Relationships between biodiversity and carbon dynamics in tropical forests

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The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

Assertion of moral rights:

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Abstract

Biological diversity and ecosystem functions, such as the production of wood and the storage of carbon, are important ecological attributes, but how are they related? Tropical forests are the most diverse terrestrial ecosystems and key players in global carbon cycling, so preserving both functions are important conservation goals. Yet little is known about diversity–function relations here.

I investigate tree diversity–function relations in African and South American old-growth tropical forests, using 323 forest plots (mostly 1-ha) from a pan-tropical network sampled using standardised techniques. I focus on aboveground biomass (AGB) and coarse woody production (AGWP). I develop methods to deal with issues that arise in calculating AGWP over long time-spans and in estimating diversity when only some individuals are identified.

Diversity–function relations are assessed using two main approaches. Firstly, I use linear models to assess whether AGB and AGWP covary with diversity across large spatial extents. These models include climate and soil variables that may drive AGB and AGWP to statistically account for these, and filters to account for spatial autocorrelation. There is no evidence of a relationship between diversity and AGB. For AGWP, there is a positive relationship with genus and family-level diversity in South America, but not in Africa.

Secondly, I investigate whether diversity is related to AGB or AGWP within the plots, thereby removing environmental differences among plots. Using mixed effects models on 0.04-ha subplots again shows AGB is unrelated to diversity. However, AGWP is positively associated with diversity in both continents, with a doubling of species richness increasing wood production by 11%.

Taken together the results represent the first evidence of widespread positive diversity–productivity relations across the two largest tropical forest continents. The lack of positive association between diversity and biomass implies a trade-off between the conservation of tropical biodiversity and carbon storage.

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1 Introduction

1.1 Justification

Tropical forests are major global centres of both biodiversity and terrestrial carbon storage. In terms of biodiversity, few studies of the complete flora of a tropical forest have been made but those that do exist show exceptional diversity. For example, Whitmore et al. (1986) found 233 species of vascular plants and 32 species of bryophyte in a 100m^2 patch of lowland rain forest in Costa Rica. The biodiversity of tropical forests is much greater than that of most other biomes, yet there is considerable variation in diversity within the tropics, with African forests typically being less diverse in tree species than their Asian and Latin American counterparts (Parmentier et al., 2007). While as many as 329 tree species ≥100 mm diameter have been observed in a 1-ha plot in central Amazonia (Laurance et al., 2010), tree diversity can be very low in monodominant tropical forests (Peh et al., 2011; Torti et al., 2001).

Despite covering only 13% of the non-Antarctic land surface area (Korner, 2009), tropical forests also play an important role in the carbon cycle, in terms of both storage and fluxes. They also currently represent a potentially significant sink of carbon. In terms of carbon storage, tropical forests contain 471 ± 93 Pg of carbon, which is 55% of the globe's forest carbon pool of 861 ± 66 Pg (Pan et al., 2011).

Of the current anthropogenic carbon emissions of c.9.3 Pg C a^{-1}, only around 45% contributes to increases in atmospheric CO_2 levels. The rest is absorbed by the oceans and terrestrial ecosystems, in roughly equal proportions (Le Quéré et al., 2013). As a component of the terrestrial carbon uptake, it is estimated that tropical forests provide a carbon sink of 1.2 ± 0.4 Pg C a^{-1} (Pan et al., 2011) and thus play an important role in buffering the warming impact of anthropogenic CO_2 emissions. There are however several mechanisms by which the carbon uptake of tropical forests could be reduced in the future (Lewis, 2006), and this could lead to a reduction in the strength of the sink, or even a positive feedback that would further enhance climate change (for example as suggested by Cox et al., 2000).

The role of tropical forests as a carbon store is receiving great attention at present, because carbon emissions from tropical deforestation and degradation account for approximately 2.9 ± 0.5 Pg C a^{-1} (Pan et al., 2011), and therefore are the second largest source of emissions after fossil fuel combustion. A scheme to reduce carbon emissions via the United Nations

Framework Convention on Climate Change (UNFCCC), termed REDD+ (Reducing Emissions from Deforestation and Forest Degradation, the '+' means including forest management activities), has played a prominent role in international climate negotiations. Under REDD+, developing countries would be paid to reduce the rate of deforestation and forest degradation, with the aim being to reduce carbon emissions from these sources. If REDD+ is implemented, it is important to ensure that any co-benefits from forest protection are maximised. These include the rights of indigenous peoples and forest dwellers, plus biodiversity, as well as other ecosystem services such as flood control, soil protection, and local microclimatic effects. Knowledge of the relationship between biodiversity and carbon storage will provide valuable information to help achieve a goal of maximising carbon storage and biodiversity conservation.

Much recent academic debate has focused on the effects of biodiversity on ecosystem functioning. In particular, the potential role of biodiversity in enhancing productivity and the resulting biomass accumulation has been a topic of considerable interest. Biodiversity could enhance productivity through various mechanisms, including some based on the effects of diversity itself, and others driven by the fact that particular species are more likely to be present in more diverse stands. However, studies have been concentrated on a limited number of ecosystems, and little work has been done in high diversity systems such as tropical forests. Further examination of ecological relationships in tropical forests can greatly improve our understanding of the role of biodiversity in highly diverse ecosystems.

I will therefore study the relationships between biodiversity and two key aspects of ecosystem function – aboveground biomass and aboveground wood production, in tropical forests of Africa and South America. I will assess whether there are bivariate diversity–function relationships within forest stands and whether these factors covary over large spatial extents. This will further our understanding of biodiversity and ecosystem functioning in high diversity systems, and will aid in the setting of priorities for tropical forest conservation.

1.2 Biodiversity

1.2.1 Defining and measuring biodiversity

The term biodiversity appears to have been first proposed by Walter Rosen in 1985 (Magurran, 2004). Since then its use has steadily grown, and the concept has gained wider recognition beyond the scientific community, in part, as a result of the 1989 Brundtland Report and the Rio

Earth Summit of 1992. There have been numerous definitions of biodiversity. A commonly cited definition is that of the United Nations Environment Programme (Heywood, 1995):

'Biological diversity' means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.

This recognises the fact that biodiversity occurs on a variety of levels, described by Harper and Hawksworth (1995) as 'genetic,' 'organismal,' and 'ecological.' Other definitions emphasise particular aspects of biodiversity, with some focussing on the measurement of biodiversity, and others considering it as a wider concept. The fact that biodiversity is such a broad concept means it cannot be fully encapsulated by any single number. Purvis and Hector (2000) describe biodiversity as 'fundamentally multidimensional,' thus a plethora of indices is available, and the choice of which one to use must be based on the aims of the study in question.

The measurement of biodiversity can be carried out on various spatial scales. Alpha diversity represents the diversity of species within plots in a particular community, while β-diversity considers the differences in species composition amongst communities, and is thus a measure of species turnover. The two measures are combined as γ-diversity to consider the total diversity of an ecosystem (Magurran, 2004). The best-known and simplest measure of α-diversity is species richness.

Solely considering species richness fails to take evenness into account. As an example, we might ask if a community containing five species, each represented by 20 individuals, is more diverse than a community containing 96 individuals of a single species, plus four more species each represented by a single individual. This can be examined using rank/abundance plots. Thus, communities may be dominated by a few highly abundant species (as modelled by a geometric series), abundance may follow a log normal distribution, or communities may contain a set of species with relatively similar abundances (following the broken stick model) (Magurran, 2004). A range of species evenness indices (such as Simpson's evenness index) can be used to quantify these relationships.

There are a range of indices that combine both richness and evenness to produce a single measure of species diversity. The Simpson Index (Simpson, 1949) is one of the most biologically meaningful measures relating to diversity, and works well even at small sample sizes. In its simplest form, known as Simpson's concentration, it gives the probability that any two individuals, randomly drawn from an infinitely large community, will belong to the same species. As such, it emphasises the evenness, rather than the richness, component of diversity.

The Shannon Index (Shannon, 1948), known as Shannon entropy, is derived from information theory. It is widely used and places equal emphasis on evenness and richness. It relies on the assumption that all species are represented in the sample. This can be a source of error, which becomes magnified at small sample sizes and in more diverse communities, unless efforts are made to estimate the full richness of the community. Fisher's α is a parametric index derived from the log series model, but may be used even when species abundance patterns do not appear to follow the log series distribution. Fisher's α is independent of sample size if $N > 1000$ (Magurran, 2004).

It can thus be seen that there are multiple ways in which biodiversity can be measured, and the use of a single index such as species richness will not fully characterise the true extent of diversity within a given community or assemblage. However, the indices described above are measured on various different scales and are not easily comparable. A solution to this problem is to use indices of the 'effective number of species' (Jost, 2006). When all species have equal abundances, diversity according to any 'effective number of species' index will be equal to species richness. When species do not have equal abundances, diversity according to different 'effective number of species' indices will diverge.

Modified forms of the popular Shannon and Simpson indices can be used as indices of 'effective number of species.' These indices can be placed within a framework (Hill, 1973), in which diversity of order 0 (^0D; species richness) means each species contributes equally to diversity regardless of abundance, diversity of order 1 (^1D; equivalent to exponential Shannon entropy) means each stem contributes equally to diversity, and diversity of order 2 (^2D; equivalent to Simpson's Reciprocal Index, the inverse of Simpson's concentration) means abundant species contribute disproportionately to diversity. This provides a coherent framework in which the various aspects of alpha-diversity can be compared. Fisher's α does not make use of species abundance data, therefore it cannot fit into this framework. However, it is a useful diversity index for situations where abundance data are not available.

1.2.1.1 Dealing with spatial scale and sample size

Occasionally it may be possible to compile a full species list for an entire community or assemblage, but in diverse tropical forests this is often not feasible and richness must be estimated. This estimation can relate to the number of species per specified number of individuals (numerical species richness), per quantity of biomass, or per area of land (species density). The use of multiple forms of estimates is also valuable because the density of individuals, for example the stem density of tropical forest trees, may vary considerably among

forest stands. Thus the comparative tree diversity of two forests as calculated per land area may not necessarily equate with their diversity as calculated per number of individuals.

To compare richness values between communities when the number of individuals varies, taxon sampling curves can be produced. These relate sampling effort (in terms of either individuals observed or samples collected) to the number of taxa found. Accumulation curves record the increases in observed richness as more individuals or samples are included in the dataset. Rarefaction curves follow a contrasting approach, in which the starting point is the full dataset, and repeated resampling without replacement is conducted to generate richness estimates for smaller numbers of individuals or samples (Gotelli and Colwell, 2001). Rarefaction is particularly useful in comparing diversity across communities, for a given number of individuals, as long as the sample size in each community is equal to or greater than the chosen number of individuals. This provides a more accurate representation of diversity than the use a simple taxa-per-individual ratio would, because richness does not normally increase linearly with abundance (Gotelli and Colwell, 2001). Such rarefaction procedures do not provide information on species abundances, thus the Shannon and Simpson indices cannot be applied to their results, but the use of Fisher's α remains possible.

Just as richness does not increase linearly with abundance, neither does it scale linearly with area. This means richness estimates derived from samples representing different spatial scales cannot be directly compared. Instead, comparisons can be achieved through the use of species-area curves. The current range of extrapolation models for species-area curves are reviewed by Tjorve (2009). Power models assume the same proportion of new species is added every time the area is doubled. Logarithmic models assume the same number of new species is added every time the area is doubled. Both of these are inflexible and often fit data poorly, but can be improved by modifying the parameterisations. The negative-exponential family of models, including the Chapman–Richards model and the Weibull distribution, have upper asymptotes, beyond which further increases in area have no effect on species number. It is also possible to fit trivariate models, which include another variable, such as climate, energy or habitat diversity, in addition to area. The choice of model depends on the amount of data and whether the curve is fitted for descriptive, explicative or predictive purposes.

If most species are common and randomly dispersed, the species-area curve will rise steeply and then decelerate when plotted on logarithmic axes. Both uneven species abundances and spatial aggregation will lower the curve, and can result in a wide range of curve shapes (Tjorve et al., 2008). Tjorve et al. (2008) show that the effect of spatial aggregation on species-area curves is weaker than the effect of uneven abundance. Aggregation of rare species affects the

curve at most scales, while aggregation of common species affects the curve only at fine scales.

1.2.1.2 Moving beyond species

The outcome of interactions among organisms, or of interactions between organisms and the environment, are influenced by the diversity of species' functional traits, defined as phenotypic characteristics that influence the performance of species or ecosystem processes, rather than by species diversity *per se*. A distinction can be made between response traits and effect traits (Lavorel and Garnier, 2002). Response traits determine how species respond to environmental or biotic factors, such as climatic conditions, competition, soil nutrient status or fire. Effect traits reveal the effect of species on the environment; this includes traits that affect productivity, biomass and the flammability of vegetation.

Functional diversity, defined by Tilman et al. (2001) as 'the value and range of the functional traits of the organisms in a given ecosystem,' can be assessed by grouping species into functional groups (Naeem and Wright, 2003) or by the use of various indices of functional trait values (Petchey and Gaston, 2002; Walker et al., 1999). With any of these indices, there may be difficulties relating to the choice of traits. Some of the chosen traits may have no impact on the ecosystem process of interest, while other traits that have significant effects may be overlooked. It can also be difficult to determine whether some of the chosen traits are more important than others and deserve greater weighting (King, 2009; Petchey and Gaston, 2006).

The concept of phylogenetic diversity provides another means of moving beyond measures that treat all species equally. Pielou (1975) recognised the importance of phylogeny when she asserted that a community in which species are divided amongst many genera would have greater diversity than a community in which the majority of species belonged to a single genus. Furthermore, if phenotypic change is assumed to take place at a constant rate, then evolutionary divergence times are likely to be correlated with the total functional differences between species (Cadotte et al., 2009). One advantage of phylogenetic measures over functional measures of diversity is that there is no danger of missing any relevant traits – the differences between species in all functional aspects will be incorporated. The downside of this is that there can be no differentiating between aspects which are relevant to the ecosystem process of interest, and aspects which are not.

Higher taxon diversity has been proposed as a simple means of incorporating phylogenetic information in biodiversity measures (Harper and Hawksworth, 1995; King, 2009), which can be applied when phylogenies are not available. The boundaries between higher taxa may vary

greatly in terms of the evolutionary time since lineages split, but species richness can also be difficult to define, for example in the case of species complexes, cryptic species and ring species (Harper and Hawksworth, 1995). Measures of higher taxon diversity are particularly useful when individuals are identified to family or genus level but not to species level.

1.2.2 Patterns of tree diversity in tropical forests

Globally, tropical forests have the highest diversity of all terrestrial biomes (Kier et al., 2005), but there are large differences in diversity levels within and between tropical regions. On a continental scale, African forests tend to have lower diversity than their South American and Asian counterparts, at least for trees (Parmentier et al., 2007). Within Amazonia (including the Guyana Shield), the forests with the highest tree α-diversity can be found in a band running across the centre of the tropical forest zone at 5°S. Forests with the lowest α-diversity are found at the extreme northern and southern fringes of the tropical forest zone, in the Guyana Shield and Bolivia (Ter Steege et al., 2003). Lowland Amazonia has been estimated to contain around 16,000 tree species, of which a small proportion can be described as 'hyperdominant', while most are rare (Ter Steege et al., 2013).

When studying γ-diversity rather than α-diversity, the heterogeneity of the abiotic environment, including topography, geology, soils and climate, becomes a dominant factor. Barthlott et al. (2007) term this 'geodiversity.' This means the global maxima of vascular plant diversity, containing greater than 5000 species per 10,000 km^2, can be found in the Chocó-Costa Rica region, the eastern Andes, Atlantic Brazil, northern Borneo and New Guinea. Central Amazonia has relatively low γ-diversity due to its lack of geodiversity (Barthlott et al., 2007).

Most research has focused on the drivers of diversity in tree species. Van der Heijden and Phillips (2009) find that the pattern of liana species richness is congruent with that of tree species richness, in that both groups are richest in wet forests with short dry seasons (but see Schnitzer, 2005). Animal diversity is closely correlated to plant diversity (Gaston, 1996), since a greater diversity of plant species will provide a greater variety of available niche space, but plant structural diversity is probably more important for animal diversity than is plant species richness *per se* (Mutke and Barthlott, 2005). Novotny et al. (2006) find that the latitudinal gradient in folivorous insect species richness appears to be a direct function of plant species richness, rather than a consequence of narrower host specificity. However, not all taxonomic groups have the same global patterns of diversity. While angiosperm diversity is highest in tropical America and SE Asia, gymnosperm diversity is highest in SW China, and is very low in Amazonia and tropical Africa (Mutke and Barthlott, 2005).

1.2.3 Drivers of tree diversity in tropical forests

Several theories have been put forward to explain the high tree diversity of tropical forests. Some of these theories focus on the origins of tropical diversity, while others focus on the maintenance of tropical diversity.

1.2.3.1 Origins of tropical tree diversity

The origins of biodiversity relate to evolutionary and biogeographical processes occurring on long timescales. High biodiversity in any region must reflect a high rate of either speciation or immigration of new species into the region, in relation to regional extinction rates. One hypothesis regarding the high biodiversity of tropical biomes proposes that higher temperatures promote faster speciation rates, due to shorter generation times, higher mutation rates, and faster physiological processes. Additionally, the relatively stronger biotic interactions in warm, wet climates could also raise speciation rates, because biotic factors are more spatially variable than abiotic factors (Currie et al., 2004). In support of this, it has been found that genetic divergence within populations of vertebrate species is generally greater at low than at high latitudes (Martin and McKay, 2004).

There has been much debate about the possibility of tropical forest 'refugia' during the glacial periods, as first proposed for Amazonia by Haffer (1969). The predominantly drier climate could have transformed large swaths of the tropics into savannas. The remaining areas of moist tropical forest would have been geographically separated, allowing allopatric speciation of tree species to occur. Possible refugia have been identified in areas of forest containing unusually high numbers of endemic species. However, pollen records from the Amazon fan, composed of fluvial sediments which provide a record of vegetation composition from across the Amazon Basin, show no increase in Poaceae pollen during the last glacial. The same is true for pollen records at Lake Pata and Carajas in Brazilian Amazonia. This suggests that most of Amazonia probably remained under forest cover throughout the last glacial period, refuting the refugium hypothesis (Colinvaux et al., 2000). But these records do show increases in pollen from montane species during the Pleistocene, suggesting temperatures were 5-7°C cooler than today.

Palynological diversity in sediments from the west Amazonian Caquetá River area has been found to be twice as high in Miocene sediments as in Holocene sediments (Van der Hammen and Absy, 1994). This could suggest that Amazonian tree diversity actually fell during the Pleistocene. Instead, most Amazonian diversity could have developed during the Tertiary

period, due to the uplift of the Andes and the new opportunities this presented (van der Hammen and Hooghiemstra, 2000).

In Africa, there is greater evidence for past reductions in tropical forest extent. Savanna expansion combined with continental uplift is thought to have prevented the dispersal of many lowland tropical species, causing widespread extinction in the Late Miocene and Pliocene (Morley, 2000). African forests are also thought to have been restricted to refuges during the coldest and driest periods of the Pleistocene, and to have suffered reductions in area during the Holocene (Maley, 2002). Parmentier et al. (2007) argue that these events could have caused the current low tree diversity of African forests. When comparing regions of low mean annual rainfall and temperature, the tree diversity of 1-ha African forest plots is equivalent and at times higher than that of Amazonian forest plots, but when comparing regions of high mean annual rainfall and temperature, tree diversity is significantly higher in Amazonian forests. This suggests that the regional pool of species adapted to warm, wet conditions has been depleted by past climatic events in Africa, while the regional pool of species adapted to cold, dry conditions has not been depleted in this way.

Simple factors relating to space and time may also influence the sizes of regional and local species pools within and among biomes. According to species-area theory, since speciation and extinction operate on timescales of millions of years, the diversity of a biome depends on a combination of its area and the length of time it has been in existence. Fine and Ree (2006) find that although the current tree diversity of eleven tropical, temperate and boreal biomes does not correlate with the current size of these biomes, significant positive correlations are found between current tree diversity and area-time over periods since the Eocene, Oligocene and Miocene. At smaller scales within a domain (a geographically contiguous portion of a biome), the overlap in species ranges will be greatest towards the centre, and this mid-domain effect could explain diversity gradients within large tropical forest regions such as Amazonia (Colwell and Lees, 2000).

1.2.3.2 Maintenance of tropical tree diversity

If there were no mechanisms promoting the maintenance of diversity at a community level, it would slowly erode through stochastic extinction, competitive exclusion, and unstable host-enemy dynamics (Wills et al., 2006). Classic hypotheses for the maintenance of diversity emphasise the importance of niche differentiation (Ashton, 1969). In tropical *terra firme* forests, one of the clearest examples of such differentiation distinguishes pioneer and shade-tolerant tree species (Swaine and Whitmore, 1988). Growth-mortality trade-offs have also

been observed, showing that interspecific variation in functional traits such as wood density may play an important role in maintaining diversity (Wright et al., 2010). Nevertheless, the frequent occurrence of many very similar sympatric species begs the question of how these species can occupy separate niches. This may in part be explained by the 'regeneration niche' concept (Grubb, 1977), which is made up of several components including production of viable seed and its year-to-year variability, seed dispersal in space and time, germination requirements, seedling establishment, and onward growth.

The warm and humid tropical climate, with its lack of seasonality, may allow denser niche packing to occur here than in other biomes. Alternatively, richness in the tropics may be greater because more species can tolerate the relatively benign environmental conditions (Currie et al., 2004). The diversity of a range of taxonomic groups closely correlates with measures of energy in northern high latitudes, and with water availability elsewhere (Hawkins et al., 2003). According to Field et al. (2005), woody plant richness can be predicted if potential evapotranspiration is known. Within Amazonia, dry season length has been found to be a strong predictor of maximum tree α-diversity, although it is only weakly correlated with average tree α-diversity (Ter Steege et al., 2003). This implies that dry season length acts to limit the maximum α-diversity of Amazonian forests, but in many areas other environmental variables become the dominant limiting factors, causing further reductions in α-diversity.

