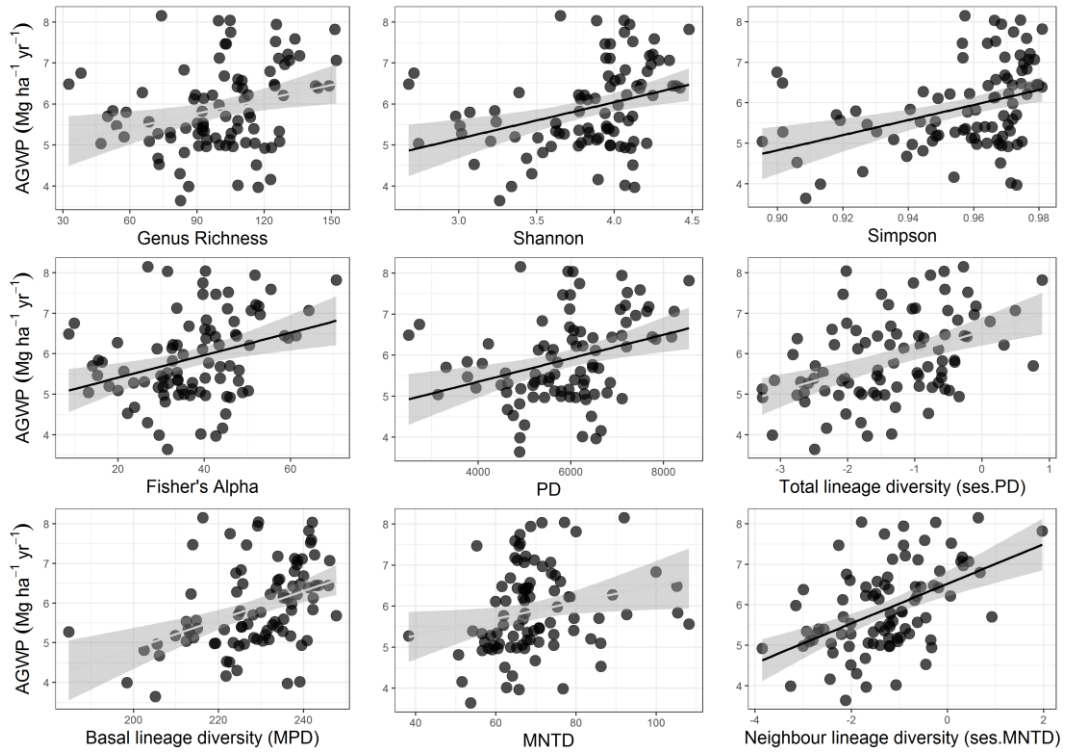
**Table A.3.8. 1** Results of Principal Component analyses of soil texture among 90 plots across Amazonia.

Soil content (%)	PC1	PC2
Sand	0.75	0.23
Silt	-0.64	0.50
Clay	-0.17	-0.84
% Variance explained	0.55	0.45

### Appendix 3.7 Results from bivariate relationships

**Table A.3.7 1** Kendall's tau for correlations between biodiversity metrics and predictor variables: aboveground wood productivity (AGWP) and aboveground biomass (AGB). Probabilities are given without (P) and with adjustment (P.adj) for multiple comparisons using a false discovery rate (please see details in the methods section).

Diversity metrics		AGWP			AGB		
		Kendall's	p	p.adj	Kendall's	p	p.adj
Common diversity metrics	Genus richness	0.19	0.01	0.01	-0.24	0.00	0.00
	Shannon	0.25	0.00	0.00	-0.28	0.00	0.00
	Simpson index	0.28	0.00	0.00	-0.28	0.00	0.00
	Fisher's alpha	0.21	0.00	0.00	-0.23	0.00	0.00
Phylogenetic diversity metrics	PD	0.22	0.00	0.00	-0.26	0.00	0.00
	Total lineage diversity	0.30	0.00	0.00	-0.19	0.01	0.01
	Basal lineage diversity	0.34	0.00	0.00	-0.32	0.00	0.00
	sesMPD	0.17	0.02	0.02	-0.27	0.00	0.00
	MNTD	0.21	0.00	0.00	-0.14	0.05	0.06
	Neighbour lineage diversity	0.33	0.00	0.00	-0.20	0.00	0.01



**Figure A.3.7.1** Bivariate relationships between above ground woody productivity (AGWP) and different biodiversity metrics across 90, one ha inventory plots. Continuous black lines indicate significant relationships after accounting for environment, stand structure variables and spatial autocorrelation (Gaussian correlation structure). Dashed grey lines indicate significant bivariate correlation between AGWP and diversity metrics (Table A.3.7.1). Significant correlations were assessed using Kendall's tau and P-values were corrected using a false-discovery rate (see methods for details).

## Sensitivity analyses in relation to potentially non-linear relationships between Simpson Index and wood productivity

The bivariate relationship between wood productivity and Simpson index may be non-linear (Figure 3.2). As a result, I tested the sensitivity of the results to specifying Simpson index with both a quadratic and linear term (Figure A.3.7.2). Specifying the association between AGWP and Simpson in this way yielded similar results, and improved model fit slightly (Table A.3.7.2). The results of the importance of different facets of diversity for promoting wood productivity were consistent: communities including more distantly related lineages (i.e. greater sesMNTD) and a higher proportion of rare genera, and a more even distribution of abundances among different genera (i.e. higher Simpson index) enhanced productivity. However, as the results are consistent using both linear and non-linear relationships, and there is no *a priori* ecological reasoning to expect increasing wood productivity at low diversity in tropical forests I retain the use of solely linear relationships in Chapter 3. The results specifying non-linear associations are provided below:

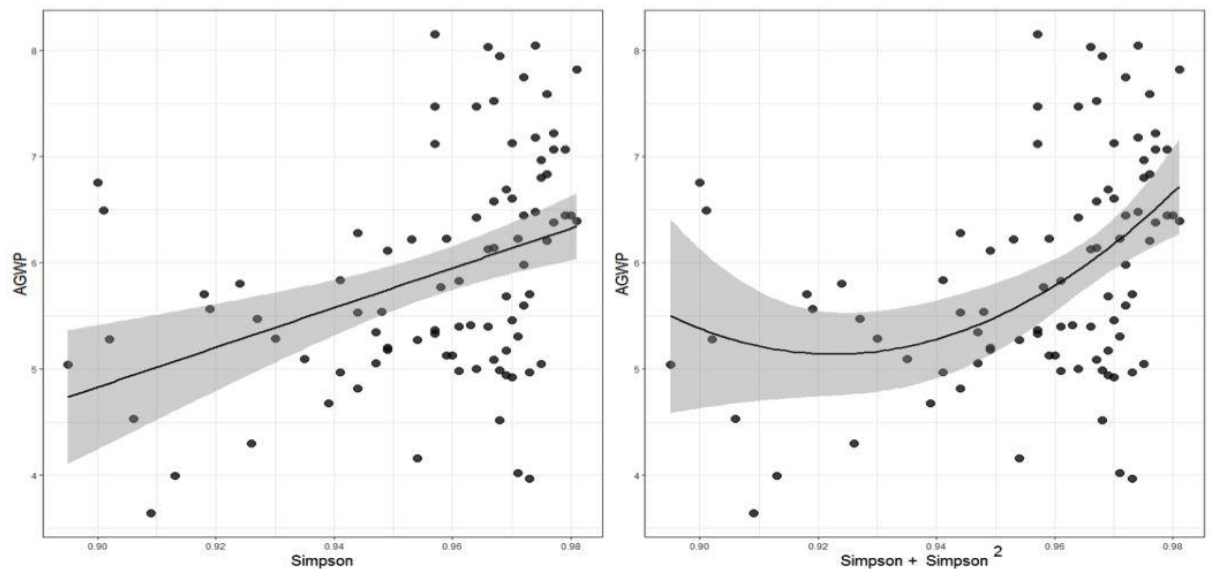


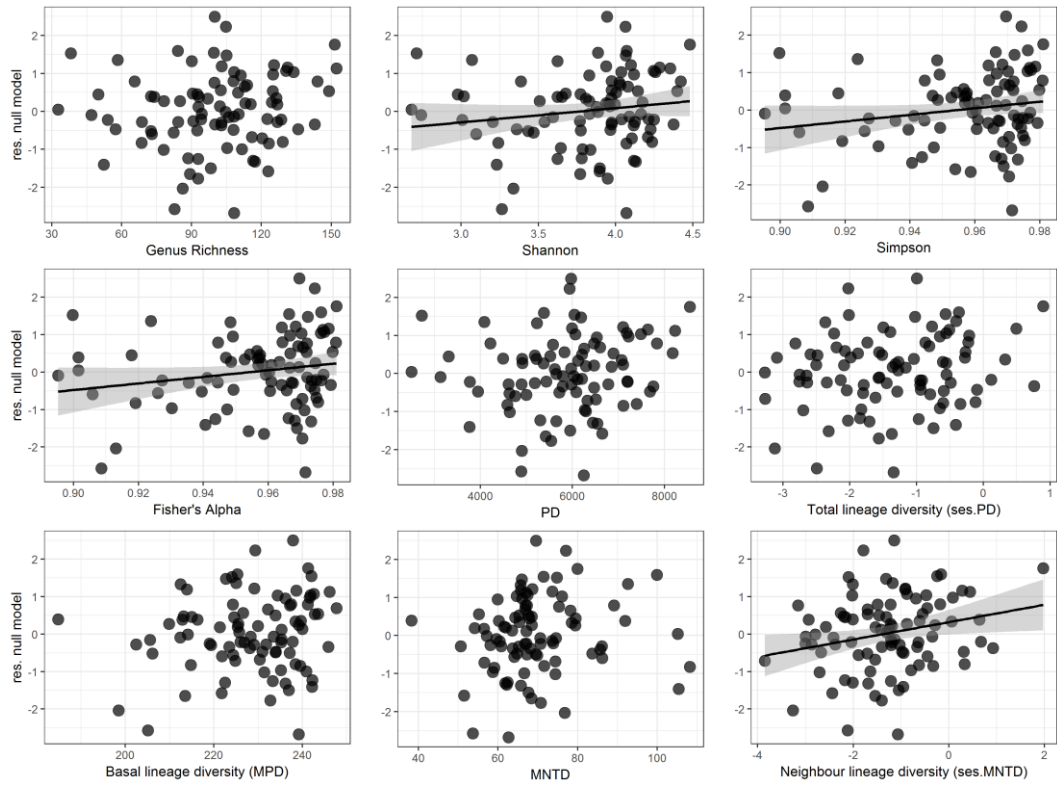
Figure A.3.7. 2. Relationships between aboveground wood productivity (AGWP) and Simpson index: a) linear relationship and b) specifying the relationship as both linear and quadratic terms.

**Table A.3.7 2 Results for generalised least square (GLS) models across 90, one ha plots for wood productivity (ln AGWP) as a function of diversity metrics, structural attributes, climate, soil variables, and accounting for spatial autocorrelation (Gaussian correlation structure). The relationship between Simpson index and wood productivity was modelled as both a linear and quadratic function.**

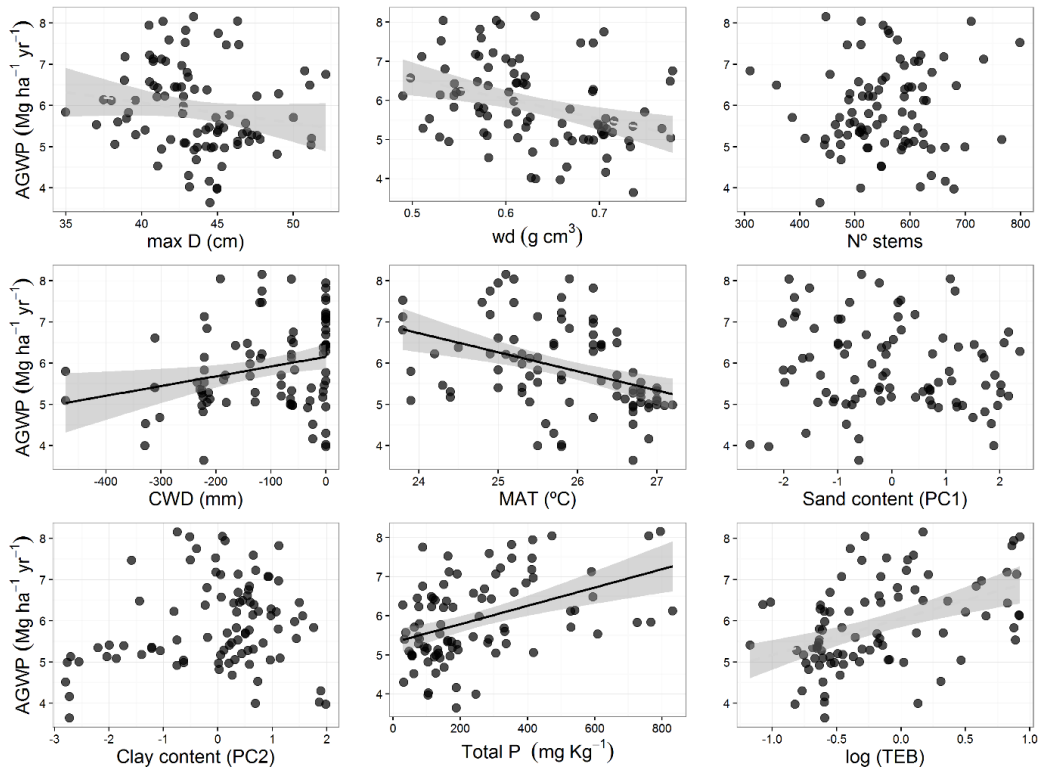
Model	AGWP		
	R <sup>2</sup>	AIC	Δ AIC
sesMNTD + simpson + simpson <sup>2</sup>	0.44	-119.20	-10.18
sesMNTD + simpson	0.41*	-116.16	-7.13
sesMNTD	0.40*	-111.68	-2.65
simpson	0.36*	-114.12	-5.09
simpson + simpson <sup>2</sup>	0.40*	-117.00	-7.97
null	0.34	-109.03	0.00

Independently of the use of either linear or non-linear relationships, the best model included a combination of both Simpson and Neighbour lineage diversity (Table 3.1; AIC=-116.16; R2= 0.41; AIC=-119.21; R2 = 0.44).