Considerable research has focused on density-dependent mechanisms that promote plant diversity. This originates from the Janzen-Connell "Escape Hypothesis," which argues that seedling mortality is disproportionately high close to adult trees of the same species or in high density conspecific seedling stands (Janzen, 1970). This is due to the impact of distance- and density-responsive pathogens and herbivores (Wills et al., 1997). Species have been found to have a higher survival rate when they are locally rare (Wills et al., 2006), and seedling diversity is significantly greater than seed diversity (Harms et al., 2000), although rare species are more strongly affected by the presence of a conspecific neighbour than common species are (Comita et al., 2010). The tropical climate means biotic factors are likely to be more important in tropical forests than in other biomes, where abiotic factors dominate (Richards, 1996). There is no cold season, which would kill many pathogens and limit the niches available to herbivores. Mean herbivory rates are higher in tropical than temperate forests (Coley and Barone, 1996), but there is still little direct evidence that density-dependent mechanisms are more important in the tropics than elsewhere.

The role of disturbance is fundamental to non-equilibrium hypotheses of diversity maintenance that assume species composition is constantly changing. Disturbance can range

in scale from individual treefall gaps to windthrow during cyclones or other storms (Nelson et al., 1994), landslides, river channel movement across floodplains (Salo et al., 1986), drought, and fire (Colinvaux, 1987). The intermediate disturbance hypothesis (Connell, 1978) states that diversity is highest when the frequency and magnitude of disturbances are at intermediate levels, because the non-equilibrium populations produced will contain a mixture of pioneer and competitive species adapted to a variety of conditions. Severe disturbance will reduce diversity, while a lack of disturbance will lead to dominance by a few highly competitive species. Both between-patch and within-patch mechanisms can be identified, involving spatial and temporal factors (Sheil and Burslem, 2003). Phillips et al. (1994) found tropical tree species richness at 25 sites to be best predicted by turnover rates (mortality and recruitment), suggesting disturbance plays an important role in maintaining tropical forest diversity.

One of the major current debates in community ecology is between the proponents of niche differentiation and the proponents of the neutral theory of biodiversity (Hubbell, 2001). Neutral theory is derived from the premise of Occam's Razor, that the simplest adequate model is preferable to more complex models. While neutral theory acknowledges that niche differences between species exist, it postulates that these have little role in influencing diversity, and all species can be treated as essentially equivalent. Instead, diversity is controlled by generic factors such as dispersal limitations and the stochastic processes that determine regeneration (Hubbell, 2008). The same view is taken of environmental and habitat differences. The role of chance is especially prominent in seedling recruitment. In diverse communities most species are relatively rare, so only a subset of the species will compete in each available gap (Hurtt and Pacala, 1995). Neutral theory also emphasises the balance between speciation, immigration and extinction, revealing links to the theory of island biogeography (MacArthur and Wilson, 1967). It can provide a useful null model for testing other aforementioned hypotheses that posit a greater role for differences between species.

1.2.3.3 Spatial scale and diversity drivers

It is likely that in fact many mechanisms drive differences in biodiversity within tropical forests, and each will contribute to variance in diversity at a particular spatial scale. The historical and evolutionary processes involved in the origins of biodiversity are better at explaining large-scale taxonomic distributions and patterns of endemism, major floristic differences between continents, and regional-scale diversity (Stropp et al., 2009). The ecological processes involved in the maintenance of diversity are better at explaining the differences that occur on smaller spatial and temporal scales, and their link to differences in abiotic and biotic conditions.

On a plot level, phyto-diversity may be predominantly affected by neutral processes (Hubbell, 2001) and gap dynamics (Molino and Sabatier, 2001). At smaller scales, mechanisms of density dependence (Comita et al., 2010) and the identity of individual trees may affect tree species diversity. Wiegand et al. (2007) found some tropical tree species act as diversity accumulators, while others act as diversity repellers, within a 20m radius. On a landscape scale, factors such as hydrology, elevation, soil type, geology and topography (Ferry et al., 2010a) are likely to determine patterns of biodiversity and carbon storage. On *terra firme* soils of southwestern Amazonia, obligate habitat restriction of tropical forest tree species is rare, but most species have significant habitat association (Phillips et al., 2003). Environmental factors accounted for 40% of observed floristic variation, while just 10% of variation was attributed to spatial autocorrelation (Phillips et al., 2003). In a Cameroonian forest, 63% of species were again found to have significant habitat association (Chuyong et al., 2011).

On a regional or continental scale, climate is a major factor affecting patterns of biodiversity and carbon storage. According to Kreft and Jetz (2007), the relatively low plant diversity of African tropical forests, in relation to their South American counterparts, can be statistically predicted purely by differences in mean annual precipitation and the mean annual number of wet days. However, Parmentier et al. (2007) show that other factors must also play a role, since the mean tree

diversity of African forests is still lower than that of Amazonian forests even when analysis is restricted to 2.5 x 2.5 km pixels of directly comparable climate. Gamma-diversity will also be controlled by landscape heterogeneity, since this determines β-diversity. Kreft and Jetz (2007) find a significant relationship between vascular plant species richness and habitat heterogeneity, defined as the number of vegetation types per region. A significant correlation is also found between species richness and topographic complexity, defined as the number of elevational bands per region, but only when potential evapotranspiration is greater than 505 mm a^{-1}. Topographic heterogeneity may be associated with high potentials for speciation during past periods of climatic change, or the recent uplift of mountain ranges (Kreft and Jetz, 2007).

At a global scale, Kreft and Jetz (2007) found land area, potential evapotranspiration, the annual number of days with rainfall, topographical and vegetational heterogeneity, vertical structure of vegetation, and floristic kingdom to be the most important predictors of vascular plant species richness. Evolutionary history also plays a role in explaining floristic differences at large spatial scales. Issues relating to the origins of biodiversity assume greater significance at these scales, and flora may represent past events and climatic conditions, rather than present

conditions. The historic dispersal of taxa is also relevant. The Southern African Cape region has more than double the number of species expected per unit area, given its current environment and topography, perhaps because of past climatic changes or habitat or pollinator specialisation (Kreft and Jetz, 2007).

1.3 Biomass

1.3.1 Defining and measuring biomass

Biomass refers to the mass of living organic matter. The carbon content of dry tree biomass has been found to be 47.4 ± 2.5% in Panamanian tropical forest (Martin and Thomas, 2011), although the content for individual species can vary by up to 5% (Elias and Potvin, 2003). The amount of carbon stored in the biomass of any vegetation depends on both the rate of carbon uptake and the length of time this carbon is stored within the vegetation (Korner, 2009). Carbon uptake is controlled by net primary productivity (NPP), the net balance between photosynthesis and respiration. The persistence of the carbon within vegetation is determined by its distribution within the plant and the longevity of the tissues in which it is stored. As most carbon is stored in woody tissue, rather than foliage, fine roots or necromass (Malhi et al., 2009), its persistence is strongly linked to the lifetime of the tree itself. An increase in tree productivity will not lead to increased carbon storage if it is simultaneously accompanied by an equal increase in mortality.

In tropical forests, direct measurement of biomass is not normally feasible, but aboveground biomass (AGB) can be estimated using allometric regression models developed from harvested trees. The use of a site-specific regression model would provide greatest accuracy, but these are very time-consuming to produce. Allometric regression models that are applicable across the tropics have been developed by Chave et al. (2005) for wet, moist, and dry forests, using 27 datasets from three continents, comprising 2,410 directly harvested trees. Tree diameter and wood density were found to be the most important predictive factors for AGB, followed by height (Chave et al., 2005). Wood density is an important variable (Baker et al., 2004), which can be represented using species level average values, while averages for higher taxonomic groupings or stand-level averages can be used if specific data are not available.

Forest inventories commonly involve direct measurements only of living trees above a certain diameter threshold, such as 100 mm or 10 mm. This means the contributions of trees below the diameter threshold, lianas, epiphytes, dead wood, and below-ground biomass are rarely measured. Belowground biomass in particular is poorly understood, while likely to be the

greatest of these additional components in most tropical forests. The belowground: aboveground biomass ratio has been measured at 0.37 in a Central Amazonian forest (2006 IPCC Guidelines for National Greenhouse Gas Inventories; Higuchi unpublished data in Phillips et al., 2008) or 0.25 in a moist semi-deciduous forest in Cameroon (Deans et al., 1996). Non-tree components are often excluded from AGB estimates (Keeling and Phillips, 2007). Phillips et al. (2008) used a set of expansion factors to estimate total net biomass gain, assuming that the other biomass and necromass components have increased proportionally with increases in the biomass of woody stems ≥100 mm diameter.

1.3.2 Patterns of tropical forest biomass

Globally the highest AGB is found in some temperate forests, such as the *Sequoia sempervivens* groves of northern California (Keeling and Phillips, 2007). Within the tropics, forests in Asia and Africa have considerably higher biomass on average than South American forests, with African forests having 45% greater biomass than South American forests; this is mainly due to differences in the AGB of large trees (Slik et al., 2013). The mean AGB of African forests is 395.7 Mg dry mass ha^{-1}, with Congo Basin forests having significantly higher biomass than East and West African forests (Lewis et al., 2013). In tropical South America, the greatest AGB is found in central and eastern Amazonia and in the Guiana Shield (Baker et al., 2004; Feldpausch et al., 2012).

Large trees are particularly important for biomass, since they comprise a high proportion of total AGB (Stegen et al., 2011) and drive 70% of the variation in AGB between tropical continents (Slik et al., 2013). In Asia, the Dipterocarpaceae occupy a dominant role as large canopy and emergent species. In all tropical continents, the dominance of wind dispersed species such as these is an indicator of forests with high density of large trees and high AGB (Slik et al., 2013). Biomass can also vary greatly at a landscape scale (Laumonier et al., 2010).

Attempts to map regional patterns of carbon storage tend to use a combination of remote sensing and ground-based data. Two recent maps of AGB across the three major tropical continents at resolutions of 1km or greater (Baccini et al., 2012; Saatchi et al., 2011) use localised inventory plot and Lidar data, with satellite images for extrapolation. These maps produce relatively convergent results at regional scales, but large uncertainties remain at smaller scales, such as in central Amazonia. These uncertainties are greatest in areas where little ground data is available (Mitchard et al., 2013). According to Baccini et al. (2012), tropical woody vegetation holds 228.7 Pg C, of which 35% is in Brazil and Indonesia.

1.3.3 Biomass drivers

Proximately, biomass is mainly determined by wood density, tree height, and basal area, which represents the number of stems and their size-frequency distribution. Baker et al. (2004) found that basal area explained 52-63% of variation in AGB, and wood density explained 30-45% of variation, in 56 mature forest plots across Amazonia. Mean wood specific gravity is 15.8% higher in central and eastern Amazonia than in northwestern Amazonia, due to spatial patterns in the diversity and relative abundance of trees with high and low wood specific gravity levels (Baker et al., 2004). It is this, rather than any systematic variation in basal area, that determines the overall regional pattern of AGB across Amazonia. Tree height is another important determinant of biomass, and a failure to include height can lead to overestimates of tropical forest biomass (Feldpausch et al., 2012).

In terms of ultimate drivers, a large number of factors have been suggested to influence biomass in tropical forests. Productivity is a key driver of biomass, but biomass is also influenced by tree longevity and turnover rates (Galbraith et al., 2013). Anything that affects productivity or turnover is likely to affect biomass. This can include trait distributions of local species pools, for example in influencing the regional variation in wood density. In Borneo soil fertility, including soil phosphorous, potassium, magnesium and percentage sand content, are positively related to AGB (Paoli et al., 2008; Slik et al., 2010). Biomass is also influenced by rainfall and temperature (Slik et al., 2013), suggesting that environmental changes could cause changes in forest functioning.

The drivers of AGB will vary with spatial scale. At a local scale, gap dynamics and recovery from disturbance will have a large effect on biomass. Immediately after disturbance, biomass will be low and possibly still falling due to delayed mortality, as found by Chave et al. (2008) in Luquillo, Puerto Rico, immediately after Hurricane Hugo. Subsequently, biomass will begin to recover, and the majority of forest stands at any given point in time will be characterised by rising biomass.

The potential risks of extrapolation from relatively small forest plots to the regional level are highlighted by the extensive debate surrounding the question of whether or not tropical forests are currently a carbon sink. Inventory plot data showed AGB of trees >100 mm diameter to be increasing by an average of 0.62 ± 0.23 Mg C ha^{-1} a^{-1} in Amazonia, suggesting a large regional carbon sink (Phillips et al., 2008). However, it has been argued that the RAINFOR network of plots do not adequately capture the full range of variation with regard to disturbance. According to Fisher et al. (2008), the rare and spatially clustered nature of tree

mortality events may mean that the plots are too small to provide an unbiased sample. However, Gloor et al. (2009) argue that the plot network is of sufficient size that unsampled large mortality events could not occur often enough to account for the observed biomass increase. It is important to be able to estimate the accuracy with which findings based on such plot networks can represent the wider variability of forests.

1.4 Productivity

1.4.1 Defining and measuring productivity

Gross primary production (GPP) is defined as the total carbon captured during photosynthesis. The portion of this that is not used in respiration in known as net primary production (NPP), which represents the net flux of carbon from the atmosphere into vegetation. Net primary production can be estimated by summing the net change in above- and below-ground biomass during a sampling interval plus the losses of biomass that was produced during that interval (Clark et al., 2001). Aboveground losses include litterfall, herbivory, and biogenic volatile organic compounds, while belowground losses include rhizodeposition and root exudation. For practical reasons, estimates of productivity rarely include belowground carbon stores and fluxes, and instead it is common practice to estimate aboveground coarse woody productivity (AGWP, Malhi et al., 2011). This is the component of productivity that contributes to most long-term carbon storage and changes in AGB.

There are several components of AGWP that typically go unobserved. It is necessary in forest plots to choose a minimum diameter threshold above which trees are measured, thus the growth of stems below this threshold is not observed. The growth of trees that subsequently die within sampling intervals must also be considered (Sheil and May, 1996), as well as tree damage (Chambers et al., 2001). These unobserved elements will be proportionately more important the longer the census interval.

Apart from the monitoring of inventory plots, other techniques used to estimate terrestrial-atmospheric carbon fluxes in tropical ecosystems include eddy covariance and aircraft-based flux measurements. These techniques are designed to measure total ecosystem carbon fluxes, including fluxes from both the vegetation and the soil. However, the assumptions required for eddy covariance measures of CO_2 fluxes are not met on calm nights, meaning correction factors are required (Ryan and Law, 2005). Due to this problem, the results from eddy covariance studies have been highly variable, and it is difficult to integrate eddy covariance outputs to directly estimate ecosystem carbon balance (Loescher et al., 2006).

1.4.2 Patterns of tropical forest productivity

Tropical forests account for around a third of global NPP (Field et al., 1998), but difficulties in measuring all components have so far precluded among-continental analyses of NPP variation. Aboveground coarse woody productivity in Amazonia varies between 1.5 and 5.5 Mg C ha^{-1} a^{-1} (Malhi et al., 2004). Within Amazonia, the most productive forests, at least in terms of AGWP, are found in western Amazonia and the Andean foothills, while forests in central and eastern Amazonia and the Guiana Shield are less productive. It is possible that this pattern represents spatial variability in the balance of carbon allocation between respiration, wood carbon and fine root production, rather than directly representing variability in gross or net primary productivity (Malhi et al., 2004).

Faster-growing species tend to have lower wood density. The spatial gradient of wood density is linked to variation in soil fertility, and its effect on coarse wood production. Differences in productivity lead to differences in recruitment and mortality rates. The high productivity and high turnover rates of western Amazonia favour fast-growing species with low wood density, while the low productivity and low turnover rates of eastern Amazonia and the Guiana Shield favour slow-growing species with high wood density (Ter Steege et al., 2006). The high seed mass of species found in this area shows that the seedlings of these species are adapted to grow under shade, in forests with low disturbance levels (Ter Steege et al., 2006).

1.4.3 Productivity drivers in tropical forests

In Amazonia at least, the most important driver of regional variability in productivity appears to be soil fertility. Quesada et al. (2012) found that soil fertility, especially total soil phosphorus, has a strong positive effect on the aboveground wood production of Amazonian forests, leading to the spatial pattern described above. Phosphorous may also be a key driver of net primary productivity, in Amazonia and beyond (Cleveland et al., 2011). However, tree turnover rates were found to be more strongly controlled by soil physical properties (Quesada et al., 2012). Poor soil physical properties could increase turnover rates by causing increased mortality, through factors such as mechanical instability on steep gradients with shallow soils, and the inhibition of deep root growth in poorly drained anaerobic soils.

Moisture availability is a commonly considered limiting factor of biomass and productivity, related to the hydraulic limitation hypothesis (Ryan et al., 2006). Basal area declines significantly at the dry periphery of the Amazonian forest zone, due to increasing dry season length, but local variability appears to be more important than regional trends, and there is little evidence for a relationship with seasonality when dry season length is less than four

months (Malhi et al., 2006). Malhi et al. (2004) found no relationship between coarse wood productivity and mean annual rainfall or dry season length in Amazonia.

Temperature is certainly one of the main factors controlling productivity at mid and high latitudes, but its role in the tropics is less clear. In a meta-analysis of published data from moist tropical forests, Raich et al. (2006) found that total net primary productivity increased with the site mean annual temperature (MAT) by an estimated 0.2–0.7 Mg of carbon ha^{-1} a^{-1} $°C^{-1}$. Forest biomass increased with site MAT by 5-13 Mg of carbon ha^{-1} $°C^{-1}$. However, this study included montane forests with altitudes of up to 4000m. In lowland Amazonian forests, Malhi et al. (2004) found a small but significant negative correlation between temperature and productivity. However, this is probably an artefact, caused by the coincidence that the more fertile soils generally occur at slightly higher elevations in Amazonia.

Biotic interactions could also affect tree productivity. For example, lianas suppress the growth of shade-tolerant saplings in gaps, and increase their mortality rates (Schnitzer et al., 2008). Many animals act as seed dispersers for tropical trees. The loss of large vertebrates through bushmeat hunting may lead to a decline in large-seeded species, which tend to also have high wood density. This could eventually reduce forest biomass and carbon storage (Brodie and Gibbs, 2009).

At small scales, gap dynamics and recovery from disturbance will also have a large effect on productivity. Immediately after disturbance, the abundance of fast-growing species will rise, as found by Chave et al. (2008) in Luquillo, Puerto Rico, while later, the abundance of fast-growing species will fall. Larger-scale disturbances and their relative impact on different landscape units could also be important. At medium to large scales, productivity also varies greatly by soil type, with differences in NPP of almost 100% found between the least fertile nutrient-poor white sand soils and the most fertile *terra preta* (Aragao et al., 2009).

Forest productivity appears to be less affected by wood density than biomass is. Baker et al. (2009) found that large-scale variation in coarse wood production across Amazonia could not be explained by variation in average species maximum height and average species wood density. Productivity instead appears to be more strongly controlled by environmental variables, as discussed above.

1.5 Biodiversity and ecosystem functioning

1.5.1 Theoretical underpinnings of biodiversity and ecosystem functioning

The diversity of life on earth is extraordinary, but it is currently being lost at a rapid rate. How will this loss affect the processes of ecosystem functioning that we all rely on? It is expected that biodiversity has a positive impact on many aspects of ecosystem functioning, and in recent years there has been much progress towards understanding these biodiversity and ecosystem functioning (BEF) relationships. Many BEF studies have used productivity or biomass as an indicator of ecosystem functioning. However, a positive correlation between biodiversity and ecosystem functions can occur for many reasons. Various types of effect have been identified to explain the correlations identified in studies.

Complementarity effects occur when improvements in ecosystem functioning are genuinely caused by increases in biodiversity, and cannot be attributed to the presence or absence of individual species. These effects may be due to niche differentiation, allowing more resources to be tapped when biodiversity is greater. This is an additive mechanism, because it is linearly related to the individual performance of each species in its own niche. Complementarity effects could also involve non-additive mechanisms, whereby the interaction between organisms produces non-linear effects, which may be positive or negative (Reiss et al., 2009). Positive non-linear effects are known as facilitation.

Selection effects involve individual species and additive mechanisms. Changes in ecosystem functioning may be correlated with biodiversity only because the plots with greater biodiversity are more likely to contain functionally important species (Huston, 1997). Selection effects can be negative, as well as positive, if species with lower than average function come to dominate diverse plots (Loreau and Hector, 2001). Selection and complementarity effects can be differentiated by studying the performance of each species in individual monocultures, then comparing these to the performance of high-diversity mixtures, after taking into account changes in abundance. If the overall performance of high-diversity plots is better than that of the best monoculture, then complementarity effects must be occurring (Tilman et al., 2001). This is known as ‘overyielding.’

Many studies have found an element of redundancy in BEF relationships (Sasaki et al., 2009). There comes a point at which further increases in biodiversity no longer have any detectable effect on ecosystem functioning. This could be a real effect, or alternatively it may not persist when additional aspects of ecosystem functioning are considered. Most studies have focused on a single process as their ecosystem functioning response variable. It is important to

simultaneously consider multiple processes, because each process is likely to be affected by a different set of species; hence, more species may be required to maintain multiple functions, compared to the number required for the maintenance of a single function (Isbell et al., 2011; Reiss et al., 2009). Therefore studies focusing on single ecosystem functions could underestimate the importance of diversity.

One of the ways in which biodiversity may affect ecosystem functioning is through its role in the promotion of stability and resilience. This is described as 'insurance' against changing environmental conditions (Loreau et al., 2001). High diversity may help to maintain stability on inter-annual and intra-annual time-scales, and improve resilience in the response to extreme events and environmental change.

As diversity increases, variability within individual populations may increase due to the rising importance of biotic interactions, but the variability of aggregate ecosystem properties often falls (Loreau et al., 2001). This is caused by the way in which different species respond differently to environmental variables. This has a stabilising effect on overall ecosystem properties. However, this effect may saturate at high levels of diversity. In a 10 year study of plant diversity in experimental grassland plots, Tilman et al. (2006) found that higher species richness caused greater inter-annual stability in aboveground plant productivity. This coincided with reduced temporal stability in the annual productivity of individual species.

One way in which stability can be studied is in relation to litterfall. Chave et al. (2010) found mean inter-annual variability in litterfall mass at 81 sites across South America to be 9.3%. A significant correlation was found between litterfall seasonality and rainfall seasonality, but this correlation was very weak ($r^2 = 0.10$), so other factors must also be important in determining litterfall seasonality. Perhaps biodiversity could be one of these factors.

Resilience is an emergent property of the ecosystem as a whole, rather than the sum of individual species contributions. A distinction can be made between equilibrium dynamics, in which a resilient community is expected to return to its pre-disturbance state, and non-equilibrium dynamics, in which it is recognised that more than one stable state is possible, and resilience represents the capacity of the community to respond to disturbance without changing to a qualitatively different community type (Thompson et al., 2009).