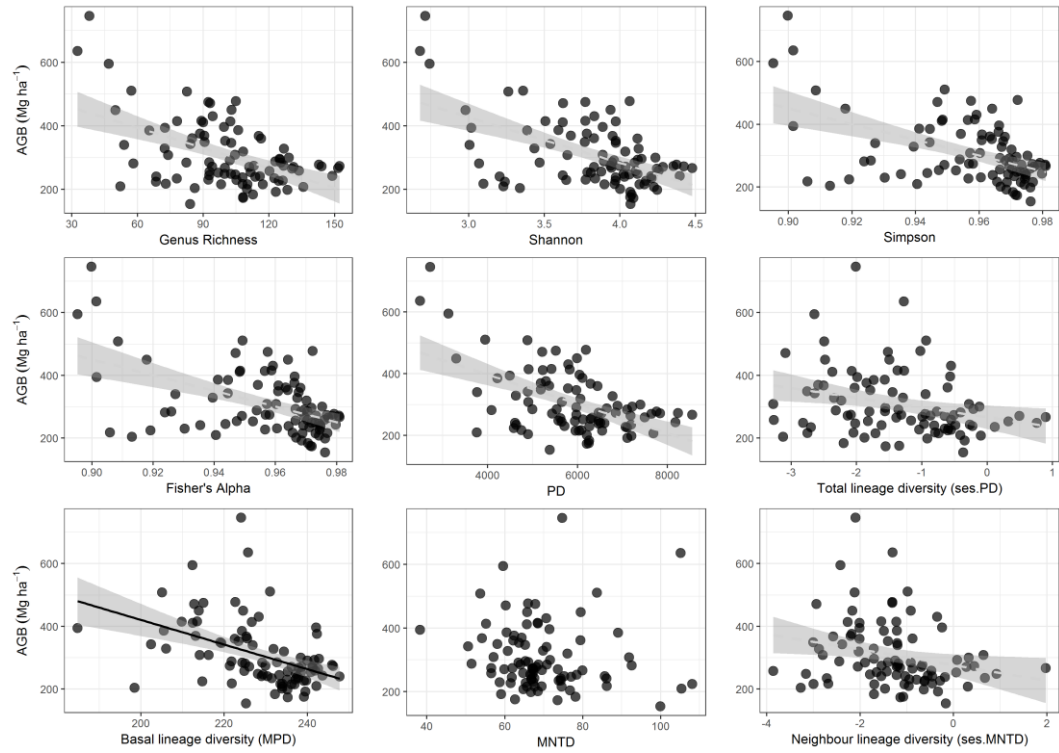




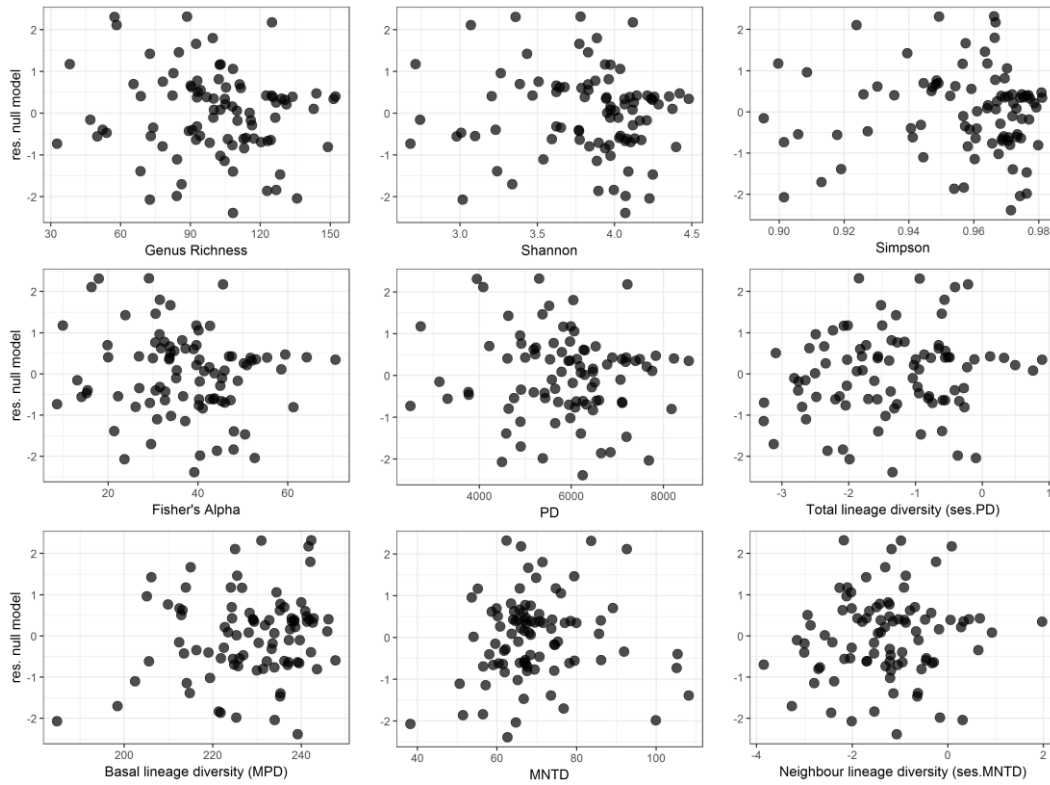
**Figure A.3.7.3** Bivariate relationships between the normalized residual from the generalised least square null model for productivity (i.e. including cumulative water deficit, mean annual temperature, and total phosphorus – see methods and Figure A.3.7.3 for details) and different biodiversity metrics across 90, one ha inventory plots.



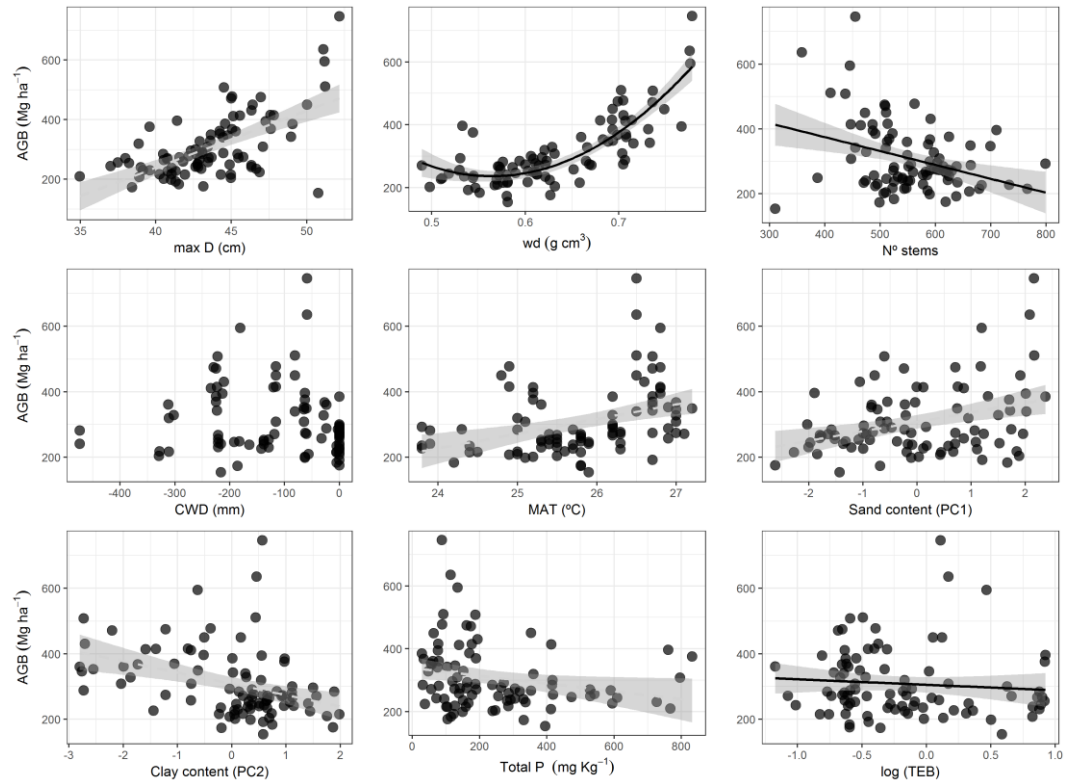
**Figure A.3.7.4** Bivariate relationships between aboveground wood productivity (AGWP) and other variables in the generalized least square models (stand structure variables, climate, and soil variables) across 90, 1 ha plots. Stand structure variables: maximum size (Max D, as the 95th percentile of the distribution of trees diameter), mean wood density (wd) and number of stems. Climate: cumulative water deficit (CWD) and mean annual temperature (MAT). Soil texture represented by PC1 (sand content) and PC2 (clay content). Soil fertility by total phosphorus (P) and total exchangeable bases (log TEB). Continuous black lines indicate significant relationships after accounting for environment, stand structure variables and spatial autocorrelation (Gaussian correlation structure). Dashed grey regression lines indicate significant bivariate relationships, significance was assessed using Kendall's tau and P-values were corrected using a false-discovery rate (see methods for details - Table A.3.7.1).