Possible causes of ecosystem change can be divided into two categories. Pulse changes involve extreme events, such as fire, drought (Newbery and Lingenfelder, 2004), disease outbreaks, flooding, hurricanes (Zimmerman et al., 1994), and storms. Press changes involve continuous

and increasing pressure on environmental means, rather than extremes, and include many factors relating to anthropogenic climate change.

In a grassland experimental study, Hector et al. (2001a) found that higher diversity increased the resistance of plots to invasion by other plant species. Conversely, Tanner and Bellingham (2006) found that less diverse forests were more resistant to hurricane disturbance in Jamaica. Tanner and Bellingham used turnover rates as a measure of forest resistance to hurricane damage, equating low turnover rates with high resistance, since low turnover strongly suggests low mortality. During the sampling period that spanned Hurricane Gilbert, turnover increased more in the three more diverse forests than in the single least diverse forest. However, turnover rates measure the resistance of individual trees to hurricane damage, rather than the resilience of the ecosystem as a whole. The more diverse forests would appear to be resilient as ecosystems, since two of these three forests showed increases in species diversity during the sampling period spanning Hurricane Gilbert.

Anthropogenic climate change could have major impacts in tropical forests, with a few models predicting that much of eastern Amazonia will be converted to savanna, due to the role of drought and fire. Lewis et al. (2004a) consider a range of mechanisms by which atmospheric change may currently be affecting tropical forests. The observed increases in AGB, growth and mortality appear to have been caused by rising levels of resource availability. Rising CO_2 levels are the most likely driver; other possible drivers could be temperature and solar radiation. The biodiversity of tropical forests is also vulnerable to climatic changes which affect potential species distributions (Miles et al., 2004), although Woodward and Kelly (2008) predict that if land use change is not considered, the impact of rising CO_2 levels will actually be to raise diversity. Changes in species composition over time within tropical forests could drive major changes in their carbon storage (Bunker et al., 2005).

One feature of anthropogenic climate change could be an increase in the magnitude-frequency of extreme events. Phillips et al. (2009a) found that the Amazon drought in 2005 caused an AGB loss of 5.3 Mg C ha^{-1} in forest subjected to a 100mm increase in water deficit. This drought was driven by elevated sea surface temperatures in the North Atlantic, and could provide a proxy for events related to future warming. Another possible effect of rising CO_2 levels across Amazonia could be the recently observed increase in the density, basal area and mean size of large lianas (Phillips et al., 2002).

1.5.2 The findings of experimental and observational studies

Experimental manipulations are commonly used in studies of biodiversity and ecosystem functioning. This allows plots to be created that contain a range of different species richness levels, including monocultures. At each richness level, there may be many different plots, each with their own randomised species composition. This approach avoids confounding factors related to the individual species chosen in lower-diversity plots (Huston, 1997). Due in part to their suitability for these type of experiments, grassland plants are particularly well studied (Fargione et al., 2007; Hector et al., 1999; Tilman et al., 2001, 2006), with strong evidence for the existence of complementarity effects. In annual grasslands, AGB and productivity are effectively equivalent. Complementarity effects have also been found in many other communities, including intertidal rocky shore seaweed assemblages (Stachowicz et al., 2008) and benthic diatom biofilms (Vanelslander et al., 2009).

In a meta-analysis of 44 independent experiments, Cardinale et al. (2007) studied the effects of plant species richness on plant productivity. They found that species richness had a significantly positive net effect on productivity in 82 out of 104 estimates. Analysis showed that both complementarity effects and selection effects were present in most studies. Complementarity effects appeared to contribute 1.9 times more to biomass than selection effects, but complementarity effects were always positive, while 43% of selection effect estimates were negative. Considering the absolute magnitude of the effects, regardless of their sign, there was no significant difference between the mean sizes of complementarity and selection effects. However, none of the studies in this meta-analysis were from forests or tropical ecosystems.

Hector and Bagchi (2007) identified species with desirable effects relating to a range of ecosystem functions in grassland biodiversity experiments. The ecosystem functions considered included above- and below-ground NPP, above-ground nitrogen levels, light interception, soil mineral nitrogen, and the decomposition of lignin and cellulose. The average proportional species overlap between functions was calculated to be 0.2 to 0.5. Ecosystem multifunctionality was found to require a greater number of species than the maintenance of individual processes, thus reducing redundancy.

In a quantitative meta-analysis of BEF studies, Balvanera et al. (2006) analysed the importance of a wide range of factors on biodiversity-ecosystem function relationships. The factors considered related to experimental design, study location, and the ecosystem properties measured. The study analysed 446 measurements of biodiversity effects from 103

publications, 252 of which were from grasslands and 398 of which involved direct manipulations of diversity. Biodiversity effects were found to be stronger when the number of species used in the highest diversity level of studies was greater (>20 species was the largest category used in analysis). This suggests that redundancy occurs little at these levels of diversity. The average effect size was close to zero for the 43 measurements of forest ecosystems, but these were all carried out in greenhouses or pots, with no field-based forest measures.

It is easier to determine the role of biodiversity when conducting experiments in greenhouses or climate chambers, where environmental conditions can be controlled, rather than in the field (Balvanera et al., 2006). However, it is unclear how the results from synthetic experimental assemblages, especially those constructed in artificial environments, translate to natural communities (Peh and Lewis, 2012). This is particularly true for communities such as mature tropical forests, since for practical reasons it is difficult to create synthetic experimental assemblages of mature forests. However, some observational studies of BEF relationships in forests have been carried out.

Observational BEF studies have been conducted in a range of temperate and boreal forest ecosystems (Table 1.1), including deciduous (Szwagrzyk and Gazda, 2007), coniferous (Chen et al., 2003), montane (DeClerck et al., 2005), Mediterranean (Vila et al., 2003, 2007), Scandinavian production forests (Gamfeldt et al., 2013), and successional forests (Caspersen and Pacala, 2001). Due to the nature of these forests and small plot sizes, maximum within-plot diversity is typically low, with the highest being 12 tree species per plot (Caspersen and Pacala, 2001). This is very different to the levels of diversity found in tropical forests.

These non-tropical studies have produced mixed results. A positive hump-shaped relationship between tree species richness and biomass production was found in temperate and boreal Swedish production forests by Gamfeldt et al. (2013). In the Midwest USA, Caspersen and Pacala (2001) found that early successional species have higher productivity, while late successional species live longer and have greater biomass. However, both total productivity and total biomass increased in conjunction with the successional diversity of the plot. A positive correlation was also found between productivity and species richness. Szwagrzyk and Gazda (2007) found a weak negative correlation between species diversity and biomass in Eastern European forests, however their plots covered a wide range of habitats and the role of environmental conditions was accounted for only through the exclusion of four subalpine plots in the analysis. A global meta-analysis, including both plantations and natural forests, has

found that both richness and evenness are positively related to forest productivity (Zhang et al., 2012).

The importance of taking full consideration of environmental factors is emphasised by Vila et al. (2003), who found a significant positive relationship between wood production and species richness in Catalonian *Pinus halepensis*-dominated forests only when climate, bedrock type, radiation and successional stage were not included in the analysis. A wider study (Vila et al., 2007), including deciduous-, coniferous-, and sclerophylous-dominated forests, found that productivity was 30% greater in mixed forests than in single species stands. When environmental and forest structure variables were included in the model, species richness remained significant but explained just 4.7% of variation in productivity.

A common feature of many temperature forests is their long history of human intervention. One third of the plots sampled by Vila et al. (2007) showed signs of wood harvesting. Human intervention and related recovery effects could significantly affect the findings of many studies, illustrating the urgent need for more work to be undertaken in tropical forests, which are often impacted relatively little from direct human activities. Relationships between biodiversity and ecosystem functioning in mature tropical forests are still poorly understood, and this is a crucial gap in the research agenda which needs to be filled.

The quantification of plant diversity and carbon storage and the relationships between them is dependent on the spatial scale of analysis. On a global scale, there may be a positive correlation between diversity and productivity, but this correlation may not exist at smaller scales, or within the ecosystems with the highest levels of diversity and productivity, such as tropical forests. Diametrically opposing relationships between biodiversity, carbon storage and agricultural value are found in different 100 x 100 km squares of the British National Grid by Anderson et al. (2009). It is also important to distinguish between the grain size used in an analysis, such as the size of monitoring plots or pixels in remote sensing data, and the spatial extent of a study, which will affect the accuracy with which results can be extrapolated to other areas.

In the tropics, positive correlations between AGB and species richness have been found in a single mature forest in Panama (Ruiz-Jaen and Potvin, 2010), as well as in a single mature subtropical forest in Puerto Rico (Vance-Chalcraft et al., 2010). Positive effects of diversity on tree growth rates were found when comparing monocultures and mixtures in Costa Rican plantations (Redondo-Brenes and Montagnini, 2006). Diversity was unrelated to AGB in managed forest in Panama (Kirby and Potvin, 2007), but positive relations were found in a

Panamanian plantation (Ruiz-Jaen and Potvin, 2011). All of these analyses are limited to single sites.

Finally, species richness was found to be positively related to both AGB and AGWP in a study of 25 forests (of which 11 had multiple census data and were thus suitable for AGWP). The sizes of these effects were uncertain, ranging from 48% to 5% for AGWP and from 53% to 7% for AGB, depending on whether or not all effects that could potentially be related to stem density were excluded (Chisholm et al., 2013). This study includes only one African forest and two Amazonian forests, only one of which was suitable for AGWP. It remains the case that across the world's most extensive tropical forests, there have been very few studies of biodiversity and ecosystem functioning, and whether such relations exist remains largely unknown.

Table 1.1: The findings of biodiversity and ecosystem functioning studies in natural and managed forest systems.

Author(s) and year	*Ecosystem or assemblage studied*	*Ecosystem functioning variable*	*Diversity measures / levels*	*Plot size and scale of study*	*Method of analysis*	*Effect found and strength*	*Other remarks*
Caspersen and Pacala (2001)	Forests in 11 US Midwest states	AGB, AGWP, mortality	1-12 species	24670, 0.4ha plots.	Null model with niche index of species	Biomass and productivity rise with both successional and species diversity	Early successional species more productive; late successional species longer lived.
Chen et al. (2003)	Coniferous forest, British Columbia and Alberta	Stand volume. Also measured tree age	1-2 species in 3 mixtures	Plot sizes from 30x30m to 12x12m.	Linear and nonlinear regression	Relationships depend on composition of mixed stands. Definitions of mixed stands varied.	Diversity improves growth best when shade tolerant and shade intolerant species are mixed. Used natural even-aged stands.
Chisholm et al. (2013)	Tropical / subtropical / temperate forests	AGB and AGWP	Species richness (c. 10-300 sp.)	25 plots for AGB; 11 plots for AGWP; at 0.04-ha, 0.25ha and 1-ha scales	Generalised least squares	Species richness positively associated with both AGB and AGWP	Strength of relationships unknown due to stem density effects (5-48% rise in AGWP with doubling of richness, 7-53% rise in AGB with doubling of richness)
DeClerck et al. (2005)	Upper montane conifer forests, California	Basal area, soil C and N, canopy closure	1-4 species	281 forest stands with trees >120 years old	Multiple regression and ANOVA	Canopy cover and basal area increased significantly with species richness.	Selected plots with similar environmental conditions. Species composition explained more variation in canopy cover.
Kirby and Potvin (2007)	Managed forest, agroforest and pasture, Panama	Above- and below-ground carbon	1-25 morphosp.	16 paired 15m-radius plots in each site	Nested ANOVA or Kruskal-Wallis test	No diversity-carbon relationship	Taboo on felling a sacred species (*Cavanillesia platanifolia*) helps maintain C stocks

Redondo-Brenes and Montagnini (2006)	Native tree plantations, Costa Rica	AGB, AGWP, basal area	1-3 species (3 mixtures)	16x16m plots	ANOVA	Most species performed better in mixtures than in pure stands	Measured height and diameter
Ruiz-Jaen and Potvin (2010)	Lowland tropical forest, Panama	AGB	Richness and dominance of 30-61 species	One 4.96-ha plot	PCNM and variance partitioning	Diversity explained 19% of variation in AGB (more than environment and space did)	Partitioned variation according to environment, space and diversity.
Ruiz-Jaen and Potvin (2011)	Panama plantation and natural forest	AGB (similar to AGWP in 6-year-old plantation)	Richness; dominance; functional traits	Two sites <20km apart	Multiple regression	AGB mainly explained by species richness in the plantation and by functional dominance in natural forest	In plantation treatments are planted with 6, 9 or 18 species. Controlled for stem density and light availability.
Szwagrzyk and Gazda (2007)	Natural forests from subalpine spruce to deciduous lowland.	AGB	1-8 species	Over 100 plots in Czech Republic, Poland and Slovakia.	Pearson's or Spearman's rank correlation coefficient.	Weak negative relationship between diversity and biomass. Pearson's r =-0.52, p=0.027.	Relationship significant when excluding subalpine plots. Environmental factors not fully accounted for. Similar results for functional groups.
Vance-Chalcraft et al. (2010)	Subtropical forest, Puerto Rico	AGB	1-14 sp., using 5 diversity measures	Four sites, over 100 0.08-ha circular plots in each	Linear and quadratic regression	Positive linear species richness–AGB relationship in the mature forest site; unimodal relationships in the other sites.	Only trees >24.2cm *D*. Three of the sites are secondary forest.
Vila et al. (2003)	Mediterranean pine forest, Catalonia	AGWP and AGWP /basal area ratio	1-5 species	10,644 plots of 10m radius across 32,000km^2 area	One-way ANOVA and general linear model	Productivity of *Pinus halepensis* higher in mixed stands. $F_{4, 442}$ =9.85, P < 0.0001	Effect no longer significant when controlling for environmental factors. No effect for *Pinus sylvestris*.
Vila et al. (2007)	Mediterranean forests, Catalonia	AGWP	1-5 sp., 1-3 functional groups	5069 plots of 15m radius. Measured trees ≥ 75 mm	General linear model	30% greater productivity in mixed forests (P < 0.0001). Species richness explains 4.7% of variation.	Wood harvesting in a third of plots, esp. those with high diversity. Species richness more important than functional group richness.

1.5.3 Ecological relationships within tropical forests

Tropical moist broadleaf forests are characterised by high rainfall throughout most of the year and low annual variability in temperature, and are dominated by evergreen broadleaf tree species. They are characterised by a complex network of ecological interactions and processes, involving biodiversity, species composition, productivity, biomass and their environmental and historical drivers (Figure 1.1). The existence of a correlation between any two of these variables does not necessarily signify a causal relationship, since correlations will also be expected if some of the drivers of biodiversity, productivity and biomass coincide. Thus the causes of any observed relationships must be carefully investigated.

Productivity is hypothesised to affect forest biomass in three ways. Firstly, increased NPP is commonly expected to result in increased basal area and biomass of trees, especially when the initial level of productivity is relatively low. However, unlike the assumptions of global vegetation models, there is no simple linear relationship between forest biomass and productivity (Keeling and Phillips, 2007). Instead, a global analysis found that AGB peaks when aboveground productivity (ANPP) is 15-20 Mg ha^{-1} a^{-1}, and plateaus when ANPP is 20-25 Mg ha^{-1} a^{-1}.There is some evidence that AGB may decline at higher levels of ANPP. Thus secondly, AGB does not continue to increase with rising ANPP because high productivity is associated with high turnover rates, and these tend to be fast-growing species with low wood density (Keeling and Phillips, 2007). Thirdly, high turnover rates are also associated with high mortality, high disturbance levels in terms of treefall gaps, and reduced longevity of individual trees. This longevity explains why temperate Californian *Sequoia* forests have higher AGB than tropical forests, despite their lower productivity (Keeling and Phillips, 2007).

Species composition is likely to affect functional traits such as wood density (Baker et al., 2004) and productivity (Tilman et al., 2001). There will also be complex relationships between species diversity and species functional composition. Higher biodiversity could increase the range of functional trait values. The functional traits of individual species can have an impact on the biodiversity found around individuals of those species, on small scales (Wiegand et al., 2007).

The warm, wet and aseasonal tropical climate has been proposed as a promoter of high tropical biodiversity, via various proposed mechanisms (Currie et al., 2004; Richards, 1996). The same factors also promote high productivity, especially on a global scale, although within relatively aseasonal moist tropical forests other factors such as soil fertility become more

important (Quesada et al., 2012). There are also relationships between the abiotic variables, for example soil fertility will be affected by the geological substrate and rainfall regime, with high rainfall totals causing reduced fertility in the old soils that occur across much of the tropics.

Of the predicted ecological relationships set out in Figure 1.1, I will investigate those that link biodiversity with productivity and biomass. High biodiversity could promote high productivity and biomass through complementarity effects such as niche partitioning and facilitation, as argued in the BEF literature (Cardinale et al., 2007), and could be associated with high productivity via selection effects. Mortality and damage due to the effects of density- and distance-dependent pathogens and herbivores (Webb et al., 2006) could ensure that both productivity and biomass are higher in diverse communities.

It might also be possible for high productivity to promote high plant diversity. The 'energy-richness hypothesis' argues that the higher productivity of tropical climates allows a greater density of individuals, and this causes high diversity. However, Currie et al. (2004) refute this, because the correlation between productivity and species richness is stronger than the correlation between productivity and the number of individuals. Another way in which productivity could affect biodiversity is through the impacts of disturbance. High productivity can cause high turnover of individuals, resulting in greater disturbance from treefall gaps. The dynamic processes associated with this disturbance could promote diversity (Phillips et al., 1994) through the inhibition of competitive exclusion (Ter Steege and Hammond, 2001).

In terms of what is known about their large-scale spatial distributions in the lowland tropics, biodiversity and productivity appear more closely linked than biodiversity and biomass. This is the case in Amazonia at least, where biodiversity and productivity are both high in the west, while AGB peaks in the northeast, where wood density is highest. However, these spatial distributions may be due to other factors, including the fertile soils and the superwet, aseasonal climate of western Amazonia, which have a positive influence on both biodiversity and productivity. It remains unclear therefore whether there is a direct causal relationship between productivity and biodiversity in Amazonia, or elsewhere in the tropics.

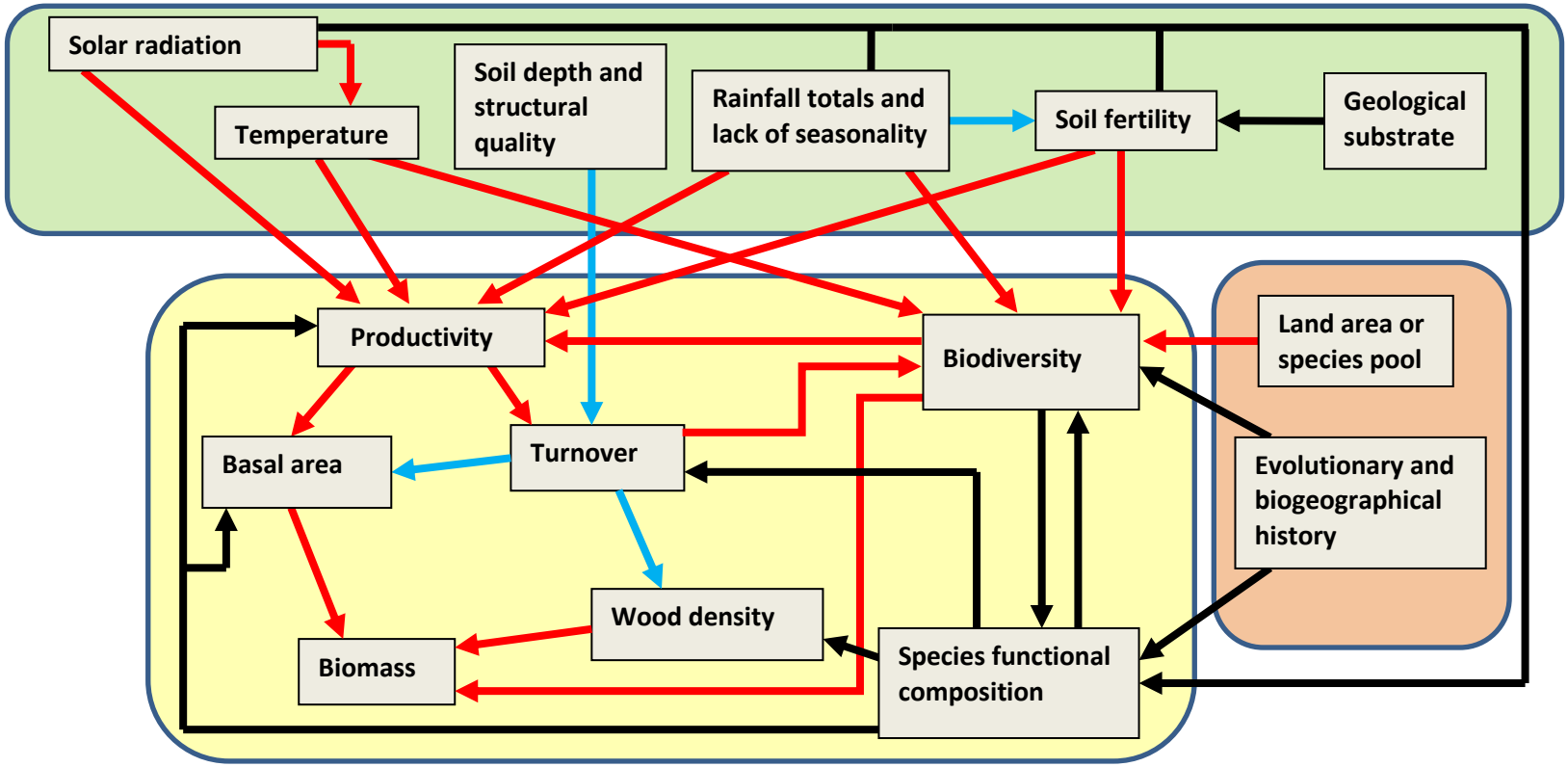


Figure 1.1: Potential local-scale ecological relationships in tropical forests, among components of biodiversity and forest carbon dynamics and their environmental and historical drivers, as predicted by biodiversity and ecosystem functioning research. Positive relationships are shown using red arrows, negative relationships with blue arrows, positive or negative relationships with black arrows. Environmental drivers are contained in the green box, historical drivers in the orange box, and effects of forest composition and ecosystem function in the yellow box.

1.6 Policy relevance of tropical forest biodiversity and carbon dynamics

Much of the recent international attention received by tropical forests has been focused on their role as a major store of carbon, rather than their importance for global biodiversity. However, it is important to take a holistic viewpoint and consider how the preservation of tropical forests can contribute to both biodiversity conservation and climate change mitigation (Talbot, 2010). Reducing the greenhouse gas emissions arising from tropical deforestation and forest degradation has great potential and relatively low costs in comparison to other means of emissions reduction. The foundations for the inclusion of measures relating to forests in the post-2012 climate protection regime were introduced at the Thirteenth Conference of the Parties to the United Nations Framework Convention on Climate Change in 2007. Measures to reduce emissions from deforestation and forest degradation were included in the 2009 Copenhagen Accord, in their expanded REDD+ form, as one of the key mitigation measures. These were further developed in the Cancún Agreements of 2010, and at Warsaw in 2013. The implementation of REDD+ will involve measures to preserve existing forests in developing countries, thereby reducing deforestation rates, and to reduce forest degradation, for example during selective logging. It could draw on various public and private sources of funding, including a possible international fund sponsored by developed countries, which could allow the offsetting of their national emissions.

The spatial scale of REDD+ monitoring and payments could be project-based (sub-national), national, or a combination of the two (Angelson et al., 2008). A project approach allows for the participation of countries that do not yet have sufficient capacity to undertake national inventories of carbon stocks, but this suffers from the problem of leakage, since deforestation may simply happen in a different place. The national approach could also suffer from international leakage. Another problem relates to the setting of an appropriate baseline from which to measure deforestation rates. If the baseline is set to reflect past deforestation rates, this will penalise countries with historically low levels of deforestation. Finally, the permanence of the emissions reductions in any scheme is uncertain, due to the risk of future deforestation, and the impacts of climate change and other possible agents of forest destruction.

The current prominence of REDD+ provides a great opportunity for a range of other benefits as well as the preservation of carbon stocks. Biodiversity conservation is a clear example of a potential co-benefit. Biodiversity provides a range of ecosystem services as well potentially

improving the resilience of ecosystems to climate change (Dutschke, 2007). However, if the focus of REDD+ projects is solely on carbon emissions prevention, then biodiversity may not benefit from these projects. Biodiversity could even suffer if REDD+ projects in low-diversity forests lead to leakage and displaced deforestation elsewhere (Grainger et al., 2009). It is therefore important for biodiversity conservation to be explicitly considered when REDD+ projects are implemented. Meanwhile, other types of conservation funding could be directed towards areas that are unlikely to benefit from REDD+ (Miles and Kapos, 2008). It is also important to ensure that the rights of the local communities in areas affected by REDD+ projects are respected, especially where these communities include indigenous peoples. Local communities should be able to actively participate in the development of projects, and receive a fair share of the financial benefits.

In order to maximise benefits in terms of both carbon storage and biodiversity, it is necessary to know how these vary across tropical forests. Thus schemes in forests with high carbon storage and high biodiversity can be prioritised. A demonstration atlas of carbon and biodiversity has been produced (UNEP-WCMC, 2008), using the IPCC Tier-1 default values for vegetation biomass (Ruesch and Gibbs, 2008), derived from a global land cover map stratified by continent, ecoregion and forest disturbance level. This means that in each continent, undisturbed evergreen tropical forests are given a single value for biomass. In this atlas, areas of high importance for aspects of biodiversity are denoted by overlaying global classification schemes such as Conservation International's Hotspots and the WWF Global 200 Ecoregions. Another study uses the same very crude dataset for biomass carbon storage, but combines this with more detailed diversity data on the global distributions of 20,697 species of mammals, amphibians and birds to infer the presence or absence of these species in hexagonal ~12,500km^2 grid cells (Strassburg et al., 2010), finding strong associations between carbon stocks and species richness. Neither of these studies provides detailed representation of co-variations in biomass and tree diversity within tropical forests. In order to better understand relationships between tree diversity and carbon storage in tropical forests, studies must analyse field monitoring data from fixed points, such as inventory plots. This can provide more accurate measures of biomass and diversity, improving knowledge of how these covary in tropical forests.

1.7 Thesis aims and objectives

1.7.1 Thesis aims

Biodiversity–function relations remain largely unknown in high diversity systems such as tropical forests. I will investigate whether any relationships exist between tree diversity and aboveground biomass or between tree diversity and aboveground coarse wood production, in 323 forest inventory plots in tropical Africa and South America. I will investigate these diversity–function relationships both across large spatial extents, accounting for variation in climate and soils, as well as within forest stands, where climate and soils do not vary appreciably.

1.7.2 Objectives

1) To develop improved methods for obtaining reliable estimates of aboveground coarse wood production using forest inventory plot data.
2) To develop improved methods for obtaining reliable estimates of tree diversity using forest inventory plot data, when not all trees are identified in the field.
3) To investigate whether bivariate correlations between tree diversity and aboveground biomass exist in tropical forests.
4) To investigate whether bivariate correlations between tree diversity and aboveground coarse wood production exist in tropical forests.
5) To investigate whether tree diversity and aboveground biomass covary in tropical forests at large spatial extents, after accounting for soil and climate differences, and any spatial autocorrelation.
6) To investigate whether tree diversity and aboveground coarse wood production covary in tropical forests at large spatial extents, after accounting for soil and climate differences, and any spatial autocorrelation.
7) To investigate whether tree diversity and aboveground biomass are related within tropical forest stands, thereby obviating the need to account for soil and climate differences and spatial autocorrelation.
8) To investigate whether tree diversity and aboveground coarse wood production are related within tropical forest stands, thereby obviating the need to account for soil and climate differences and spatial autocorrelation.

1.7.3 Chapter Outline

In Chapter 2, methods are developed to deal with three longstanding issues that particularly affect the estimation of wood production from forest plot data over long time periods, namely, changes in the height of the point of measurement of tree diameter, differing length of census intervals, and the treatment of stems that newly pass the minimum diameter threshold. In Chapter 3, methods are developed for the estimation of tree richness and diversity. Due to the exceptionally high diversity of tropical forests, it is usual for some trees to remain unidentified in the field. Accounting for these, I use a suite of indices to compute diversity for 61 African and 91 South American forests.

In Chapter 4, I investigate diversity–AGB and diversity–AGWP relations in tropical forests across large spatial extents. I first test for bivariate correlations, then investigate whether relationships emerge or diminish after accounting for soil and climate variables and for spatial autocorrelation. If tree diversity and function, particularly biomass, are found to covary across large spatial extents, this could have important implications for forest conservation and carbon mitigation policies. In Chapter 5, I investigate whether diversity and AGB or diversity and AGWP are directly related in forest stands. Using mixed models in a quasi-experimental approach, I am able to avoid the problem of covarying environmental factors, whilst also controlling for differences in forest structure. The use of a suite of inter-comparable diversity indices enables conjectures to be made about the likely processes that may be driving any observed diversity–function relationships. In Chapter 6, the results from the previous chapters are synthesised and their impact on the current state of knowledge assessed.

1.7.4 Use of forest plot data

Forest plot data are sourced from a global database, ForestPlots.net (Lopez-Gonzalez et al., 2011; Phillips et al., 2009b), which now contains data from over 1000 tropical forest inventory plots censused following standard protocols. Many of these forest plots belong to the RAINFOR (Amazon Forest Inventory Network, www.rainfor.org, Malhi et al., 2002a) and AfriTRON (African Tropical Rainforest Observatory, www.geog.leeds.ac.uk/projects/afritron, Lewis et al., 2009) networks, and have been established and surveyed by a large number of international collaborators.

Personally, I have taken part in the recensusing of 7 plots in Bolivia that are used in the current analysis (LCA-13, LCA-16, MBT-02, MBT-04, MBT-05, MBT-07 and MBT-08 as well as four other plots that are not used, two because of a recent history of anthropogenically influenced fire

disturbance, one because less than 60% of stems were identified to species level, and one because palms had not been measured according to the standard protocol in previous censuses and comprised >30% of stems) and a further 11 plots in Cameroon (DJK-01, DJK-02, DJK-03, DJK-04, DJK-05, DJK-06, NGI-01, NGI-02, NGI-03, EJA-04 and EJA-05). This included inputting the census data from these plots into ForestPlots.net, and for the Bolivian plots, inputting the data from previous censuses conducted by collaborators IBIF (the Bolivian Institute of Forest Research). I have devised the standardised version of 20 x 20 m subplots used in Chapters 3 and 5, and ensured that where these are used, all trees are assigned to subplots, and the positions of most trees are recorded according to a standardised system of coordinates. I also devised the coding system for assigning trees to morphospecies, as explained in Chapter 3.

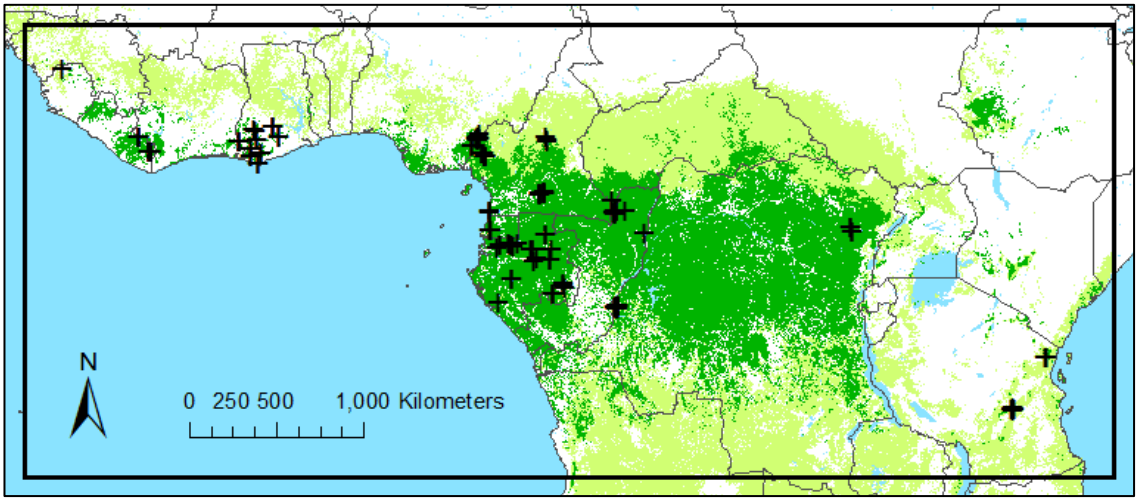
Plot selection criteria vary in Chapters 2, 3, 4 and 5 and overlapping sets of plots are used in each of these chapters. The locations of all of the plots used are shown in Figure 1.2. In all chapters, plots are selected that are from old-growth, closed-canopy, African and South American lowland tropical forest, that are not known to have been directly impacted by humans (e.g. logging, fire). All trees ≥ 100 mm diameter have been censused and the data have been checked for possible errors. Where standard protocols have not been followed for particular taxonomic groups (normally Arecaceae) and these groups need to be excluded, they comprise < 30% of stems. The plots have been visited by a botanist and scientific names are used for species, with ≥ 80% of stems identified to genus level and ≥ 60 % of stems identified to species level. Swamp forests, montane forests and forests with mean annual temperatures < 20°C are excluded. Whenever productivity is used in analyses, plots must have been sampled at least twice over a period of at least 3 years.

In Chapter 2, to assess issues relating to the estimation of wood production over long time-spans, plots were selected that had a minimum of three censuses over a period of at least ten years. In every census, the height at which the diameter of each tree was measured was recorded and the information retained in ForestPlots.net. To ensure the set of plots complying with these conditions remained coherent, only plots from western Amazonia were included. Since this is the only chapter which does not involve measurement of diversity, in this chapter alone plot dimensions were not limited to ≤ 500 m and plots containing multiple soil types were allowed.

In Chapter 3, a single dataset is used for analysis of diversity both within entire 1-ha plots and within 20 x 20 m subplots. Therefore, only plots of 1-ha size were used, in which all trees could

be assigned to 20 x 20 m subplots. In Chapter 4, relationships of tree diversity with AGB and AGWP are assessed among 1-ha plots, therefore all plots are 1-ha in size, but there is no requirement for trees to be assigned to subplots. Chapter 5 deals with analysis of diversity–function relations within plots, thus all plots must have at least five 20 x20 m subplots, with all trees assigned to a subplot, but the plots do not need to be 1-ha in size. All of the plots used in Chapter 5 are sampled at least twice over a period of at least 3 years, because productivity is required for all of the analyses in this chapter.

(a)



(b)

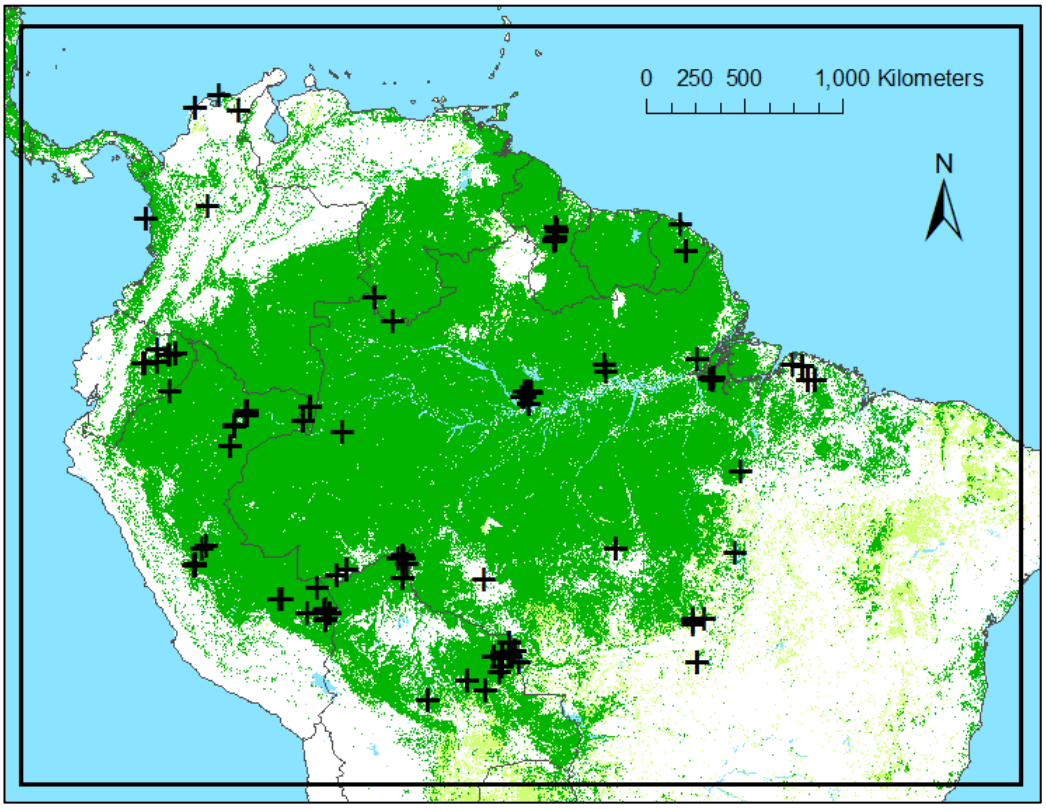


Figure 1.2: Locations of all of the forest plots used in the thesis. Maps show (a) African and (b) South American plots. Using Global Land Cover 2000 classes, broadleaved evergreen and fresh water regularly flooded forests are shown in dark green, broadleaved deciduous and burnt forests and mosaics of forest and other natural vegetation are shown in light green (from Global Land Cover 2000 database, 2003).

2 Methods to estimate aboveground wood productivity from long-term forest inventory plots

2.1 Abstract

Forest inventory plots are widely used to estimate biomass carbon storage and its change over time. While there has been much debate and exploration of the analytical methods for calculating biomass, the methods used to determine rates of wood production have not been evaluated to the same degree. This affects assessment of ecosystem fluxes and may have wider implications if inventory data are used to parameterise biospheric models, or scaled to large areas in assessments of carbon sequestration. Here, I use a dataset of 35 long-term Amazonian forest inventory plots to test different methods of calculating wood production rates. These address potential biases associated with three issues that routinely impact the interpretation of tree measurement data: (1) changes in the point of measurement (POM) of stem diameter as trees grow over time; (2) unequal length of time between censuses; and (3) the treatment of trees that pass the minimum diameter threshold ("recruits"). I derive corrections that control for changing POM height, that account for the unobserved growth of trees that die within census intervals, and that explore different assumptions regarding the growth of recruits during the previous census interval. For the chosen dataset, I find that annual aboveground coarse wood production (AGWP; in Mg dry mass ha^{-1} a^{-1}) is underestimated on average by 9.2% if corrections are not made to control for changes in POM height. Failure to control for the length of sampling intervals further results in a mean underestimation of 2.7% in annual AGWP in these plots for a mean interval length of 3.6 years. Different methods for treating recruits result in mean differences of up to 8.1% in AGWP. In general, the greater the length of time a plot is sampled for and the greater the time elapsed between censuses, the greater the tendency to underestimate wood production if corrections are not made. I recommend that POM changes, census interval length, and the contribution of recruits should all be accounted for when estimating productivity rates, and suggest methods for doing this.

2.2 Introduction

The role of forests in carbon cycling has gained increasing attention in recent years. Globally, forests represent a carbon stock of 861 ± 66 Pg C, with 42% of this in live biomass (Pan et al., 2011). The greatest carbon stocks and fluxes are found in the tropics, with major impacts associated with both natural processes and anthropogenic land-use change activities. Tropical forests contain an estimated 55% of global forest carbon (Pan et al., 2011) and account for 34% of terrestrial gross primary production (Beer et al., 2010). Between 1990 and 2007, tropical intact forests were estimated to represent a carbon sink of 1.2 ± 0.4 Pg C a^{-1}. This is of similar magnitude to the net anthropogenic carbon loss in tropical forests due to deforestation and secondary regrowth (Pan et al., 2011).

Methods for estimating aboveground live carbon stocks from discrete permanent sample plots are relatively well-established in tropical forests, with different plot networks having largely converged on common field methods (e.g. Condit, 1998; Phillips et al., 2009b; TEAM Network, 2010) and similar analytical techniques (e.g. Chave et al., 2008; Lewis et al., 2013; Phillips et al., 2009a). However, the estimation of aboveground wood production from the same type of long-term plots has not been given the same degree of attention. For all ecologists interested in understanding and comparing key aspects of forest ecosystem functioning, as well as for forest management, the quantification of atmosphere-biosphere carbon fluxes and the effects of climate variability on forest productivity (Tian et al., 1998), having access to reliable and comparable estimates of wood production is critical. For example, wood production must be accurately estimated in order to assess the role that tropical forests appear to play in buffering the increase in atmospheric CO_2 concentration caused by human activity. In future, the carbon uptake of tropical forests could be reduced or even reversed (Huntingford et al., 2013), and if this were to occur by warming or drying it could lead to positive feedback further enhancing climate change (Friedlingstein et al., 2006).

My interest lies in coarse wood production as the major long-lived component of net primary production (NPP). As the portion of gross primary production (GPP) that is not lost in respiration, NPP is determined by both GPP and carbon use efficiency. Components of NPP include aboveground and belowground wood production; leaf, flower, and fruit production; fine root production; and the production of volatile organic carbon compounds and root exudates (Malhi et al., 2011). Coarse wood production represents tissues that contribute to the long-term storage and sequestration of biomass carbon, and is also the component with

the greatest relevance to forestry studies (Blanc et al., 2009). For these reasons, in additional to practical concerns, most inventory plot studies measure the aboveground fraction of coarse wood production (AGWP).

The estimation of AGWP normally involves the repeated measurement of stem diameter (*D*) for all stems within a defined area (an inventory plot), across a number of census intervals. Aboveground biomass (AGB) estimates for each census are obtained using allometric equations. However, there remains no single agreed method for the derivation of AGWP from these repeated measures. Although here I consider solely methodological effects on productivity estimation, equivalent methods can also, if required, be used for the calculation of losses of live coarse wood from the system through mortality. This will avoid any apparent imbalances in net fluxes being driven by methodological artefacts.

To obtain the most accurate estimates of AGWP, it is preferable to use a long sampling period. This reduces the signal-to-noise ratio, minimising the impact of hydrostatic flex that may affect the measurement of some trees (Sheil, 1995), and minimising small measurement errors, which can have disproportionate influence across short census intervals. It also ensures that AGWP estimates represent an average of different years with different conditions, reducing uncertainties relating to the impacts of short-lived disturbances and stochastic mortality events, as well as potentially larger-scale events such as droughts or insect outbreaks. Long sampling periods therefore enable more accurate comparisons between plots. However, long sampling periods and long intervals between individual censuses also increase the chance of encountering problems associated with three factors that affect AGWP estimation, as explained below.

Firstly, individual trees naturally tend to increase in height, stem and crown diameter over time. As a tree grows, the need for stabilisation is satisfied in many tropical species by progressive development of root buttresses. Other species may have adventitious or prop roots that move upwards through time. The point of measurement (POM) for stem diameter is normally set at 1.3m or a fixed height above buttresses, but as deformities creep up the trunk, POM changes are often necessary (Sheil, 1995). These will affect an increasing number of trees with increasing time elapsed since the first measurement. The new POM will typically be at a higher point, where the stem has lower *D* due to stem taper (Fang and Bailey, 1999). The existence of stem taper, which can vary greatly between species (Poorter and Werger, 1999), means that *D* measurements taken at different POMs are not directly comparable, and

treating them as such would bias growth estimates (King, 2009; Niklas, 1995). Procedures are therefore required to correct for this impact.

Secondly, the unobserved growth of trees that subsequently die within an interval represents a source of bias closely related to interval length (Sheil and May, 1996). The longer the interval, the more unobserved growth there will be, both from previously measured stems and from unmeasured stems that pass the minimum diameter threshold and subsequently die within the same interval unrecorded (Lewis et al., 2004b; Malhi et al., 2004; Sheil and May, 1996). Clearly, the relative importance of this effect increases with increasing census interval length.

A third origin of uncertainty in AGWP measurements is the approach used to deal with recruits, i.e. those trees that have reached the minimum measured *D* threshold by the end of a given census interval. Since these trees were not measured at the start of the interval, their growth within the interval is unknown. Two common approaches have been used: assuming growth over the interval is only that greater than the diameter measurement threshold in the study (typically 100 mm; i.e. a new recruit of 110 mm is assumed to have grown 10 mm); or recruits were 0 mm in the previous census interval (Clark et al., 2001; Malhi et al., 2004). The fraction of AGWP associated with recruits, and the concomitant degree of uncertainty, will increase with mean census interval length.