**Figure A.3.7.5** Bivariate relationships between aboveground biomass (AGB) and different biodiversity metrics across 90, one ha inventory plots. Continuous black lines indicate significant relationships ( $p < 0.05$ ) after accounting for environmental factors; stand structure variables and spatial auto correlation. Dashed grey regression lines indicate significant bivariate correlation between AGB and diversity metrics (Table A.3.7.1). Significant correlations were assessed using Kendall's tau and P-values were corrected using a false-discovery rate (see methods for details).

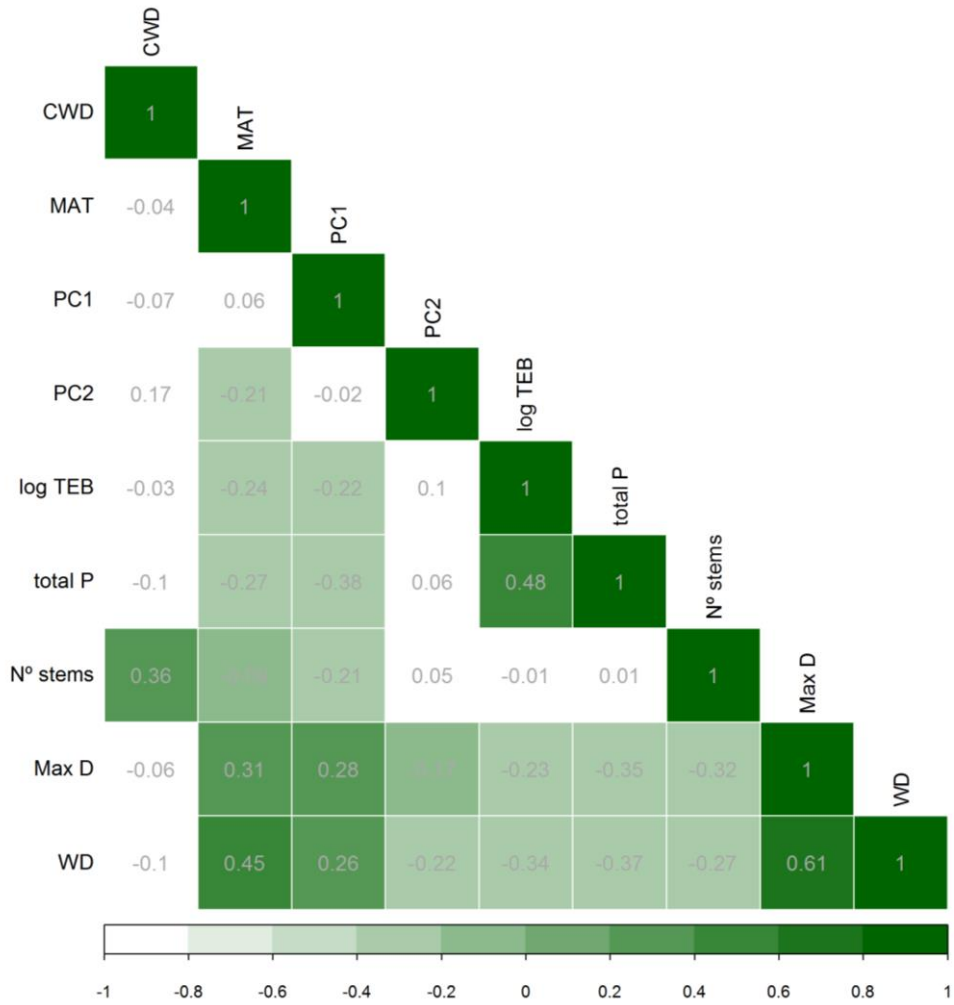


**Figure A.3.7.6** Bivariate relationships between the normalized residual from the generalised least square null model (i.e. including wood density, number of stems and total exchangeable bases – see Figure A.3.7.6 for details) and different biodiversity metrics across 90, one ha inventory plots.



**Figure A.3.7.7** Bivariate relationship between aboveground biomass (AGB) and other variables in the mixed model (stand structure variables, climate, and soil variables) across 90, one ha plots. Stand structure variables: maximum size (Max D, as the 95th percentile of the distribution of trees diameter), mean wood density (wd) and number of stems. Climate: cumulative water deficit (CWD) and mean annual temperature (MAT). Soil texture represented by PC1 (sand content) PC2 (clay content). Soil fertility: total phosphorus (P) and total exchangeable bases (log TEB). Continuous black lines indicate significant relationships even when accounting for environment, stand structure variables and spatial autocorrelation (Gaussian correlation structure). Dashed grey regression lines indicate significant bivariate relationships, significance was assessed using Kendall's tau and P-values were corrected using a false-discovery rate (see methods for details).

Bivariate relationships between aboveground biomass and functional characteristics highlighted unusually permanent forest plot with high potential tree size (50.7 cm) and low biomass (155.18 Mg ha<sup>-1</sup>). Although it is generally observed a significant and positive relationship between biomass and potential tree size (i.e. forest plots encompassing trees species that can achieve very large potential size store greater biomass; Figure A.3.7.6;), this plot is indeed realistic. Even though this plot contains species that achieve very large potential tree sizes such as *Ceiba pentandra*, *Cariniana strelensis*, *Ficus maxima*, *Chorisia insignis* and *Schizolobium amazonicum* (Fauset *et al.* 2015; Coelho de Souza *et al.* 2016) it also include a very large number of bamboos that directly reduce aboveground biomass. In the southwest Amazon bamboo forest dominate large intact areas, encompassing at least 161 500 km<sup>2</sup> (de Carvalho *et al.* 2013) and when compared to nearby forests without bamboo and under similar environmental conditions, bamboo presence reduce aboveground biomass up to 40% (Barlow *et al.* 2012). However, despite this plot being realistic, I ran GLS analyses for both wood productivity and aboveground biomass without plot DOI-02 and show that the results presented here are insensitive to this specific plot. Although the correlation between potential tree size and aboveground biomass increased slightly ( $\tau=0.41$   $p<0.001$ ;  $\tau=0.44$   $p<0.001$ , with and without plot DOI-02 respectively) results are basically the same. Best model for wood productivity includes both Simpson Index and neighbour lineage diversity (AIC=-115.28; R<sup>2</sup>=0.41), which provides a better fit in comparison to the null model including solely cumulative water deficit, mean annual temperature and total phosphorus (AIC=-109.5; R<sup>2</sup>=0.35). Similarly to results including all the plots, for aboveground biomass, a model containing basal lineage diversity provided slightly better fit (AIC=-72.9; R<sup>2</sup>=0.70) in relation to the null model including wood density, total exchangeable bases and number of stems (AIC=-70.19; R<sup>2</sup>= 0.68).



**Figure A.3.7.8** Matrix of correlation coefficients from the predictors used to select the best null model. Significant correlations were assessed using Kendall's tau ( $\tau$  shown in grey) and P-values were corrected using a false-discovery rate, lack of correlation ( $p \leq 0.05$ ) is evidenced by a black square.