Other factors could influence productivity estimates, for example the choice of procedures used to deal with missing or extreme values, the choice of allometric equation, the carbon fraction (Martin and Thomas, 2011), the belowground: aboveground biomass ratio assumed (Deans et al., 1996) and estimation of wood density (Flores and Coomes, 2011). These are important concerns, but beyond the scope of this paper's focus on methodological considerations related to processing accurately collected data.

I present procedures developed to minimise the biases associated with POM changes and census interval length, and make explicit how the treatment of recruits can alter results, using a large number of forest plots to assess impacts on AGWP rates. I review a set of methods for AGWP estimation, evaluate the biases, and provide recommendations for the estimation of AGWP from permanent sample plots in tropical forest.

2.3 Materials and Methods

Thirty five long-term forest inventory plots from western Amazonia were selected from a single database (www.forestplots.net, Lopez-Gonzalez et al., 2011), all part of the RAINFOR network. To ensure that plots were appropriate for the investigation of how methodologies for POM changes, census interval length and recruitment affect productivity, only plots with at least three censuses over a period of at least 10 years were used, in which POMs had been recorded in each census. To ensure accurate wood density values could be used, I selected plots that had been visited by a botanist, with ≥80% of stems identified to genus level (mean 97%) and ≥60% of stems identified to species level. All plots were in mature old-growth forests. Plot size ranges from 0.88 ha to 1-ha, with mean number of census intervals of 4.9 and mean interval length of 3.6 years. The sites span lowland western Amazonia, from seasonal forests near the savanna margins in the south to the wet upper Amazon. The selected plots are listed in the attached CD (Table A2.1).

I estimated the aboveground biomass (AGB) of each stem ≥100 mm *D* at each census, including monocotyledons which were treated in the same way as dicotyledons. AGB was estimated using the Chave et al. (2005) moist forest equation, $AGB = exp\ (-2.977 + ln\ (\rho D^2 H))$, where *D* is stem diameter (in cm) at reference height, *H* is the height of the stem (in m) and ρ is stem wood density (in g cm^{-3}) (Figure 2.1). Height was inferred from diameter using the regional height-diameter Weibull equation of Feldpausch et al. (2012). I estimated the wood density of individual stems using a pan-tropical database (Chave et al., 2009; Zanne et al., 2009). The most resolved taxonomic level available was used, following the method of Lewis et al. (2009), using continent-specific wood density taxon reference values.

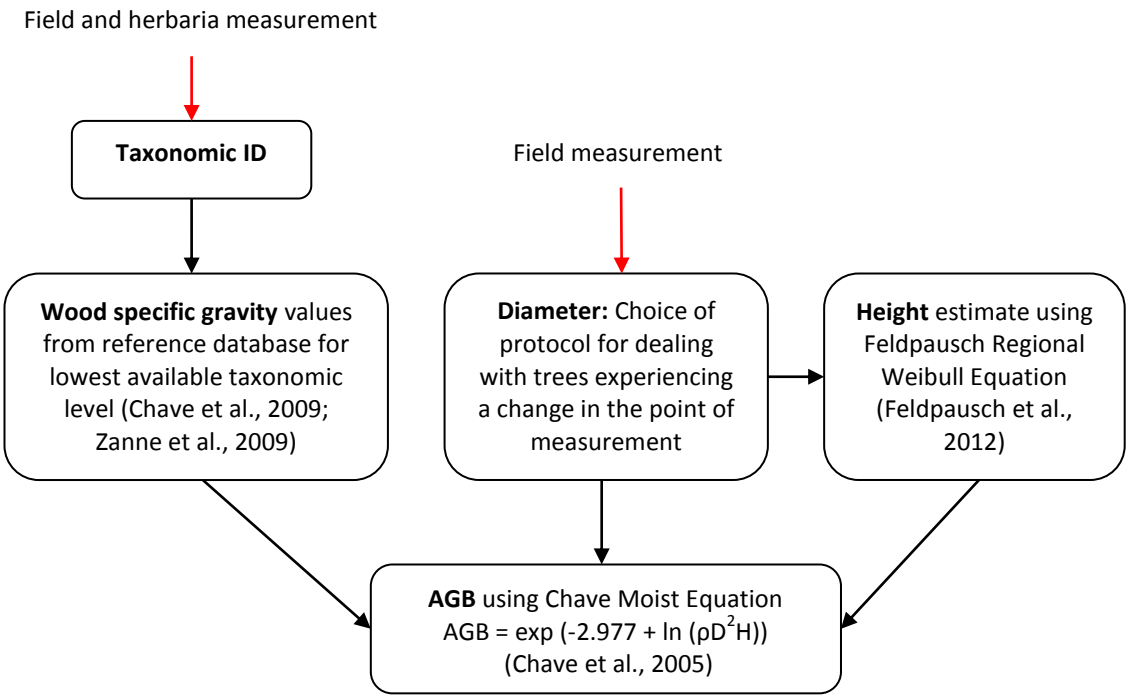


Figure 2.1 Procedure for estimating the AGB of a single stem.

Diameter was measured for all stems with D ≥100 mm, using diameter tape at a height of 1.3 m, or above buttresses or other stem deformities. When such deformities threatened to encroach the current POM I changed to a new POM, recording the diameter at both the old and new POMs. Stem taper can be estimated by the ratio of D at old POM (D_{old}): D at new POM (D_{new}). This ratio is used to calculate standardised estimates of D_{old} for each census after a POM change and of D_{new} for each census prior to a POM change, with D_{mean} denoted as the mean of D_{old} and D_{new} (Figure 2.2).

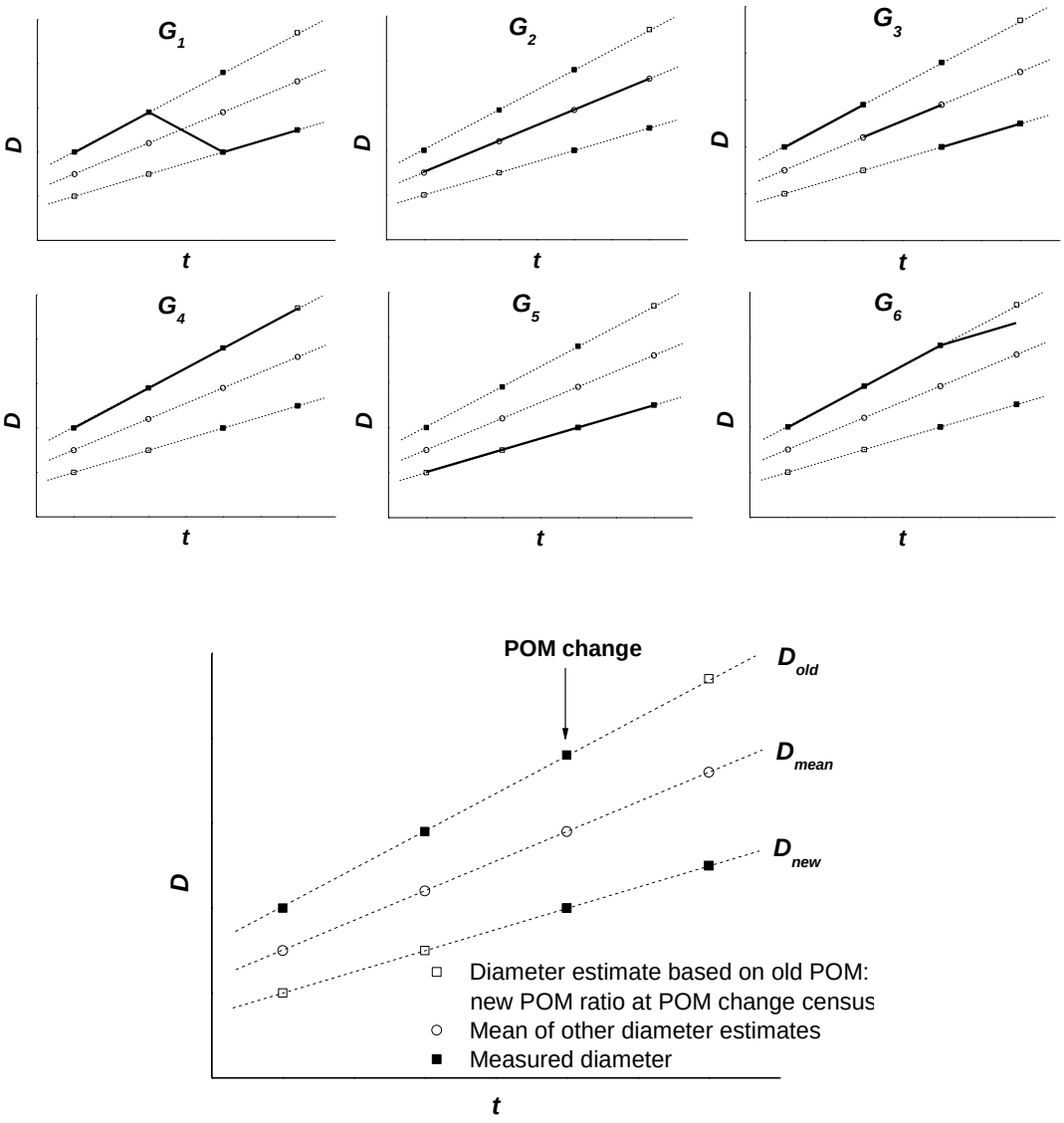


Figure 2.2: Diameter and growth measures for a hypothetical stem which has undergone a POM change. Growth measurement protocols are shown as the bold lines in the insets. G_1*:* Uses measured diameter in all censuses, regardless of POM changes; G_2*:* Uses estimated diameter at a standardised POM height (D_{mean}) in all censuses, representing the mean of D_{old} and D_{new}; G_3*:* Uses a combination of estimated diameter at D_{mean} in censuses with POM changes and measured diameter in other censuses; G_4*:* Uses diameter at D_{old} in all censuses; G_5*:* Uses diameter at D_{new} in all censuses; G_6*:* After a POM change the increment at D_{new} is added to the original diameter at D_{old}.

A number of techniques were used to avoid or minimise potential errors arising from missing diameter values, typographical errors, or extreme *D* growth ≥40 mm a^{-1} or total *D* growth ≤-5 mm across a single census interval (i.e. losing 5 mm, as trees may shrink by a small amount due to hydrostatic effects in times of drought, and measurement errors can be both positive and negative). For stems belonging to species known to experience very high growth rates, or

noted as having damaged stems, these values were accepted. I used interpolation, where possible, or extrapolation to correct errors. If neither of these procedures were possible I used the mean growth rate of all dicotyledonous stems in the same plot census, belonging to the same size class, with size classes defined as $100 \leq D < 200$ mm, $200 \leq D < 400$ mm, and $D \geq 400$ mm, to estimate the missing diameter value. Of all stem growth increments, 1.7% per census were assigned interpolated estimates of diameter, for 0.9% I used extrapolated estimates, and for 1.5% I used mean growth rates.

To estimate the AGWP of a given plot across a single census interval, I summed the change in AGB for each tree present at both the start and end of the interval, plus the AGB of new recruits present at the end of the interval, and divided the result by the interval length. Having calculated mean annual AGWP of each census interval, I then calculated mean annual AGWP across the entire period during which a given plot had been sampled, weighting the AGWP of each individual census interval by the length of the interval.

I used multiple methods to estimate wood production, in response to the three problems of POM changes, census interval length, and recruitment. These included a designated 'suggested scenario' involving corrections relating to POM changes and census interval length, and a 'baseline scenario' that lacked these corrections. This enables the quantification of how AGWP estimates using other method combinations deviate from these two reference cases. Since the recommended treatment of recruits itself depends on the specific question being asked by a researcher, I used the same method of treatment of recruits in both the baseline and the suggested scenarios.

2.3.1 Treatment of POM changes

A number of approaches for treating POM change trees were tested to explore their impact on AGWP estimates (Figure 2.2). My first method provides no correction for stems with POM changes (denoted *'G_1'*). This is used in the baseline scenario. At any given census, this is normally expected to provide the best measure of stem diameter at that particular census, and could therefore be appropriate for biomass estimation. However, when stems undergo POM changes, changing the height at which this diameter is taken, the existence of stem taper means that estimates of wood production will be biased downwards across these intervals.

To avoid the bias inherent in G_1 and to help quantify its impact, five alternatives were explored (Figure 2.2). In the second method, denoted *'G_2',* I use the estimated diameter at a standardised POM height (D_{mean}) in all censuses, with D_{mean} representing the mean of D_{old} and

D_{new}. The third method, 'G_3', uses a combination of techniques from G_1 and G_2. Thus, for all census intervals not involving a POM change, the directly measured diameters were used to calculate growth (as in G_1), but for census intervals involving a POM change, D_{mean} was used to calculate growth across that interval (as in G_2). G_3 is used in the suggested scenario. The three final techniques are similar to G_2 in that they all maintain a constant POM height across all censuses for each tree. With G_4 this POM is at D_{old} in all intervals, with G_5 it is at D_{new} in all intervals, and with G_6, which follows the method of Clark et al. (2013), the measured diameter increment at D_{new} after a POM change is added to the original diameter at D_{old}.

2.3.2 Treatment of differing census interval length

The longer a census interval, the greater the proportion of growth that will go unobserved within the interval. Census interval correction is required to account for two sources of error – unobserved growth from trees that were known to have died during the interval, and unobserved growth from trees that both recruited and died during the interval. I used two different methods to derive correction factors that accounted for the effects of census interval length on observed AGWP. In the results, the baseline scenario does not include any correction for census interval length, while the suggested scenario uses the second correction method.

First, I used a parametric technique based on the methods of Malhi et al. (2004), denoted 'CIC_1', but with the corrections applied to AGWP rather than basal area growth rates (as in Phillips et al., 2009a). For this, I calculated AGWP across all of the one-, two- and three-census periods within each plot, grouping consecutive censuses to create the two- and three-census periods. I included every possible combination of consecutive censuses within a given plot, except for those of greatly different lengths (ratios of 1: 3 or greater), which were excluded to minimise variation in the length of these intervals. Any censuses that I excluded in this way were excluded from the estimates of AGWP across all single censuses as well as the estimates of AGWP across the two- and three-census periods. I derived growth using G_2 to avoid problems associated with POM changes in the two- and three-census periods.

Next I calculated the mean length and mean annual AGWP of all of the single censuses in a plot, all of the two-census periods, and - for plots with at least four censuses – all of the three-census periods. I regressed mean annual AGWP against mean interval length separately for each plot (Figure 2.3), and used the resulting gradients to calculate the corrected AGWP estimates for each census interval as follows:

$$AGWP_{corr} = AGWP_{obs} - c*t$$

Where $AGWP_{corr}$ is the corrected mean annual productivity, $AGWP_{obs}$ is the observed mean annual productivity, c is the required annual correction (the gradient in Figure 2.3) and t is the census interval length, in years. For four plots in which all consecutive censuses were of greatly different lengths (HCC-23, HCC-24, SUC-03, and TIP-01), I corrected AGWP using the mean c derived from all other plots (-0.058).

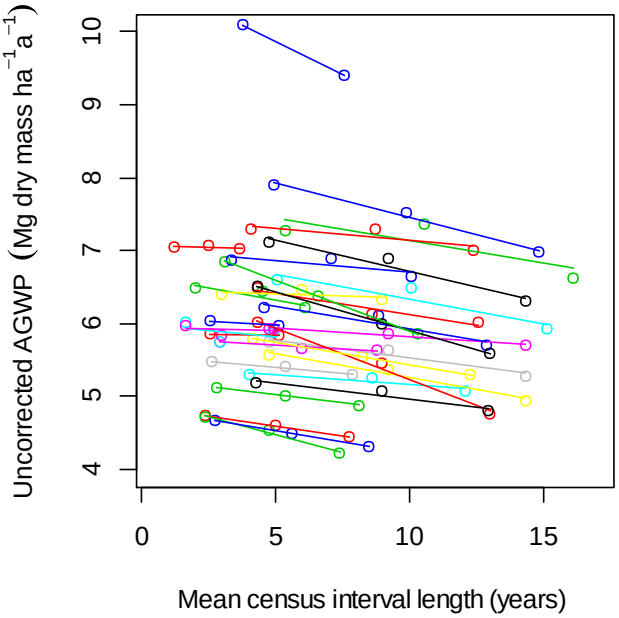


Figure 2.3: The census interval effect, showing how uncorrected AGWP is higher when census intervals are shorter. Each line represents a single plot, with each point representing the mean uncorrected AGWP of all single censuses, all possible two-census periods, or all possible three-census periods within that plot, excluding consecutive censuses of greatly different lengths (ratios of 1: 3 or greater).

In the second method for census interval correction, denoted 'CIC_2', an individual stem-based approach is used. Since data are collected on the growth of individual stems, the most accurate corrections should be those that use these measurements to estimate the growth both of known stems that die during the interval and of stems that recruit and die unobserved during the interval. To estimate the growth of known stems that died during the interval, these stems were assumed to have died at the mid-point. I calculated the unobserved growth up to the mid-point using the median growth of all dicotyledonous stems in the plot within the same size class, using the size classes defined above.

The number of unobserved recruits (U_r) was estimated as the product of the number of stems in the plot (N), the time-weighted mean annual mortality rate in the plot (M), the time-weighted mean annual recruitment rate in the plot (R) and the census interval length (t): U_r =

*N*M*R*t*. My use of time-weighted mortality and recruitment estimates representing the entire period across which a plot has been sampled reduces the impact of the variability of these processes over short time-spans. I assumed the diameter growth rate of unobserved recruits to be the median rate for dicotyledonous stems in the 100-199 mm size class. This was chosen as a lower estimate than the size class mean growth rate or the mean growth rate of recruits, since stems are reported to have reduced growth in the months immediately prior to mortality (Chao et al., 2008). I assigned stem wood density as the same as the plot mean in that census. I assumed these stems recruited on average one-third of the way through the interval and died two-thirds of the way through the interval, allowing growth over a time period equal to one-third of the interval. The estimated unobserved growth from the known stems that died and the unobserved recruits were added to the AGWP of each census interval.

2.3.3 Treatment of newly recruited stems

To estimate AGWP across a census interval, the productivity of trees that surpass the minimum diameter threshold of 100 mm during the census interval must be included, in addition to the gain in AGB of trees that were present at both censuses. The productivity of these new recruits is uncertain, since their diameter is unknown at the start of the census interval. I used three methods to quantify the productivity of new recruits.

For my first method, denoted 'R_1', I assumed the recruits had a diameter of 0 mm in the census prior to recruitment. This is unlikely in practice, but allows the growth of stems <100 mm *D* to be implicitly included in productivity estimates. For this reason it is commonly used. For the second method ('R_2'), the recruits were assumed to have had a diameter of 100 mm in the census prior to recruitment. Note that to ensure comparability of biomass gain and loss the same 100 mm core must also be subtracted from the biomass of each dead tree when using R_2. These two methods respectively delimit the maximum and minimum possible growth rates of recruited stems. R_1 is used in both my baseline scenario and my suggested scenario.

For the third method ('R_3') I extrapolated the growth rate of each individual stem backwards from the census immediately following recruitment. If the mean of the measured *D* of a newly recruited stem and the extrapolated *D* of the same stem in the previous census was <100 mm, I did not include growth of this stem in the measure of recruitment using R_3 (i.e. zero growth assumed across the interval for this stem), thereby following equivalent methods to delimit the lower end of the 100-199 mm size class as would be used to delimit any other stem size class. Where the plot had no census following recruitment, meaning growth rates of recruits

could not be extrapolated, I used the 86th percentile growth rate of stems from the same plot census in the 100-199 mm size class, since this was found to provide the closest approximation of the mean growth of recruits. Mean estimated stem diameter for the census prior to recruitment, excluding stems for which I assumed zero growth as explained above, was 97.4 mm.

2.4 Results

My 'baseline scenario' involves ignoring POM changes, ignoring census interval length and assuming the R_1 growth of recruits (from 0 mm diameter), and yields a long-term mean AGWP of 5.44 Mg dry mass ha^{-1} a^{-1} (n = 35; Table 2.1). By contrast, the 'suggested scenario' which incorporates corrections for POM changes (G_3) and census interval length (CIC_2), while retaining R_1 recruitment, gave a mean AGWP estimate of 6.17 Mg dry mass ha^{-1} a^{-1} (13.4% greater). Thus, it appears that disregarding these issues would substantially underestimate the true AGWP of these forest plots. In turn I discuss the three potential biases and their impacts on the dataset analysed.

Table 2.1: Mean annual AGWP across all plots, using methods developed to deal with three issues in AGWP calculation across long time-spans. Some important combinations of methods are listed first, followed by each possible remaining combination that involves G_1, G_2 or G_3.