### Appendix 3.8 Coefficients from the generalised least square models

**Table A.3.8.1** Full coefficients for all generalised least square models across 90 plots for natural logarithm of aboveground wood productivity (AGWP) as a function of diversity metrics, functional and structural attributes, climate, soil variables and using a Gaussian spatial correlation structure.

Variable	Value	SE	t-value	p-value	AIC	R2	Variable	Value	SE	t-value	p-value	AIC	R2
<b>Null Model</b>							<b>Genus richness</b>						
(Intercept)	1.75	0.02	87.62	< 0.0001	-109.03	0.34	(Intercept)	1.77	0.02	75.04	0.00	-104.64	0.34
CWD	0.05	0.02	2.75	0.01			GR	0.03	0.02	1.44	0.15		
MAT	-0.06	0.02	-2.69	0.01			CWD	0.05	0.02	2.06	0.04		
total P	0.05	0.02	3.17	0.00			MAT	-0.05	0.03	-2.05	0.04		
							total P	0.04	0.02	2.50	0.01		
<b>Shannon Index</b>							<b>Simpson Index</b>						
(Intercept)	1.75	0.02	88.04	0.00	-113.48	0.35	(Intercept)	1.75	0.02	89.54	0.00	-114.12	0.36
Shannon	0.04	0.02	2.57	0.01			Simpson	0.04	0.02	2.68	0.01		
CWD	0.04	0.02	1.77	0.08			CWD	0.04	0.02	1.85	0.07		
MAT	-0.05	0.02	-2.34	0.02			MAT	-0.05	0.02	-2.32	0.02		
total P	0.05	0.02	3.07	0.00			total P	0.04	0.02	2.90	0.00		
<b>Fisher's Alpha</b>							<b>Phylogenetic Diversity (PD)</b>						
(Intercept)	1.75	0.02	89.85	0.00	-112.94	0.37	(Intercept)	1.75	0.02	88.78	0.00	-111.26	0.36
Fisher	0.04	0.02	2.42	0.02			PD	0.03	0.02	2.04	0.04		
CWD	0.04	0.02	2.04	0.04			CWD	0.04	0.02	1.97	0.05		
MAT	-0.05	0.02	-2.67	0.01			MAT	-0.05	0.02	-2.40	0.02		
total P	0.05	0.02	3.23	0.00			total P	0.05	0.02	3.21	0.00		
<b>Standardized phylogenetic diversity (sesPD)</b>							<b>Mean Pairwise Distance (MPD)</b>						
(Intercept)	1.76	0.02	76.76	0.00	-105.38	0.38	(Intercept)	1.75	0.02	88.67	0.00	-111.91	0.34
sesPD	0.03	0.02	1.72	0.09			MPD	0.05	0.02	2.22	0.03		
CWD	0.05	0.02	2.56	0.01			CWD	0.03	0.02	1.43	0.16		
MAT	-0.05	0.03	-1.96	0.05			MAT	-0.04	0.02	-1.69	0.09		
total P	0.04	0.02	2.27	0.03			total P	0.04	0.02	2.46	0.02		



Variable	Value	SE	t-value	p-value	AIC	R2	Variable	Value	SE	t-value	p-value	AIC	R2
<b>Mean nearest taxon distance (MNTD)</b>							<b>Standardized mean nearest taxon distance (sesMNTD)</b>						
(Intercept)	1.75	0.02	87.99	0.00	-108.20	0.36	(Intercept)	1.75	0.02	92.51	0.00	-111.68	0.40
MNTD	0.01	0.01	1.06	0.29			sesMNTD	0.03	0.01	2.18	0.03		
CWD	0.05	0.02	2.84	0.01			CWD	0.05	0.02	2.58	0.01		
MAT	-0.05	0.02	-2.42	0.02			MAT	-0.05	0.02	-2.35	0.02		
total P	0.05	0.02	2.95	0.00			total P	0.04	0.02	2.70	0.01		
<b>Best Model - Simpson + sesMNTD</b>							<b>GR + sesMNTD</b>						
(Intercept)	1.75	0.02	93.61	0.00	<b>-116.16</b>	0.41	(Intercept)	1.76	0.02	78.32	0.00	-106.03	0.39
simpson	0.04	0.02	2.55	0.01			GR	0.02	0.02	1.14	0.26		
sesMNTD	0.03	0.01	2.00	0.05			sesMNTD	0.03	0.01	1.87	0.07		
CWD	0.03	0.02	1.71	0.09			CWD	0.04	0.02	1.96	0.05		
MAT	-0.04	0.02	-2.02	0.05			MAT	-0.05	0.02	-1.93	0.06		
total P	0.04	0.02	2.46	0.02			total P	0.03	0.02	2.19	0.03		
<b>Shannon + sesMNTD</b>							<b>Fisher + sesMNTD</b>						
(Intercept)	1.75	0.02	91.84	0.00	-115.19	0.40	(Intercept)	1.75	0.02	93.22	0.00	-114.09	0.41
shannon	0.04	0.02	2.39	0.02			fisher	0.03	0.02	2.08	0.04		
sesMNTD	0.03	0.01	1.92	0.06			sesMNTD	0.02	0.01	1.77	0.08		
CWD	0.03	0.02	1.66	0.10			CWD	0.04	0.02	1.96	0.05		
MAT	-0.04	0.02	-2.06	0.04			MAT	-0.05	0.02	-2.38	0.02		
total P	0.04	0.02	2.62	0.01			total P	0.04	0.02	2.79	0.01		

**Table A.3.8.2** Full coefficients for all generalised least square models across 90 plots for natural logarithm of aboveground wood productivity (AGB) as a function of diversity metrics, functional and structural attributes, climate, soil variables and using a Gaussian spatial correlation structure.

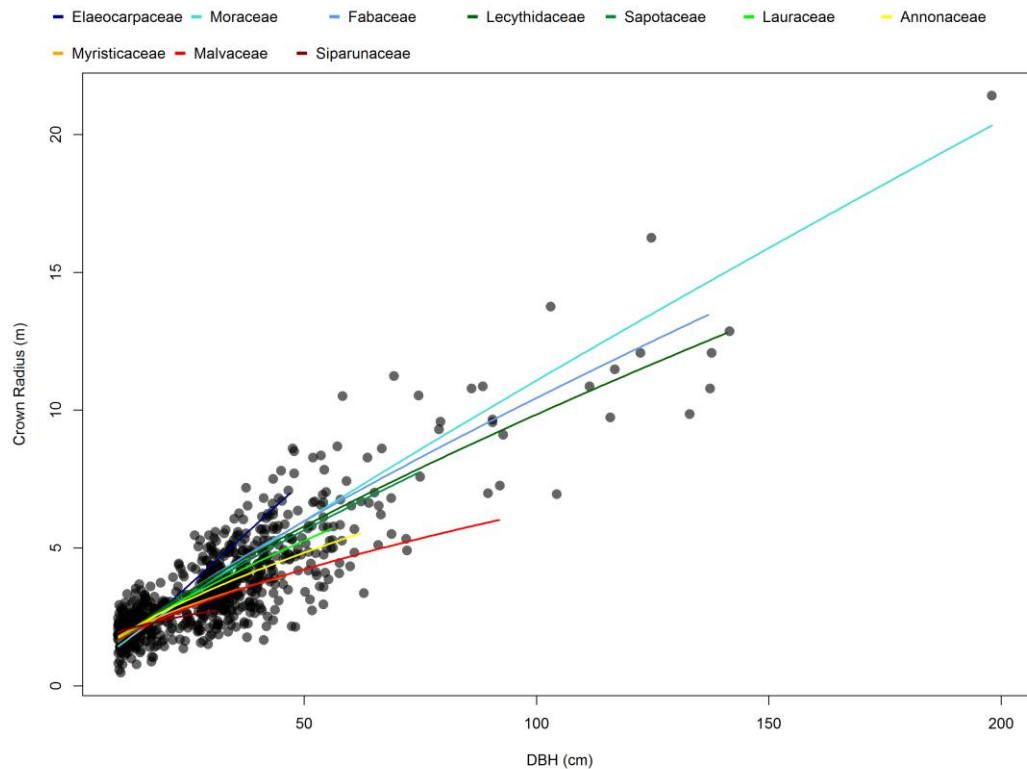
Variable	Value	SE	t-value	p-value	AIC	R2	Variable	Value	SE	t-value	p-value	AIC	R2
<b>Null Model</b>							<b>Genus richness</b>						
(Intercept)	5.67	0.02	229.62	0.00	-66.94	0.67	(Intercept)	5.67	0.02	229.90	0.00	-66.86	0.68
logTEB	0.05	0.02	2.03	0.05			GR	-0.03	0.02	-1.35	0.18		
N°stems	0.04	0.02	2.41	0.02			logTEB	0.05	0.02	1.97	0.05		
WD	-0.76	0.35	-2.17	0.03			N°stems	0.06	0.02	2.75	0.01		
WD <sup>2</sup>	1.05	0.35	3.01	0.00			WD	-0.71	0.35	-2.00	0.05		
							WD <sup>2</sup>	0.99	0.35	2.82	0.01		
<b>shannon</b>							<b>simpson</b>						
(Intercept)	5.67	0.02	228.36	0.00	-64.99	0.67	(Intercept)	5.67	0.02	228.79	0.00	-65.28	0.67
Shannon	-0.01	0.02	-0.21	0.83			Simpson	0.01	0.02	0.57	0.57		
logTEB	0.05	0.02	2.01	0.05			logTEB	0.05	0.02	2.06	0.04		
N°stems	0.05	0.02	2.34	0.02			N°stems	0.04	0.02	2.21	0.03		
WD	-0.74	0.38	-1.97	0.05			WD	-0.86	0.39	-2.20	0.03		
WD <sup>2</sup>	1.03	0.38	2.73	0.01			WD <sup>2</sup>	1.15	0.39	2.95	0.00		
<b>Fisher's Alpha</b>							<b>Phylogenetic Diversity (PD)</b>						
(Intercept)	5.67	0.02	231.11	0.00	-66.40	0.68	(Intercept)	5.67	0.02	228.64	0.00	-66.48	0.67
Fisher	-0.02	0.02	-1.18	0.24			PD	-0.03	0.02	-1.21	0.23		
logTEB	0.05	0.02	2.04	0.04			logTEB	0.05	0.02	2.01	0.05		
N°stems	0.05	0.02	2.58	0.01			N°stems	0.06	0.02	2.72	0.01		
WD	-0.72	0.35	-2.02	0.05			WD	-0.70	0.35	-1.96	0.05		
WD <sup>2</sup>	1.00	0.35	2.83	0.01			WD <sup>2</sup>	0.97	0.35	2.76	0.01		

Variable	Value	SE	t-value	p-value	AIC	R2
<b>Standardized phylogenetic diversity (sesPD)</b>						
(Intercept)	5.67	0.02	230.11	0.00	-65.12	0.68
sesPD	0.01	0.02	0.44	0.66		
logTEB	0.05	0.02	1.92	0.06		
N°stems	0.04	0.02	2.33	0.02		
WD	-0.79	0.36	-2.21	0.03		
WD <sup>2</sup>	1.08	0.36	3.03	0.00		
<b>Mean nearest taxon distance (MNTD)</b>						
(Intercept)	5.67	0.02	227.85	0.00	-64.97	0.67
MNTD	0.00	0.02	-0.19	0.85		
logTEB	0.05	0.02	2.00	0.05		
N°stems	0.04	0.02	2.03	0.05		
WD	-0.74	0.37	-2.01	0.05		
WD <sup>2</sup>	1.03	0.37	2.79	0.01		

Variable	Value	SE	t-value	p-value	AIC	R2
<b>Mean Pairwise Distance (MPD)</b>						
(Intercept)	5.67	0.02	234.74	0.00	<b>-69.41</b>	0.69
MPD	0.06	0.03	2.08	0.04		
logTEB	0.05	0.02	2.07	0.04		
N°stems	0.03	0.02	1.64	0.11		
WD	-0.90	0.35	-2.55	0.01		
WD <sup>2</sup>	1.22	0.35	3.45	0.00		
<b>Standardized mean nearest taxon distance (sesMNTD)</b>						
(Intercept)	5.67	0.02	226.86	0.00	-65.11	0.67
sesMNTD	-0.01	0.02	-0.43	0.67		
logTEB	0.05	0.02	2.03	0.05		
N°stems	0.04	0.02	2.45	0.02		
WD	-0.74	0.36	-2.09	0.04		
WD <sup>2</sup>	1.03	0.35	2.91	0.00		

### **Appendix 3.9 Crown architecture**

Crown architecture is thought to be associated with wood productivity in temperate forests (Jucker *et al.* 2015). I investigated whether there were differences in the relationship between crown radius and tree diameter across distinct tree families. Crown radius data for 2457 trees with diameter  $\geq 10$  cm, belonging to 52 different families were used (Goodman *et al.* 2014). I explored whether there were differences in tree architecture among families using ANCOVA. Variation among families was assessed by the interaction between family and tree diameter, with crown radius (Cr) as the dependent variable. The relationship between crown radius and tree diameter was further explored using a power relationship  $Cr = aD^b$  (Poorter *et al.* 2006). I found that the allometric relationship between crown radius and diameter varied widely across families (Figure A.3.9.1). Different families showed significant differences in the slope and intercept of their allometric relationships ( $p < 0.001$ ).



**Figure A.3.9.2** Size-dependent relationships between crown radius and tree diameter across different families. Each family is represented by a different curve and the curve ends at the biggest individual measured for a particular family.

### **Appendix 3.10 Aboveground biomass – switch in sign for basal lineage diversity (MPD)**

There was a change in sign in the relationship between biomass and MPD from univariate to multivariate analyses. The direction of the relationship changed from negative as suggested by simple bivariate correlations to a weak positive relationship after accounting for confounding environmental and stand structure variables in multivariate model. This change in the direction of the relationships from univariate to multivariate analyses could be an outcome of correlation amongst the explanatory variables (Gelman & Hill 2006). However, despite the strong negative correlation between wood density and MPD ( $\tau = -0.51$ ,  $p < 0.001$ ), I ensured that variance inflation factor (VIFs) for all variables were smaller than five (Kutner *et al.* 2005) (i.e. VIFs: WD=2.33; N° stems: 1.34; TEB=1.35; MPD=2.08). However, even though there is a significant relationship between MPD and biomass after accounting for wood density, the residuals of the null