Method	*Treatment of POM change*[a]	*Treatment of recruits*[b]	*Census interval correction*[c]	*Mean annual AGWP across all plots, with bootstrapped 95% confidence intervals (Mg dry mass ha^{-1} a^{-1})*
Baseline scenario	G_1	R_1	*Without CIC*	5.44 (5.12 - 5.79)
Suggested scenario	G_3	R_1	CIC_2	6.17 (5.82 - 6.55)
Using D_{old}	G_4	R_1	CIC_2	6.26 (5.89 - 6.63)
Using D_{new}	G_5	R_1	CIC_2	6.00 (5.66 - 6.34)
After Clark et al. (2013)	G_6	R_1	CIC_2	6.24 (5.87 - 6.61)
A	G_2	R_1	*Without CIC*	5.95 (5.61 - 6.32)
B	G_3	R_1	*Without CIC*	6.01 (5.65 - 6.37)
C	G_1	R_2	*Without CIC*	4.96 (4.65 - 5.29)
D	G_2	R_2	Without *CIC*	5.48 (5.13 - 5.83)
E	G_3	R_2	Without *CIC*	5.53 (5.18 - 5.89)
F	G_1	R_3	*Without CIC*	4.95 (4.64 - 5.29)
G	G_2	R_3	Without *CIC*	5.47 (5.14 - 5.83)
H	G_3	R_3	Without *CIC*	5.52 (5.16 - 5.89)
I	G_1	R_1	CIC_1	5.71 (5.38 - 6.08)
J	G_2	R_1	CIC_1	6.22 (5.87 - 6.60)
K	G_3	R_1	CIC_1	6.27 (5.92 - 6.66)
L	G_1	R_2	CIC_1	5.23 (4.91 - 5.59)
M	G_2	R_2	CIC_1	5.74 (5.40 - 6.10)
N	G_3	R_2	CIC_1	5.79 (5.44 - 6.18)
O	G_1	R_3	CIC_1	5.22 (4.90 - 5.58)
P	G_2	R_3	CIC_1	5.73 (5.39 - 6.10)
Q	G_3	R_3	CIC_1	5.79 (5.43 - 6.17)
R	G_1	R_1	CIC_2	5.61 (5.29 - 5.96)
S	G_2	R_1	CIC_2	6.12 (5.78 - 6.47)
T	G_1	R_2	CIC_2	5.11 (4.81 - 5.45)
U	G_2	R_2	CIC_2	5.63 (5.30 - 5.99)
V	G_3	R_2	CIC_2	5.68 (5.34 - 6.04)
W	G_1	R_3	CIC_2	5.11 (4.79 - 5.45)
X	G_2	R_3	CIC_2	5.62 (5.29 - 5.98)
Y	G_3	R_3	CIC_2	5.68 (5.33 - 6.04)

[a] G_1: No correction for POM changes; G_2: Uses standardised POM height at D_{mean} in all censuses; G_3: Uses combination of diameter at D_{mean} in censuses with POM changes and directly measured diameters in other censuses; G_4: uses diameter at D_{old} in all censuses; G_5: uses diameter at D_{new} in all censuses; G_6: after a POM change the increment at D_{new} is added to the original diameter at D_{old}.

[b] R_1: Assumes recruits have a diameter of 0 mm in the census prior to recruitment; R_2: Assumes recruits have a diameter of 100 mm in the census prior to recruitment; R_3: Extrapolates stem growth rates backwards from the census following recruitment.

[c] CIC_1: Parametric correction for census interval length; CIC_2: Stem-by-stem correction for census interval length.

2.4.1 Effect of POM change protocol

When census-interval corrections and recruitment are treated as in the suggested scenario (CIC_2, R_1), but diameter is used as measured in the field (G_1 protocol), i.e. ignoring the effect of POM changes, estimated mean annual AGWP is 5.61 Mg dry mass ha^{-1} a^{-1}, 9.2% lower than the suggested scenario (which uses G_3). By contrast, if instead growth is based on the mean of growth at the new and old POM (G_2), annual AGWP across all plots is estimated as 6.12 Mg dry mass ha^{-1} a^{-1}, just 0.9% lower than the suggested scenario (Figure 2.4). Alternatively, using a fixed POM at D_{old} (G_4) produces a mean annual AGWP of 6.26 Mg dry mass ha^{-1} a^{-1}, a fixed POM at D_{new} (G_5) gives 6.00 Mg dry mass ha^{-1} a^{-1}, and adding the diameter increment at D_{new} to the original diameter at D_{old} (G_6) yields 6.24 Mg dry mass ha^{-1} a^{-1}.

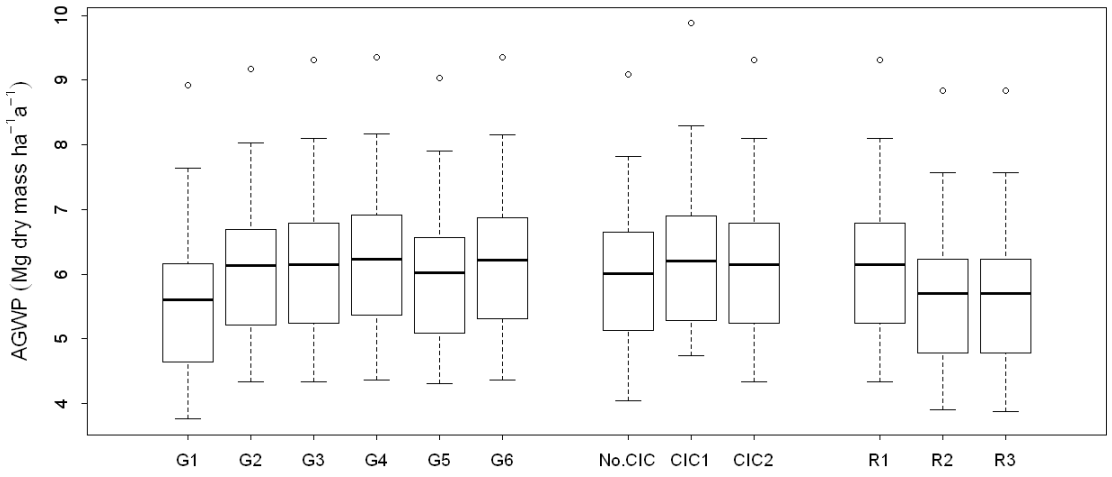


Figure 2.4: Variation in estimated mean annual AGWP with choice of analytical method. Each group of boxplots shows the effect of changing a single factor, with the other methods based on the standard suggested scenario in which corrections for both POM changes (G_3) and census interval length (CIC_2) have been made. From left to right, the single factors are POM change protocol, method of census interval correction, and treatment of recruits.

The impact of POM changes is linked to the total length of the sampling period. As trees grow and time elapses, the greater the proportion of stems that will have undergone POM changes. By the final census, on average 16.8 years after the initial census, a mean of 10.5% of stems present have had their POM changed. Nevertheless, the impact of POM changes does not appear to be linked to mean interval length or baseline scenario productivity (Figure 2.5).

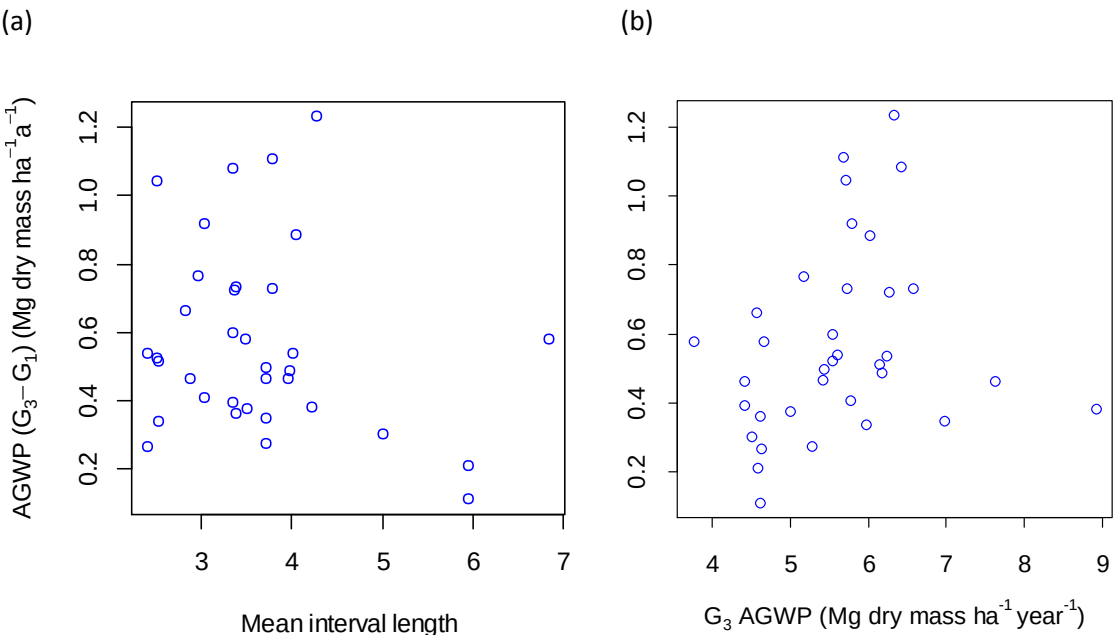


Figure 2.5: Effect of (a) mean interval length; and (b) AGWP (using the suggested scenario) on the estimated bias associated with POM changes. This is calculated as the difference between AGWP using G_3 (suggested scenario) and AGWP using the G_1 protocol.

2.4.2 Effect of census interval correction

The length of census intervals also has a noticeable impact on productivity estimates. Without correcting for census interval length, mean AGWP (using G_3 and R_1) is estimated at 6.00 Mg dry mass ha^{-1} a^{-1}, 2.7% less than the suggested stem-by-stem method (CIC_2), which gives an estimate of 6.17 Mg dry mass ha^{-1} a^{-1}. When parametric (CIC_1) rather than stem-by-stem census interval corrections are applied, AGWP is estimated at 6.27 Mg dry mass ha^{-1} a^{-1} (Figure 2.4).

The corrections applied in each plot using method CIC_1 are shown in Figure 2.3. Dividing the gradients in this graph by the mean uncorrected AGWP values in each plot, I derive a simple formula that shows the mean proportional annual correction:

$$AGWP_{corr} = AGWP_{obs} + 0.0091\ AGWP_{obs} * t$$

Where $AGWP_{corr}$ is the corrected mean annual productivity and $AGWP_{obs}$ is the observed mean annual productivity within a census interval of length t, in years. This gives a correction of 0.91% per census-interval year. Using either method of census interval correction, the corrections appear closely related to interval length (Figure 2.6).

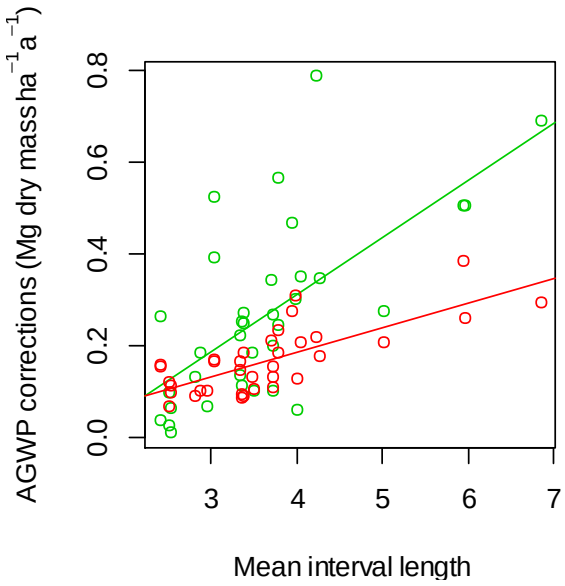


Figure 2.6: Effect of census interval length on the magnitude of AGWP corrections to account for stems that die within intervals. Each circle represents a plot; using parametric (CIC_1) AGWP corrections (in green); and stem-by-stem (CIC_2) AGWP corrections (in red), with regression lines.

2.4.3 Effect of treatment of recruits

When growth of recruits is assumed to start from 100 mm *D* at the time of the previous census (R_2), rather than from 0 mm *D* (R_1), mean AGWP falls 7.9% to 5.68 Mg dry mass ha^{-1} a^{-1} (Figure 2.4). The difference in estimated AGWP between R_1 and R_2 will be greatest when AGWP is low and when mean interval length is long, since under these circumstances recruits comprise the highest proportion of total wood production (Figure 2.7). Considering solely the productivity of the recruits, with R_1 mean annual AGWP of recruits was 0.73 Mg dry mass ha^{-1} a^{-1}, while switching to R_2 reduced this by 65.7% to 0.25 Mg dry mass ha^{-1} a^{-1}. Back-extrapolation of individual stem growth rates from later censuses (R_3) produces a mean AGWP of 5.68 Mg dry mass ha^{-1} a^{-1}, similar to R_2 and 8.1% lower with R_1, with 0.24 Mg dry mass ha^{-1} a^{-1} for the recruits only.

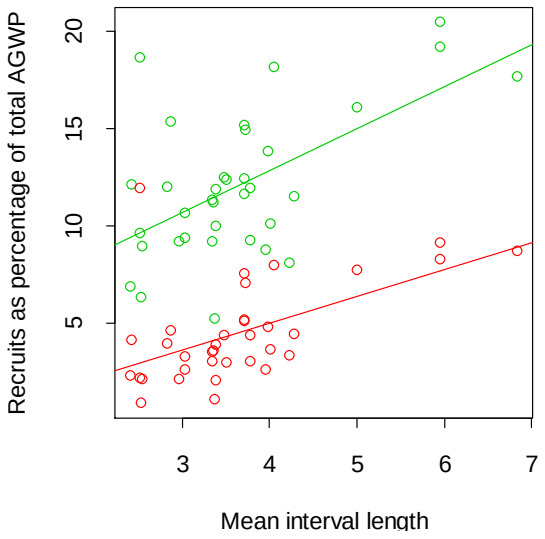


Figure 2.7: How the percentage of wood production represented by recruits changes with mean interval length. Each circle represents a plot, using R_1 (in green) and R_2 (in red), with regression lines.

2.5 Discussion

I have shown that the choice of methods for estimating AGWP can have an important impact on the values obtained, with mean AGWP from the baseline scenario and suggested scenario differing by 13.4%. This becomes especially important when estimating AGWP across long periods, since potential sources of bias tend to increase with time. Problems related to POM changes, census interval corrections and recruited stems are discussed in turn.

Changes in the point of measurement of stems are made in response to buttress growth, but pose a challenge for interpreting long-term tree measurement data. For census intervals with POM changes, use of directly measured diameters as in G_1 does not provide an appropriate measure of growth because it involves comparing diameters at different points along a tapering trunk (Niklas, 1995). Using a fixed POM across these intervals (i.e. same measurement height at the start and end of the census), as in G_2 and G_3, gives a more appropriate measure of growth. Of all the methodological variants tested, the greatest single impact on AGWP estimates was caused by incorrect use of G_1 instead of using a protocol to account for the impact of POM changes.

There are several potential methods of correcting for POM changes. In the G_2 protocol, D_{mean} is used for all census intervals, not just those involving POM changes. Diameter estimates at new POMs for the censuses prior to a POM change, and at old POMs for the censuses following a POM change, rely on the assumption of an unchanging old POM: new POM ratio. This may add

some uncertainty, since the degree of stem taper can change during ontogeny (Metcalf et al., 2009), but has the advantage of internal consistency in providing an estimate of tree diameter and growth at an unvarying location through time, and this internal consistency is potentially helpful for analysis of biomass dynamics. Fixing the POM at either D_{old} (G_4) or D_{new} (G_5) is conceptually similar to G_2, with these techniques being, respectively, slightly less or more conservative with regard to growth estimates. Adding instead the diameter increment at D_{new} to the original diameter at D_{old} (G_6, used by (Clark et al., 2013)) provides a further means to correct for POM changes that in effect fixes the POM height. The G_3 protocol has the advantage of maximising the use of actual diameter measurements taken in the field (i.e. for all censuses except those involving POM changes) which lends itself to among-site comparisons of stand-level AGWP.

While there are subtle differences between each of these approaches, all five of the POM-change analytical methods produce rather similar estimates of AGWP. All five contrast sharply to the use of directly measured diameters throughout, which clearly underestimates productivity. By contrast to my methods based on stem characteristics, a promising site-specific approach has been developed to deal with these challenges involving species-based Bayesian models to represent stem taper and diameter growth rates (Metcalf et al., 2009), but this is unlikely to be feasible when dealing with large numbers of rare tropical species across multiple sites, for which sufficient data to calibrate stem taper may not be available.

A second set of challenges with deriving AGWP estimates relates to their sensitivity to the length of measurement interval. Most trees that die will nevertheless still have grown since the last census before dying; similarly some trees will both recruit and die, unmeasured, within a single census interval (Sheil and May, 1996). The failure to observe the full growth of these stems affects mortality estimates as well as productivity estimates, and when calculating net fluxes it is necessary to follow equivalent procedures for the correction of mortality estimates to those used for the correction of productivity estimates.

My two different census-interval correction methods both produced results relatively close to the 0.67% median annual correction (with range 0.04 – 1.39%) derived by Malhi et al. (2004). Of the two methods, the individual-stem based method (CIC_2) has the potential to provide the most accurate corrections, reflecting real fluctuations in mortality rates and making the maximum use of the available data. This method works for a single interval and is not dependent on a large dataset to provide accurate parameter estimates.

Nevertheless, CIC_2 remains subject to uncertainties. Several authors have reported that stems grow at below-average rates in the years or months prior to mortality (Bigler and Bugmann, 2003; Chao et al., 2008; Vasconcelos et al., 2012; Wyckoff and Clark, 2002). Similarly, unobserved recruits that die may have lower than average taxon-level wood density, as this has been shown to be a predictor of mortality (Chao et al., 2008; Kraft et al., 2010). Both these factors may cause my assumed growth in CIC_2 to be too high, although I deal with this by using median growth estimates for the unobserved growth of known stems that die and of unobserved recruits, as explained above. However, there are also reasons suggesting that growth in CIC_2 is underestimated, due to the above-average diameter growth rates typical of high turnover, low wood density species. On balance, since CIC_2 on average gives slightly lower growth than CIC_1, assumed growth in CIC_2 appears if anything to be slightly conservative.

A third persistent challenge to estimating forest AGWP results from stems in inventory plots not being measured until they reach a certain diameter threshold, one of the most common being 100 mm. Moving to a lower threshold would not benefit the interpretation of existing long-running datasets, and even in inventory plots with 10 mm *D* thresholds (Chave et al., 2008) the problem remains conceptually equivalent, although the potential range of AGWP values associated with the treatment of recruits is naturally greatly reduced. Assuming growth from 0 mm (R_1) typically overestimates the actual growth of the stem in that interval, since it normally takes many years for a stem to reach a diameter of 100 mm. Backwards extrapolation of growth rates of recruited stems (R_3) produces plot-level AGWP very similar to estimates made assuming growth from 100 mm (R_2). Although R_3 provides the most accurate measure of the growth of an individual recruit across the relevant census interval, it is difficult to ensure comparability of biomass gain and loss using this method, due to the stem-specific minimum diameters used.

In comparison to the other methods, R_1 allows for an implicit partial inclusion of the growth of stems below the minimum diameter threshold. Nevertheless, it must be recognised that AGWP estimates made using R_1 fail to include the productivity of stems that die before reaching 100 mm *D* (Malhi et al., 2004). For this reason, the R_1 protocol is not equivalent to the use of a lower diameter threshold. Yet R_1 remains a closer approximation of true AGWP (no lower threshold) than the other methods that exclude all growth below the minimum diameter threshold.

Due to the considerations outlined above, the choice of method for correcting the problem of unobserved growth from recruited stems is in some senses more complex than for the other

two factors investigated. On balance, R_1 is preferred when the aim is to provide an approximation of total AGWP and to contribute to estimating stand-level fluxes and stocks. Method R_2 is suggested in two situations. Firstly, if productivity is being compared to other stand attributes or functions classified by size class, then method R_2 may enable equivalency in the samples used for each variable. Secondly, using R_2 can reduce bias caused by temporal fluctuations in recruitment rates. The accuracy of AGWP estimates made using R_1 depends on the length of time across which mean rates are calculated. If analysing variability in growth rates from one census interval to the next, AGWP may be unduly influenced by the number of stems which happen to pass the 100 mm threshold during a given interval. Therefore R_2 may be preferred for the analysis of short-term variability in AGWP.

2.6 Conclusion

The protocols described here provide a set of suggested methods for estimating AGWP that can minimise the influence of a number of known time-sensitive biases (relating to POM changes, unobserved growth within census intervals and the treatment of newly recruited stems), and which may be broadly applicable to long-term forest plot data. In western Amazonia these corrections increase estimates of AGWP by 13.4% compared to the baseline scenario in which these measurement problems are ignored. The largest bias observed was that associated with ignoring POM changes which results in large underestimates of AGWP; correction methods differ but tend to provide broadly similar results. Census interval corrections are also often necessary for more accurate AGWP estimation. The associated underestimation of AGWP increases with interval length, thus corrections are needed to compare data from plots with differing census interval lengths. Assumptions relating to recruits depend on the specific question being asked. Assuming recruits grew from 0 mm in the previous census interval likely provides a closer approximation of total AGWP than other methods, but other procedures may be more relevant to the specific questions addressed. Together, these suggested techniques should help to improve the quantification of aboveground coarse woody production and the comparability of future studies.

3 Estimating taxonomic richness and diversity using tropical forest inventory data

3.1 Abstract

As global centres of terrestrial biodiversity, tropical forests present a distinct challenge to attempts to quantify their richness and diversity. To permit analysis of tree diversity, appropriate methods must deal both with the incomplete taxonomic inventories that are commonly a result of high diversity, and with the requirement of appropriately representing the many-faceted concept of diversity itself. While traditional field identification and specimen collection techniques are vital components of any botanical survey, analytical methods must be developed to account for tropical trees that cannot be fully identified. Each individual tree can be placed in one of three categories: (1) those assignable to distinct morphospecies; (2) those that can be shown to belong to taxa that are unique within the plot; and (3) those that remain unidentified. Here I present methods for the inclusion of all these individuals in richness estimates. I also use a range of diversity metrics to represent richness and evenness across multiple taxonomic levels and to control for varying stem density. Using the resulting estimates of diversity, I compare tropical forests in Africa and South America, conducting all analyses at scales of 1-ha and 0.04-ha. In a census of 152 forest plots of 1-ha each, mean species richness per plot using the preferred approach for dealing with unidentified stems is 126.1; the minimum and maximum bounds of species richness are a mean 115.2 and 160.8 species per plot. The mean species richness per hectare of South American forests is double that of African forests, while mean alpha diversity (Fisher's α) is three times that of African forests. These differences remain when the higher stem density of South American forests is accounted for. Mean species richness per 0.04-ha subplot has much less scope for variation than per 1-ha plot, since the number of unidentified stems per subplot is very low. At both scales, the use of stem-based as well as area-based diversity measures can prevent conflation of observed diversity with stem density. Comparing species richness, exponential Shannon entropy and Simpson's Reciprocal Index of diversity, I find strong linear correlations between these measures within the selected plots, while species richness is exponentially related to genus and family richness at a 1-ha scale.

3.2 Introduction

3.2.1 The challenge of tropical diversity

Containing at least two-thirds of global terrestrial biodiversity (Gardner et al., 2009), tropical forests also represent unparalleled centres of botanical diversity, with up to 329 tree species recorded per hectare (Laurance et al., 2010). Tree diversity is not constant throughout the tropics. African forests are more species poor than their South American and Asian counterparts (Parmentier et al., 2007), and diversity gradients exist within each continent (Ter Steege et al., 2003), having various hypothesised drivers such as climate and geographical location with a domain (Colwell and Lees, 2000). But not all tropical forests have high tree diversity; forests can vary greatly at local scales, and monodominant forests are a frequent occurrence in Africa especially (Torti et al., 2001).