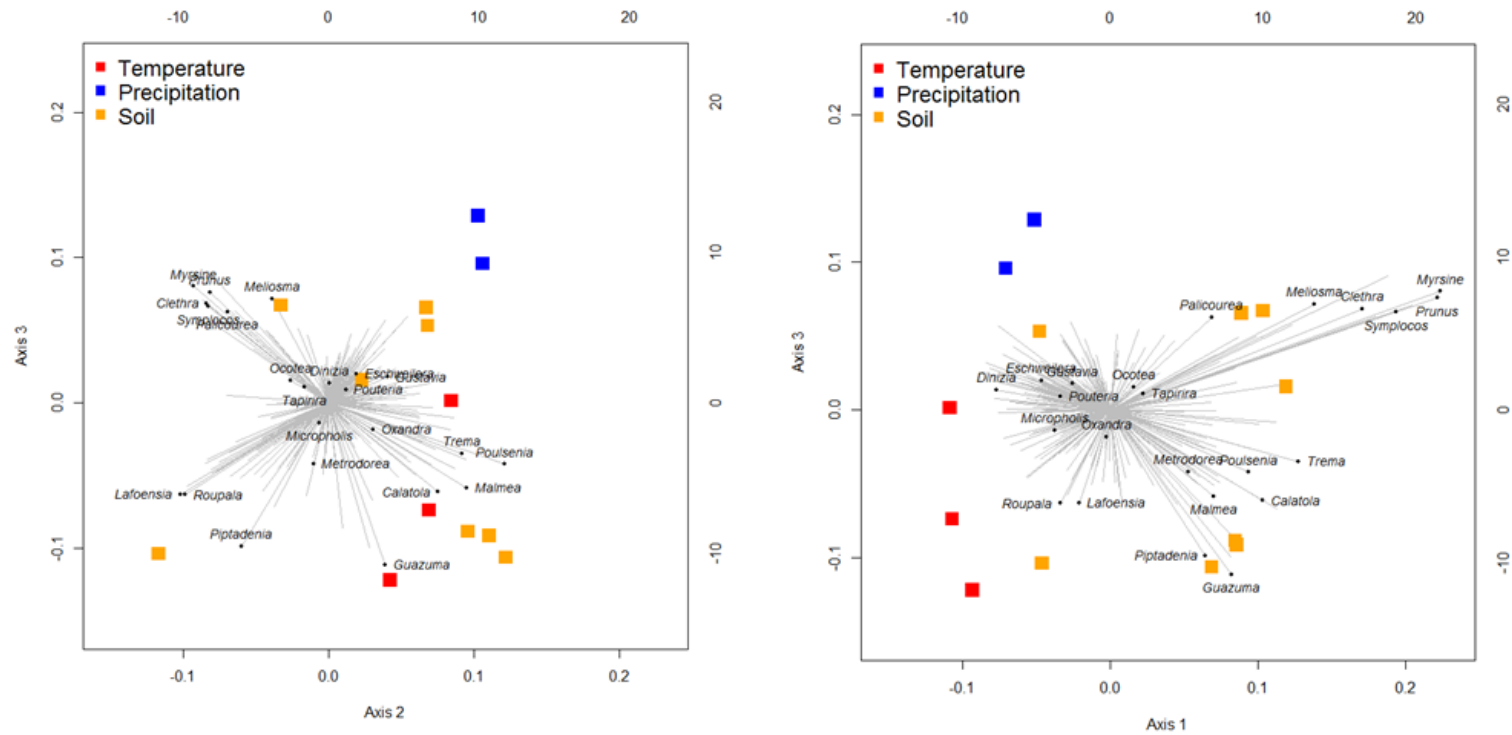
model (i.e. wood density as a quadratic and linear terms, number of stems and total exchangeable bases) are not related to MPD (Figure A.3.7.9). This inconsistency in the relationship, associated with the lack of association between MPD and residuals from the null model, suggests that biomass and MPD are weakly related at best.

## Appendix 4 Supplementary information Chapter 4

### Appendix 4.1 Principal component analyse for niche variables

**Table A.4.1** Principal component analyses for niche variables for 310 tree and palm calculated using inventory data from 788 forest plots across the Neotropics (Lopez-Gonzalez *et al.* 2009), climate (Hijmans *et al.* 2005; Chave *et al.* 2014) and locally collected soil data (Quesada *et al.* 2010; Quesada *et al.* 2012). The first PCA axis is largely associated with temperature and explains 44.6% of the variation, the second PCA axis mainly associated with soil fertility and sand content and explains 21.1% of the variation, whilst the third axis associates with precipitation gradient and explains 14.6% of the variation.

Niche variable	PC1	PC2	PC3
MAT	-0.35	0.22	-0.24
Max.T	-0.30	0.14	-0.39
Min.T	-0.35	0.27	0.00
CWD	-0.17	0.33	0.41
MAP	-0.23	0.34	0.31
Ca	0.22	0.39	-0.34
Clay	-0.15	0.22	0.17
K	0.33	-0.11	0.22
Mg	0.27	0.31	-0.29
P	0.38	0.07	0.05
Sand	-0.15	-0.38	-0.33
Silte	0.29	0.22	0.21
TEB	0.28	0.36	-0.29



**Figure A.4.1.1** Panel showing the additional Principal Component Analyses axis: PC2 versus PC3 and PC1 versus PC3. PCA using Euclidian distance as a measure of the variation in genus-level environmental niches related to temperature, precipitation and soil variables. Key genera are labelled in the graph.



#### **Appendix 4.2 Environmental niche mapped in the phylogeny**

Please see figure supplement 4.2 located in the back cover folder and refer to the electronic material (Appendix 4.2) – Phylogeny of tropical forests tree and palm genera with frequency  $\geq 10$  plots with branches coloured according to niche variables. One niche variable within each niche category: (a) temperature represented by mean annual temperature ( $^{\circ}\text{C}$ ), (b) precipitation, by mean annual precipitation (mm) and (c) soil fertility by total exchangeable bases (mg.kg). Nodes highlighted by red circles indicate clades encompassing lineages with values lower than expected by chance, whilst blue circles indicate clades including lineages showing higher values than expected by chance. Nodes highlighted in grey give a sense of topology. Nodes are numbered as following: 1) Magnoliids 2) Monocots 3) Rosids 4) Asterids 5) Ericales 6) Aquifoliales 7) Myristicaceae 8) Salicaceae 9) Clusiaceae 10) Sapindaceae 11) Primulaceae 12) Apocynaceae 13) Papilionoideae.

#### **Appendix 4.3 Other processes rather than divergent selection driving the extent of phylogenetic signal**

Other processes rather than selection could be affecting the extent of phylogenetic signal for environmental niches. However, I argue that divergent selection is likely to be the process driving the patterns found here: lower phylogenetic signal than expected under a null Brownian motion model of evolution (i.e. Lambda lower than 1). Strong selection for a single optimum across a whole clade can also lead to lower extent of similarity among related lineages (Revell *et al.* 2008; Munkemuller *et al.* 2015). However, if there was strong convergent selection across a whole clade (i.e. all angiosperms) and niche values were biased towards certain value I expect that Ornstein-Uhlenbeck with a single optimum would have provided a better fit for the environmental niches. Thus, the best fit of Lambda over Ornstein-Uhlenbeck supports the role of divergent selection (Chapter 4 Table 2). Additionally, estimates of phylogenetic signal increase once I expand the range of temperature niches (i.e. I find greater phylogenetic signal for thermal

preferences when including genera restricted or more abundant in upland forests – Chapter 4 Figure 4). Because all mountane genera have preferably similar lower temperature niches, if selection would have been driven convergence to an optimal value I would expect a decrease in the phylogenetic signal once I have broadened the temperature gradient. Moreover, lower phylogenetic signal than expected under a null Brownian motion could be an artefact of sampling scheme. If all individuals were found in similar environments I would expect that environmental niches would be converging to a single optimum. However, here I have sampled across large portions of these environmental gradients and there is substantial variability in mean niche values across all niche axes. Finally, high errors in quantifying environmental niches can also lead to decrease in the extent of signal. However, here I included a full range of environmental conditions that are associated with species distribution which is likely to have allowed more consistent niche estimates. For instance, across the soil axis lineages from the extreme nutrient poor Cerrado soils to lineages in more nutrient rich soils in the western Amazon were included (e.g. *Emmotum*, *Roupala* and *Vouacapoua* versus *Trema*, *Malmea* and *Attalea*). On the temperature gradient, lineages from the colder Andes to warmer plots in the transitional forests in Mato Grosso-Brasil were included (e.g. *Roupala*, *Guazuma*, *Diospyros* versus *Brunellia*, *Clethra*, *Hedyosmun*). Additionally, the analyses presented here encompassed a wide precipitation gradient including forests in the wetter western Amazon versus drier Cerrado in central Brasil (e.g. *Senefeldera*, *Hymenolobium*, *Iriartella*, versus *Piptadenia*, *Anadenanthera*, *Mimosa*).

## Appendix 5 List of genera and their respective index of Evolutionary Distinct and Globally Endangered (EDGE)

**Table 5.1** List of Angiosperm tree genera and their respective Evolutionary Distinct and Globally Endangered (EDGE) index. ED is the evolutionary distinctiveness and GE is the global extinction risk from the World Conservation Union Red List Categories.

Genus	ED	GE	EDGE
Duguetia	45.71222	4	6.616595
Sorocea	60.11257	3	6.192159
Mollinedia	23.75334	4	5.981549
Rinorea	41.77702	3	5.835443
Cupania	19.84028	4	5.809476
Carapa	39.2336	3	5.774144
Couepia	15.96206	4	5.603568
Trichilia	32.11354	3	5.579384
Ilex	64.13907	2	5.562819
Guatteria	57.87635	2	5.461734
Sloanea	55.06096	2	5.412734
Protium	53.51346	2	5.384742
Allophylus	26.23491	3	5.383941
Aegiphila	25.93445	3	5.372848
Styrax	51.22666	2	5.341887
Euplassa	50.11479	2	5.320368
Swartzia	49.88585	2	5.315879
Casearia	24.29555	3	5.31007
Anthodiscus	49.45298	2	5.307336
Talisia	24.06805	3	5.301036
Herrania	22.41512	3	5.232823
Copaifera	44.81042	2	5.210806
Inga	21.70369	3	5.201969
Pouteria	9.917303	4	5.162938
Gustavia	20.5285	3	5.148819
Grias	20.5285	3	5.148819
Rollinia	40.95806	2	5.122965
Miconia	19.41396	3	5.09566
Symplocos	37.48869	2	5.036659
Naucleopsis	37.43609	2	5.035291
Dipteryx	37.34993	2	5.033047
Platymiscium	36.35574	2	5.006781
Buxus	69.35548	1	4.946708
Tapirira	31.3768	2	4.863737
Lecythis	15.13149	3	4.860215
Piper	127.9944	0	4.859769
Minquartia	59.86744	1	4.801846
Aphelandra	28.95538	2	4.786003

Genus	ED	GE	EDGE
Guarea	27.79044	2	4.746338
Vantanea	27.6555	2	4.74164
Machaerium	27.37801	2	4.731909
Juglans	55.41538	1	4.725889
Meriania	26.70543	2	4.707923
Eugenia	12.82763	3	4.70611
Mouriri	52.70244	1	4.676606
Pourouma	51.69033	1	4.657579
Bulnesia	51.33869	1	4.650883
Palicourea	24.81416	2	4.637218
Pseudoxandra	24.72639	2	4.633812
Cecropia	49.87328	1	4.622485
Quararibea	24.27209	2	4.615995
Ruagea	23.42076	2	4.581728
Ampelocera	47.57675	1	4.576292
Thyrsodium	23.18637	2	4.572084
Caesalpinia	23.1334	2	4.569891
Citharexylum	23.10413	2	4.568677
Simira	22.96219	2	4.562771
Sebastiania	22.88885	2	4.559706
Graffenrieda	22.7649	2	4.554504
Zeyheria	21.79147	2	4.512681
Calyptranthes	21.6471	2	4.506326
Centrolobium	21.10433	2	4.482068
Caraipa	20.86737	2	4.47129
Jacqueshuberia	20.43112	2	4.451138
Huberodendron	18.80592	2	4.372275
Capparis	17.16197	2	4.285624
Unonopsis	16.87975	2	4.269963
Persea	16.77385	2	4.264023
Corythophora	16.24259	2	4.233677
Ladenbergia	15.43375	2	4.185631
Eschweilera	15.13149	2	4.167068
Parathesis	15.08412	2	4.164127
Erythrina	30.89855	1	4.155708
Couratari	14.33748	2	4.116594
Schinopsis	14.28342	2	4.113063
Guadua	59.47231	0	4.102186
Magnolia	59.08403	0	4.095744
Nectandra	13.93926	2	4.090287
Alnus	57.76773	0	4.073593
Bauhinia	57.71951	0	4.072772
Lafoensia	57.71639	0	4.072719
Aspidosperma	28.27886	1	4.070013
Psidium	13.43685	2	4.056078
Chrysophyllum	13.39524	2	4.053192
Coussarea	26.77925	1	4.017437
Tocoyena	12.57429	2	3.994472
Micropholis	12.2378	2	3.969371
Ficus	51.63379	0	3.963358
Sarcaulus	12.1269	2	3.960958

Genus	ED	GE	EDGE
Pterogyne	24.73884	1	3.941148
Chamaecrista	49.84154	0	3.928714
Abarema	11.02378	2	3.873181
Pentaplaris	22.94464	1	3.868892
Ormosia	44.65787	0	3.821176
Alchornea	21.55346	1	3.809036
Parkia	42.84958	0	3.780765
Campomanesia	19.39599	1	3.708486
Alseis	18.99479	1	3.688619
Manilkara	18.63703	1	3.670564
Alexa	38.10376	0	3.666219
Senna	37.12812	0	3.640952
Cereus	8.430094	2	3.6302
Macrolobium	36.39547	0	3.62155
Helicostylis	35.50185	0	3.597363
Guettarda	17.07306	1	3.58757
Cordia	34.01878	0	3.555885
Pereskia	33.9202	0	3.553066
Bocoa	33.69749	0	3.546667
Cariniana	16.03557	1	3.528451
Hymenaea	32.09561	0	3.499401
Andira	31.61714	0	3.484838
Diplotropis	31.50745	0	3.481469
Mauritia	15.03138	1	3.467696
Geissanthus	14.69769	1	3.446661
Cavanillesia	14.54482	1	3.436875
Clathrotropis	29.2933	0	3.410927
Pradosia	13.95092	1	3.39792
Phytelephas	13.46442	1	3.364839
Cojoba	27.83124	0	3.361459
Schefflera	27.71239	0	3.357329
Dalbergia	27.37801	0	3.345615
Platypodium	26.33031	0	3.307996
Bactris	12.06349	1	3.262969
Stryphnodendron	24.89611	0	3.254093
Chiococca	23.05222	0	3.180227
Pterocarpus	22.5903	0	3.160836
Calliandra	22.56249	0	3.159656
Enterolobium	22.47915	0	3.156113
Wettinia	10.68949	1	3.151838
Guapira	21.9277	0	3.132346
Macrosamanea	21.62368	0	3.118997
Cynometra	19.46989	0	3.018955
Tabebuia	18.02528	0	2.945769
Itaya	17.85319	0	2.936682
Couropita	16.03557	0	2.835303
Tachigali	15.23376	0	2.787093
Opuntia	15.20483	0	2.785309
Geonoma	14.77099	0	2.758172
Cleistocactus	13.94903	0	2.704646
Samanea	12.42911	0	2.597425

Genus	ED	GE	EDGE
Aiphanes	11.8265	0	2.551513
Ecclinusa	11.82249	0	2.551201
Astrocaryum	11.04677	0	2.488797
Iriarteia	10.07014	0	2.404252
Chromolucuma	9.917303	0	2.390349
Stetsonia	9.807196	0	2.380212
Aniba	9.689305	0	2.369244
Ocotea	8.683009	0	2.270373
Syagrus	8.412354	0	2.242023