Tropical forests are typically characterised not just by their extremely high diversity, but also by the rarity and low population densities of most species. Across Amazonia, ter Steege et al. (2013) estimate that the rarest 11,000 tree species account for just 0.12% of individuals. Of the three factors responsible for rarity according to Rabinowitz (1981), most tropical forest tree species have widespread geographical distributions and little habitat specificity, but population densities are typically low (Pitman et al., 1999). At local scales, this means that while common species may form oligarchies (Pitman et al., 2001), rarity is the norm for most species. In central Amazonia, Laurance et al. (2010) found that on average, 56% of tree species in a group of 66 plots of 1-ha size were represented by a single individual. In these circumstances, the accurate identification of all of the trees in a forest plot will likely be extremely difficult.

Abundant ecosystem services are provided by tropical forests, including carbon sequestration (Pan et al., 2011); regional climate and hydrological regulation; potential new medicines and numerous directly-harvested forest products. These services could be threatened by biodiversity loss caused by habitat destruction (FAO and JRC, 2012), harvesting certain species, and climate change (Miles et al., 2004). Quantifying tropical diversity is vital to enable these threats to be properly assessed, to estimate potential extinction rates (Bradshaw et al., 2008) and the vulnerability of individual species and of the tropical forest biome itself (Huntingford et al., 2013).

3.2.1.1 The importance of accounting for every tree

The species diversity found within tropical forests presents great challenges to efforts to estimate the richness of the flora in these ecosystems. Specimen collection remains a

cornerstone of botanical inventories, yet tropical forest inventory plots normally contain a number of trees that cannot be fully identified. In addition, it is frequent for botanists working in tropical forests to be able to designate certain trees as conspecifics, without knowing the identity of the species in question. In order to obtain accurate richness estimates, these unidentified individuals should not simply be ignored, but this does happen (Parmentier et al., 2007). By accounting for the various categories of trees that are not fully identified, it is possible to better represent the total richness of the assemblage. This same principle applies to other high diversity systems such as coral reefs and (on a different order of magnitude) insect assemblages, as well as to tropical forest trees.

Obtaining a richness estimate that represents a complete census of every individual above a given diameter threshold within the sample area has important implications for the estimation of diversity. The choice of diversity indices is often made with regard to data sets that represent limited samples taken from unknown larger populations. The distinction between a census and a sample is a crucial one. Some diversity indices, including the Shannon Index (see section 3.2.2 below), have been criticised for depending on the assumption that all species present in the assemblage are represented in the sample. At small sample sizes or in diverse assemblages, where many species remain unrepresented within the sample, this can lead to bias in diversity index values. This bias does not exist in the case of a complete census, but for this to be the case, any unidentified stems must be properly accounting for prior to the estimation of diversity.

3.2.2 The representation of diversity

Biological diversity is a multifaceted concept that cannot be expressed by a single number. Considering solely the community level diversity (α-diversity) that exists within a particular locality, this represents a function of both the number of taxa (richness) and the comparative abundances of those taxa (evenness), and it can thus be characterised in many different ways. Therefore the choice of diversity index is an important issue that can complicate comparisons between studies. To enable greater insight the use of multiple indices, each of which emphasise different aspects of diversity, may be beneficial.

Three of the most commonly used indices of diversity are the Shannon Index, the Simpson Index, and Fisher's α. The Shannon Index is derived from information theory (Shannon, 1948). Properly known as Shannon entropy (Jost, 2006), it quantifies the uncertainty in predicting the species identity of an individual picked at random from the sample:

$$H' = -\sum_{i=1}^{R} p_i \, log \, p_i$$

where p_i is the proportion of stems belonging to species *i*. The simplest form of the Simpson Index (Simpson, 1949) is Simpson's concentration. This measures the inverse of diversity and can be represented biologically as the probability that two individuals, randomly drawn with replacement from an infinitely large community, belong to the same species (Magurran, 2004):

$$\lambda = \sum_{i=1}^{R} p_i^2$$

Both the Shannon and Simpson Indices make use of species abundance data. For the Simpson Index, the proportional species abundances are squared; this reflects species dominance. Thus the Simpson Index provides a representation of diversity that is more strongly influenced by evenness than by richness.

Fisher's α is a parametric index derived from the log series distribution (Fisher et al., 1943), which is widely used to explore the diversity of tropical forests (Parmentier et al., 2007; Ter Steege et al., 2003). According to the log series distribution, species abundances are represented by:

$$\alpha x, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3}, \ldots \ldots \frac{\alpha x^n}{n}$$

where each term represents the number of species that are predicted to have 1,2,3,.....*n* individuals within the sample. To calculate Fisher's α, only the sample size and species richness are required, which means it can be used widely where abundance data is not available. When *n* > 1000, α is independent of sample size (Magurran, 2004).

3.2.2.1 Comparing richness and evenness using 'effective number of species' indices

A frequently encountered problem with the representation of diversity is the difficulty in making comparisons between different indices. Indices follow many different forms, some taking values between 0 and 1, others values between 0 and infinity. The concept of 'effective number of species' (Macarthur, 1965) is recommended by Jost (2006) as a means to compare the values of multiple indices. If there are 20 species of equal abundance, any index of 'effective number of species' will give a value of 20. If species do not have equal abundance, the value given by different 'effective number of species' indices will diverge, but will all represent an equivalent diversity to a certain number of species of equal abundance. For example, a value of 20 obtained using a given diversity index could denote 20 species of equal

abundance, 25 species of marginally unequal abundance, or 50 species of highly unequal abundance. Modified forms of the well-known Shannon and Simpson indices can be used to represent effective number of species (Jost, 2006): these modified forms are exponential Shannon entropy (exp(*H'*)) and Simpson's Reciprocal Index of diversity ($1/\lambda$), and will henceforth be referred to simply as Shannon diversity and Simpson diversity. Species richness is another example of an effective number of species index.

The key differentiator among the different indices of 'effective number of species' is the relative weight they give to rare versus dominant species, as formalised by Hill (1973). Indices corresponding to Hill numbers ${}^0D$ (diversity of order 0), ${}^1D$ (diversity of order 1) and ${}^2D$ (diversity of order 2) are the most widely used, and range from giving greater emphasis to rare species, to giving greater emphasis to dominant species. These Hill numbers refer, respectively, to species richness (${}^0D$), Shannon diversity (${}^1D$), and Simpson diversity (${}^2D$).

With species richness (${}^0D$), each species contributes equally to the richness value, with no regard to the abundance of the species in question. Therefore, stems belonging to rare species are given relatively greater weighting than stems belonging to common species. With Shannon diversity (${}^1D$), the contribution of each species to the diversity index value is directly proportionate to its abundance. With Simpson diversity (${}^2D$), dominant species provide a greater contribution than rare species, in proportion to their abundance, to the diversity index value. The use of this framework thus allows direct comparisons to be made of the effects of rare versus dominant taxa.

3.2.2.2 Comparing diversity across different levels of taxonomic classification

If phenotypic change takes place at a roughly constant rate, then there will likely be a correlation between evolutionary divergence times and the total functional differences between species (Cadotte et al., 2009). This represents an important argument for interest in phylogenetic relatedness and diversity. The most accurate representations of these aspects of diversity involve the construction of phylogenies and usage of explicit measures of phylogenetic diversity. However, higher taxon diversity can also be used to incorporate a degree of phylogenetic information in diversity metrics. The precise relatedness of higher taxa can be highly variable, in terms of time since lineage splitting (Harper and Hawksworth, 1995). Nevertheless, the use of taxonomic classifications can provide results that are apparently robust (King, 2009; Petchey and Gaston, 2006). Identification of trees to genus and family level can also provide useful information in the case of individuals that cannot be identified to species level.

3.2.3 Spatial scale and sample size

Diversity estimates are strongly affected by both the area sampled and the number of individuals observed. Different processes may influence diversity at different spatial scales, which in tropical forests could range from the influence of individual trees (Wiegand et al., 2007) to effects related to the geographical area and historical persistence of entire biomes (Fine and Ree, 2006). When comparing diversity estimates that may be drawn from different numbers of individuals or from sample areas of differing size, consideration must always be taken of an appropriate form of standardisation to account for both of these factors. A further consideration is that sample size may govern the choice of diversity indices, since some indices become increasingly biased at low sample sizes, and thus the most appropriate index may vary with sample size and therefore by extension also with spatial scale.

Diversity does not scale linearly with area, but has been hypothesised most commonly to follow a power law (Arrhenius, 1921). This is typically modelled linearly in log-log space, suggesting that the number of taxa increases by the same proportion each time the area is doubled, although other functions such as logarithmic models and negative exponential models are also used (Tjorve, 2009). Other parameters such as climate, habitat diversity, or isolation, in addition to area, may also affect the number of taxa, and can be accounted for by the use of trivariate models. Relationships between area and the number of taxa can be represented using taxon area curves, the shape of which will be influenced by the abundances and spatial aggregation of taxa (Tjorve et al., 2008).

To avoid the problems associated with spatial scale when comparing diversity between different sites, a simple approach is to always use equivalent plot areas at each site. However, in natural ecosystems this does not guarantee equal sample sizes, because stem density varies naturally. Unequal sample sizes may cause bias in observed diversity estimates, since diversity will be constrained by the number of individuals present. This problem is relevant even when the ‘sample size’ actually represents the entire population of individuals present in a given area. Taxon sampling curves are often used to express the relationship between the number of individuals or samples and the number of taxa represented. Rarefaction curves are a form of taxon sampling curve produced by repeated re-sampling without replacement from the pool of *N* individuals or samples (Gotelli and Colwell, 2001). These provide a useful method to estimate the diversity at each site for any given number of individuals, up to the total *N* present at the site, and it is possible to use these stem-based diversity measures alongside measures of the diversity of a given area.

3.2.4 The present study

Here I use a set of tropical forest inventory plots from Africa and South America to present methods for richness and diversity estimation, intended to be capable of dealing with the reality of incompletely-identified, 'messy' taxon inventory data which characterise the large majority of tropical forest plots. All analyses are carried out at two scales: for entire 1-ha plots, and for 20 x 20 m, 0.04-ha subplots within those same plots. At each scale I use both area-based and stem-based measures of tree diversity, to control for stem density and taxon area relationships.

A range of techniques are developed for dealing with stems that are not fully identified, including the classification of distinct morphospecies, the identification of additional stems which can be shown to belong to taxa not otherwise represented within the plot, and further methods to deal with the remaining unidentified stems. Having thus accounted for all unidentified stems, I then use diversity indices that represent the Hill numbers ${}^{0}D$, ${}^{1}D$, and ${}^{2}D$ to provide directly comparable estimates of α-diversity appropriate for forest inventory plot censuses that span the richness–evenness spectrum, as well as Fisher's α, which can be used when abundance data is not available. Diversity is also compared across the taxonomic levels of species, genus and family. I present the resulting estimates of richness and diversity, exploring differences between African and South American forests, and investigating how the observed values vary according to the diversity index used, and the differences with taxonomic level from species to family.

3.3 Methods

3.3.1 Plot selection

Forest plot data were obtained from a single database hosted at www.forestplots.net (Lopez-Gonzalez et al., 2011). This is the most extensive available global dataset of tropical forest plots, containing over 1000 plots from four tropical continents, in which plot establishment and remeasurement has followed specified guidelines (Phillips et al., 2009b). Within this large set of potentially useable data, I applied further guidelines in order to maximise among-plot comparability.

The analysis was restricted to lowland South America and Africa, as these represent by far the largest blocks of lowland tropical forest extant on Earth. All selected plots belong to structurally undisturbed old-growth closed-canopy tropical forests, with all trees ≥100mm

diameter sampled and allocated to 20 x 20 m subplots. Furthermore, to maximise the between-plot comparability of the diversity indices measured at the whole plot scale, all selected plots are 1-ha in area. Likewise, to maximise comparability of the diversity indices measured at the subplot scale, all subplots are the same size and shape.

In order to explore the quantification of α-diversity, I aim to minimise the chances of including appreciable between-community diversity (β-diversity) in the diversity metrics being evaluated. For this reason plots known to contain two different soil types are excluded, and maximum allowable plot length is set at 500 m, because within-plot habitat heterogeneity is likely to increase with distance between the opposite ends of a plot, inflating diversity estimates (Condit et al., 1996). Forests with mean annual temperature <20°C and forests classed as montane are also excluded, as they differ in structure and function from lowland tropical forests.

Finally, to ensure confidence in the diversity estimates, I only used plots that had been visited by a professional botanist, and in which ≥60% of stems were fully identified to species level and ≥80% of stems were fully identified to genus level. In a small number of plots (see attached CD, Table A3.1) Arecaceae or other monocotyledonous taxa (*Phenakospermum sp.*) were not always measured fully in compliance with the given protocols; in these plots, I excluded the relevant taxonomic groups. In no cases did such excluded taxa comprise >30% of stems, and in most cases they were <10% of stems. In total 152 tropical forest inventory plots from Africa and South America were selected as meeting the *a priori* criteria. There are 61 plots from Africa and 91 from South America; eight of these African plots are from monodominant forests in Cameroon and the Democratic Republic of Congo.

3.3.2 Estimating Taxonomic Richness

Richness is estimated at three taxonomic levels: species, genus and family. Methods for estimating richness vary slightly with taxonomic level; species-level methods are shown in Figure 3.1 and methods for all taxonomic levels are explained below. All richness estimates are based on initial plot censuses, because some plots were visited by trained botanists during their first census only, so levels of taxonomic identification are sometimes slightly greater at the point when the plot was established. Identical methods are followed at scales of both 1-ha and 0.04-ha, and the richness estimates thus produced can be described as being area-based. Analyses are carried out using R version 3.0.2 (R Core Team, 2013).

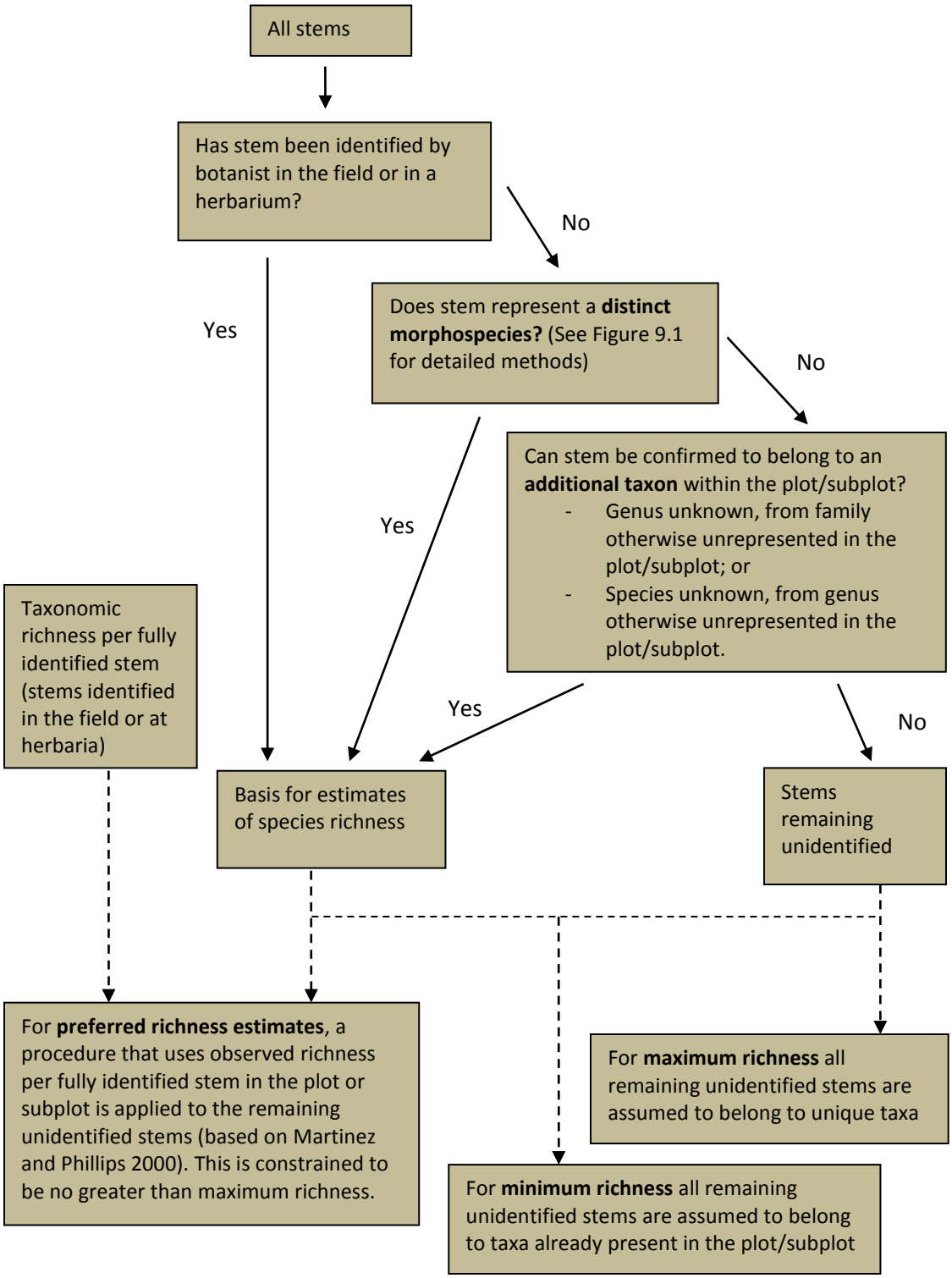


Figure 3.1: Methods for species richness estimation at the plot or subplot scale. Solid arrows show a decision tree of the processes taken for each individual stem. Dotted arrows show how these stem data are used in the calculation of the preferred richness estimates and the minimum and maximum richness bounds, at a plot or subplot scale.

3.3.2.1 Identifying trees

The majority of taxonomic identifications are based on direct field surveys of vegetative and/or reproductive features. Other trees are identified through the collection of voucher specimens and their analysis at herbaria. The proportion of trees from which vouchers have been collected varies from plot to plot. Voucher collection is important in allowing cross-referencing of identifications, to ensure consistency despite potential changes in preferred taxonomic names. In some plots, vouchers were only collected from a few unidentified stems, while in others the majority of trees were represented. In the ForestPlots.net database, orthography of all taxonomic names is standardised to avoid the incorporation of erroneous taxa or spelling mistakes. This standardisation follows the African Flowering Plant database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php) for African plots, and The Plant List (http://www.theplantlist.org/) for South American plots. At the family level, all identifications conform to the APG II list (APG II, 2003).

3.3.2.2 Morphospecies classification

A frequent feature of forest inventories in highly diverse tropical forests is that while stems cannot be fully identified to a scientifically accepted name, they are nevertheless believed to belong to a particular species, referred to as a "morphospecies." The decision tree used to classify trees to morphospecies is shown in Appendix A Figure 1, and the codes are shown in Appendix A Table 1. I distinguished morphospecies on the basis of the botanists' comments. When these comments denoted numbered morphospecies (E.g. *'sp.1' or 'Fabaceae_1'*), scientific names not accepted by the database (E.g. *'tomentosa (not accepted in database),'*), or affinity to scientific names that were not already represented in the plot (E.g. *'cuspidata aff.'*), the associated stems were assumed to correspond to unique morphospecies, according to the core morphospecies definition used in the majority of analyses.

In other cases, comments had been noted that could potentially represent morphospecies, but where the veracity of these morphospecies was less certain. This includes comments denoting unique vernacular names, botanists' field codes, stems compared (*cf.*) to scientific names, or where voucher numbers from collected specimens were associated with a stem. There is a risk here that vernacular names may in some cases be applied to more than one species, and even to species that are not closely related. In addition, a single species can have multiple vernacular names. To prevent spurious errors in morphospecies identification, in the core approach I did not assume that these uncertainly-identified stems belonged to distinct morphospecies.

However, in order to further investigate likely diversity values, I developed an extended morphospecies definition and conducted additional analyses detailing the effects of assuming morphospecies status for stems with comments including unique vernacular names, botanists' field codes, stems compared (*cf.*) to scientific names, and voucher collection. This extended approach enables diversity to be estimated using a fuller representation of potential species concepts, but the core approach is used in all of the main analyses because it makes use only of morphospecies definitions which have little potential for ambiguity, thus there is less chance of accidentally including incorrect taxa. As well as being more reliable, the core approach is also more repeatable, not being affected by potentially inconsistent vernacular names, which may be applied more frequently in some plots than in others.

3.3.2.3 Taxa known to be unique within the plot

In addition to stems belonging to fully identified taxa and to morphospecies, the species and genus richness estimates include contributions from stems that have not been fully identified (i.e. they are identified only to family or genus level), but are nevertheless shown to belong to taxa that are unique within the plot. These are included for the purposes of the present study, since this is concerned with taxonomic richness and diversity, rather than species identity and functional characteristics of individual species. However, for each of these partially identified taxa, only one stem per taxa can be positively identified as adding to the plot richness. Any additional stems remain unidentified, since it is not known whether they belong to the same or different species/genera.

At the species level, total species richness is based on the sum of (i) uniquely identified species, (ii) stems identifiably assigned to a distinct morphospecies, using botanists' comments, (iii) stems identified only to the genus level and assigned to a genus not otherwise represented within the plot, and (iv) stems identified only to the family level and assigned to a family not otherwise represented within the plot. At the genus level, generic richness is based on the count of uniquely identified genera, plus stems identified only to the family level and assigned to a family not otherwise represented in the plot. At the family level, the richness estimates were based on a simple count of the number of uniquely identified families in the plot conforming to the AGPII list.

3.3.2.4 Absolute minimum, maximum and 'preferred' richness estimates

After following the steps described above, a procedure was required for dealing with the stems that remained unidentified. The presence of these stems means the exact taxonomic

richness often cannot be known. Instead, minimum and maximum possible richness values were calculated, as well as an intermediate estimate of richness which is the estimate used in the 'preferred' approach (Table 3.1). The minimum and maximum richness values constrain the range of possible error, thus they can be used to reveal the robustness of results obtained using the values of the preferred richness estimate.

For minimum richness, the most extreme case is assumed: that all remaining unidentified stems belong to taxa already represented within the plot/subplot. To calculate maximum richness, the opposite extreme case is assumed: that each of the remaining unidentified stems belongs to a unique taxon (Table 3.1). For generic and family maximum richness under this approach, all of the stems belonging to each distinct morphospecies were treated as a single unidentified species, since each morphospecies is assumed to represent a species.

The calculated minimum richness almost certainly underestimates the true diversity of a plot, while the calculated maximum possible richness clearly overestimates the true diversity in most cases. The preferred estimate of richness was derived using a procedure based on the method of Martinez and Phillips (2000). Thus, taxonomic richness per identified stem was calculated in each plot or subplot, including only stems that were fully identified at a given taxonomic level. Remaining unidentified stems could then be assigned to additional discrete taxa using a procedure based on this ratio of richness per stem (Table 3.1).

Even for stems unidentified at the species level, there is normally some taxonomic information available at the family or genus level. Thus, for the preferred richness estimates, the remaining unidentified stems within each plot or subplot were organised by available taxonomic information. The stems in each of these groups were then assigned to one or more additional taxa, by multiplying the number of stems in the group by the taxonomic richness per identified stem in the plot or subplot, unless this product could be rounded to zero, in which case the stems were assumed to belong to an existing taxon. Where the stems within a group were assigned to more than one additional taxon, these taxa were assumed to have equal abundances. The preferred estimates are expected to provide the closest approximation of area-based richness values, and I use these in the majority of analyses.

Table 3.1: The calculation of each of the area-based richness estimates at the species, genus and family levels. This includes the minimum and maximum bounds of potential richness and a set of preferred richness estimates.

Taxonomic level	*Minimum richness estimates*	*Maximum richness estimates*	*Preferred richness estimates (used for ^0D)*
Species	$Min_s = I_s + M_s + a + b$	$Max_s = I_s + M_s + a + b + U_s$	$Best_s = I_s + M_s + a + b + \Sigma([U_{st}*P_s])$
Genus	$Min_g = I_g + a$	$Max_g = I_g + a + U_g$	$Best_g = I_g + a + \Sigma([U_{gt}*P_g])$
Family	$Min_f = I_f$	$Max_f = I_f + U_f$	$Best_f = I_f + [U_f*P_f]$

Where: I_s = richness of stems identified to species level; I_g = richness of stems identified to genus level; I_f = richness of stems identified to family level; M_s = morphospecies richness; a = richness of stems unidentified at genus level that are the unique representatives of a particular family in the plot concerned; b = richness of stems unidentified at species level that are the unique representatives of a particular genus in the plot concerned; U_s = stems remaining unidentified at species level (belonging to none of the previous categories); U_g = stems remaining unidentified at genus level (belonging to none of the previous categories); U_f = stems remaining unidentified at family level (belonging to none of the previous categories); U_{st} = stems remaining unidentified at species level and having particular information available at higher taxonomic ranks; U_{gt} = stems remaining unidentified at genus level and having particular information available at higher taxonomic ranks; P_s = number of species per identified stem; P_g = number of genera per identified stem; P_f = number of families per identified stem; [ ] denotes rounding to the nearest integer.

3.3.3 Stem-based diversity measures

As a means of dealing with differences in stem numbers per plot, estimates of the richness of species, genera and families in each plot were made using individual-based rarefaction at both the plot (1 ha) and subplot (0.04-ha) scales. This provides stem-based measures of diversity, in addition to the area-based measures described in the previous section. At the plot scale I calculated richness per 300 stems, a figure chosen to allow rarefied richness to be calculated for all but two plots (see attached CD, Table A3.1), while remaining sufficiently large to minimise error. At the subplot scale richness per ten stems was calculated, requiring the exclusion of 126 of the 3800 subplots.

3.3.4 Use of diversity indices

A range of indices were used to represent different aspects of diversity, each being calculated at the scales of both 1-ha (plot) and 0.04-ha (subplot). Using species, genus and family abundance data, I chose indices to represent the three most commonly used Hill numbers (Hill, 1973), allowing direct comparisons of the effects of rare versus dominant taxa. Richness (representing ^0D) gives greater proportional weight to stems from rare taxa, Shannon diversity ($\exp(H')$, representing ^1D) allows all stems to contribute equally to the diversity metric, and Simpson diversity ($1/\lambda$, representing ^2D) gives greater proportional weight to stems from abundant taxa (see equations in section 3.2.2). I calculated each of these measures at each of

the three taxonomic levels. Relationships between species level ^{0}D, ^{1}D and ^{2}D, and between species, genus and family richness, are investigated at both the plot and subplot scales, to find which function, if any, best approximates these relationships.

I also calculated Fisher's α (see equation in section 3.2.2), a widely used measure in tropical forests. Fisher's α does not require abundance data, which enables its use with the stem-based rarefaction data. Fisher's α is calculated at the plot scale using both the area-based and the stem-based species richness values, and at the subplot scale using the area-based species richness values. Its distribution is explored to determine whether or not it is an appropriate measure of diversity at these scales.

3.4 Results

For a set of South American and African lowland tropical forest plots, I find mean species richness of 126.1 tree species per hectare, with means of 79.5 genera per ha and 34.4 families per ha (Table 3.2). Within the same forests, estimated mean richness per 0.04-ha is 14.6 species, 12.9 genera and 9.9 families. Mean diversity values as 'effective number of species' decrease from ^{0}D to ^{1}D to ^{2}D, (i.e. from richness towards evenness), as would be expected, with species level ^{1}D (Shannon diversity) of 69.6 per ha and ^{2}D (Simpson diversity) of 40.1 per ha.

Table 3.2: Mean values of a set of tree richness and diversity indices across a large range of lowland tropical forest plots. The core morphospecies approach is always used. All indices are calculated using the preferred richness estimates. Stem-based techniques show diversity values per 300 stems at the plot scale and per 10 stems at the subplot scale. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

		Mean ^{0}D (area-based richness)	*Mean ^{1}D (area-based*	*Mean ^{2}D (area-based)*	*Mean Fisher's α (area-based)*	*Mean richness (stem-based)*	*Mean Fisher's α (stem-based)*
1 ha (plot) scale	Species	126.1	69.6	40.1	64.1	94.5	60.7
	Genus	79.5	36.8	21.0	-	65.0	-
	Family	34.4	15.7	10.4	-	30.7	-
0.04-ha (subplot) scale	Species	14.6	13.1	11.7	44.2	8.1	-
	Genus	12.9	11.2	9.6	-	7.6	-
	Family	9.9	8.1	6.8	-	6.5	-

3.4.1 Estimation of richness

Accounting for trees that are unidentified at a given taxonomic level reduces uncertainty in richness estimates, especially at the species level. Using field and herbaria identifications, of

the average 508.9 stems per plot, a mean 87% of trees are identified to species level – this of course does not differ between the plot and subplot scales (Table 3.3). Richness estimates based solely on these data would be biased downwards – at the subplot scale mean species richness (at 12.2) would actually be recorded as lower than genus richness (at 12.6), simply because fewer trees are identified to species level than to genus level. This clearly shows the importance of accounting for unidentified individuals.

Once morphospecies and trees known to belong to additional taxa have been accounted for, a mean 93% of trees at the plot level and 97% of trees at the subplot level can placed in species concepts (Table 3.3). There is still uncertainty in richness estimates due to stems that remain unidentified. The minimum and maximum richness estimates provide the upper and lower bounds of this uncertainty, which varies greatly with the scale of analysis and with taxonomic level. At the 1-ha scale, the difference between the minimum (Min_s) and maximum (Max_s) mean species richness values is 28.4%.

At the 0.04-ha scale the difference between Min_s and Max_s is only 6.1%. The low level of uncertainty at the subplot scale is to be expected since within a 0.04-ha subplot there are very few unidentified stems, so the effect of these stems on estimated richness is necessarily minimal. Genus and family richness are more tightly constrained than species richness, especially at the plot scale. At this scale, mean maximum genus richness (Max_g) is 11.7% greater than mean minimum genus richness (Min_g), and mean maximum family richness (Max_f) is 14.4% greater than mean minimum family richness (Min_f).

Table 3.3: The effects of accounting for unidentified stems on richness estimation. Mean richness computed using only trees that have been fully identified at the appropriate taxonomic level in the field or at herbaria, compared to richness measures that take into account trees identified to a taxon concept such as a morphospecies, and that deal variously with the remaining unidentified stems. Richness values are calculated using three different methodologies to obtain the minimum and maximum possible richness and a preferred estimate of the likely richness.

		1 ha (plot) scale			*0.04-ha (subplot) scale*		
		Species	Genus	Family	Species	Genus	Family
Mean proportion of fully identified trees		0.87	0.98	0.99	0.87	0.98	0.99
Mean richness per fully identified tree		0.23	0.16	0.07	0.7	0.64	0.5
Mean richness using fully identified trees only		102	77.6	34	12.2	12.6	9.8
Mean proportion of trees identified to a taxon concept		0.93	0.98	0.99	0.97	0.98	0.99
Mean area-based richness (^{0}D)	Min	115.2	77.7	34	13.9	12.7	9.8
	Preferred	126.1	79.5	34.4	14.6	12.9	9.9
	Max	160.8	88	39.7	14.8	13	10
Mean absolute uncertainty in richness estimate		45.6	10.3	5.7	0.9	0.3	0.2

The proportion of stems not fully identified (i.e. not identified in the field or at herbaria) to species level (N_s) is linearly related to the uncertainty in species richness (U_s), measured as the difference between Min_s and Max_s (Figure 3.2). At the plot scale, U_s = 368.3 N_s (constrained to pass through the origin), so an uncertainty in species richness of 20 species is predicted when 94.6% of stems are fully identified to species. This is a strong relationship with an R^2 of 0.81. Uncertainty in species richness is also linearly related to the proportion of stems not fully identified to genus and family levels (R^2 = 0.48 for stems not identified to genus, 0.28 for stems not identified to family). Thus, an uncertainty in species richness of 20 species is predicted when 98.6% of stems are fully identified to genus, or when 98.7% of stems are fully identified to family. Strong linear relations also exist between the numbers of stems not fully identified to various taxonomic levels and the uncertainty in species richness values (Figure 3.3). Thus an uncertainty in species richness of 20 species is predicted when 27 stems are not fully identified to species (R^2 = 0.90), or when 7 stems are not fully identified to genus (R^2 = 0.55), or when 5 stems are not fully identified to family (R^2 = 0.34).

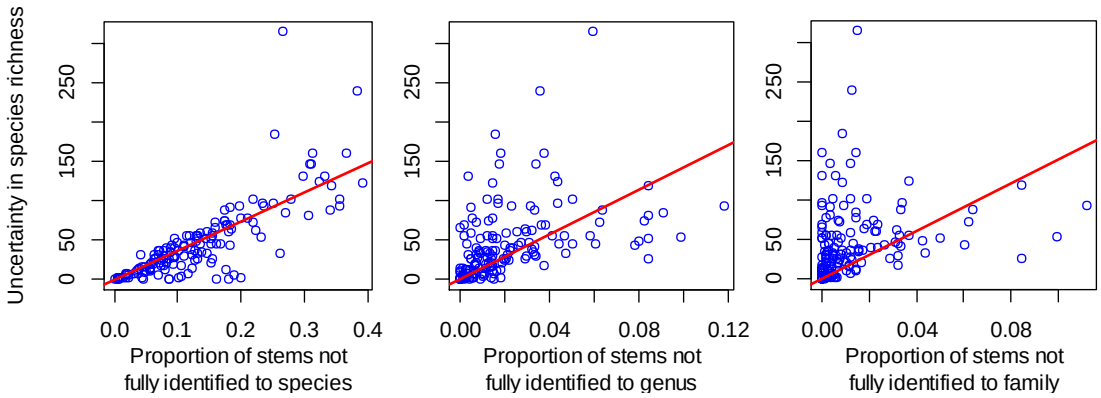


Figure 3.2: Relating uncertainty in species richness estimates (in terms of the potential number of species present) to the proportion of stems that are not identified in the field or at herbaria, for various taxonomic levels. Linear regressions (in red) are constrained to pass through the origin.

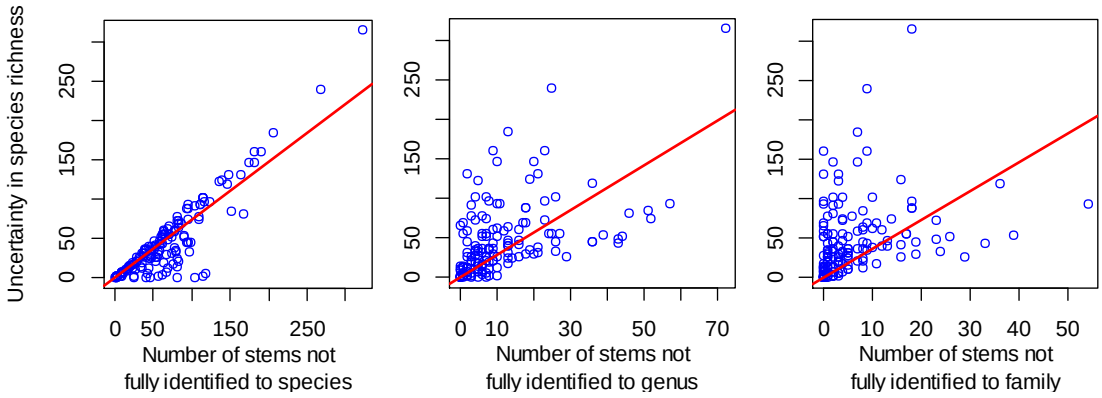


Figure 3.3: Relating uncertainty in species richness estimates (in terms of the potential number of species present) to the number of stems that are not identified in the field or at herbaria, for various taxonomic levels. Linear regressions (in red) are constrained to pass through the origin.

3.4.1.1 The effects of using the extended morphospecies definition

Using the extended morphospecies definition (Table 3.4), diversity estimates do not vary greatly from those produced using the core morphospecies definition (Table 3.2). The greatest differences are for species at the 1-ha scale, where mean Max_s is 4.7% lower and mean Min_s is 3.8% higher. Thus, the extended morphospecies approach enables reduced uncertainty in species richness values, but the preferred estimate of species richness at the 1-ha scale (127.4 species ha^{-1}) according to the extended morphospecies approach remains within 1% of the equivalent estimate using the core morphospecies definition. At a 0.04-ha scale, richness estimates using the core and extended morphospecies definitions are virtually identical.

Table 3.4: Mean values of a set of tree richness and diversity indices across a large range of lowland tropical forest plots, using an extended morphospecies definition. Richness values are calculated using three different methodologies to obtain the minimum and maximum possible richness and a preferred estimate of the likely richness. The other diversity indices are calculated using the preferred richness estimates. Stem-based techniques show diversity values per 300 stems at the plot scale and per 10 stems at the subplot scale. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

		1 ha (plot) scale			*0.04-ha (subplot) scale*		
		Species	Genus	Family	Species	Genus	Family
Mean area-based richness (^{0}D)	Min	119.6	77.7	34	14	12.7	9.8
	Preferred	127.4	79.5	34.4	14.6	12.9	9.9
	Max	153.3	87.1	39	14.7	13	10
Mean ^{1}D (area-based		69.8	36.8	15.7	13.1	11.1	8.1
Mean ^{2}D (area-based)		39.8	21	10.4	11.7	9.6	6.8
Mean Fisher's α (area-based)		65.3	-	-	44.1	-	-
Mean richness (stem-based)		95.5	65	30.7	8.1	7.6	6.5
Mean Fisher's α (stem-based)		61.9	-	-	-	-	-

3.4.1.2 The appropriateness of Fisher's α

At a 1-ha scale, Fisher's α provides a useful measure of diversity, with a distribution only slightly more skewed than that of species richness (Figure 3.4). However, Fisher's α does not provide a sensible estimate of diversity when sample size is small and diversity is high. This is the case at a 0.04-ha scale, where Fisher's α rises exponentially when species richness approaches stem density.

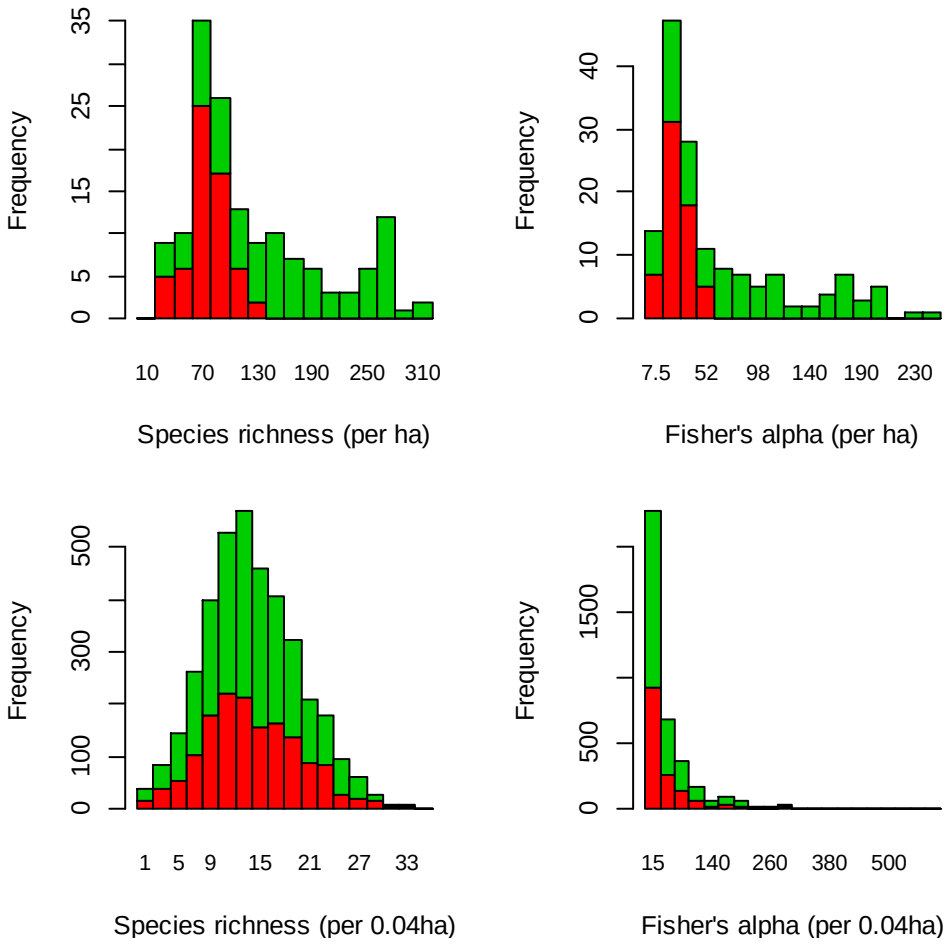


Figure 3.4: Distributions of species richness and Fisher's α at 1-ha and 0.04-ha scales. Red bars signify African forests, green South American. Fisher's α per 0.04-ha rises exponentially when species richness approaches stem density.

3.4.2 Comparisons between diversity metrics

3.4.2.1 The effects of spatial scale

Proportional differences between diversity measures are much greater at the 1-ha scale than at the 0.04-ha scale. For example, within a 0.04-ha subplot, mean family richness is 67.8% of mean species richness, while within a 1-ha plot mean family richness is just 27.3% of mean species richness. Proportional differences across the spectrum of richness and evenness follow similar patterns. Per hectare, mean species level Simpson diversity (^2D) is 31.8% of mean species richness (^0D), but per 0.04-ha mean species level ^2D is 80.1% of mean ^0D (Table 3.2). Stem density appears to exert a strong control on all forms of richness and diversity at the 0.04-ha scale, with this constraint reducing the differences between these diversity measures. This can be observed by regarding the stem-based richness estimates, which have rather large means of 8.1 species and 6.5 families per 10 stems.

3.4.2.2 Diversity metrics at the plot level

There is a strong correlation (Spearman's r = 0.99) between the minimum (Min_s) and preferred ($Best_s$) species richness estimates at the plot level (Figure 3.5). The correlations of Max_s with Min_s (r = 0.84) and $Best_s$ (r = 0.88) are less strong, with some extreme outliers due to plots having exceptionally high stem density. These include plot ALP-40 which has 1207 stems, of which 892 can be identified to species level (including stems classified as morphospecies or additional taxa), giving Min_s of 35, $Best_s$ of 45, and Max_s of 350, and BNT-02, which has 697 stems of which 457 are identified to species level, with Min_s of 127, $Best_s$ of 182, and Max_s of 367.

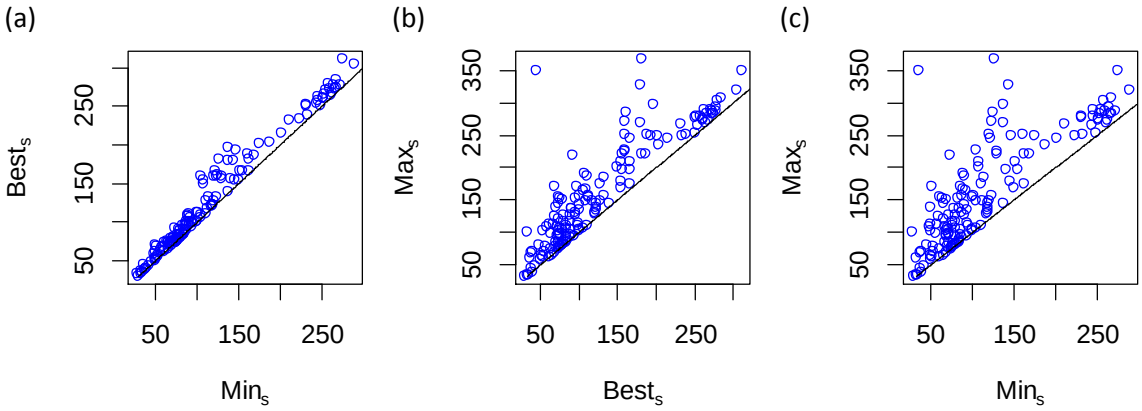


Figure 3.5: Comparing species richness estimates at the plot level. The line y=x is shown in black. (a) Comparing minimum and preferred richness estimates, (b) comparing preferred and maximum richness estimates (c) comparing minimum and maximum richness estimates.

Diversity metrics based on preferred richness estimates all show strong relations at the plot level (Figure 3.6). Area-based species richness (^{0}D) is linearly related to ^{1}D (r = 0.96) and ^{2}D (r = 0.90). Exponential functions relate species richness to genus (r = 0.97) and family (r = 0.90) richness. In all of these relationships, variance increases at higher levels of diversity as these measures begin to diverge.

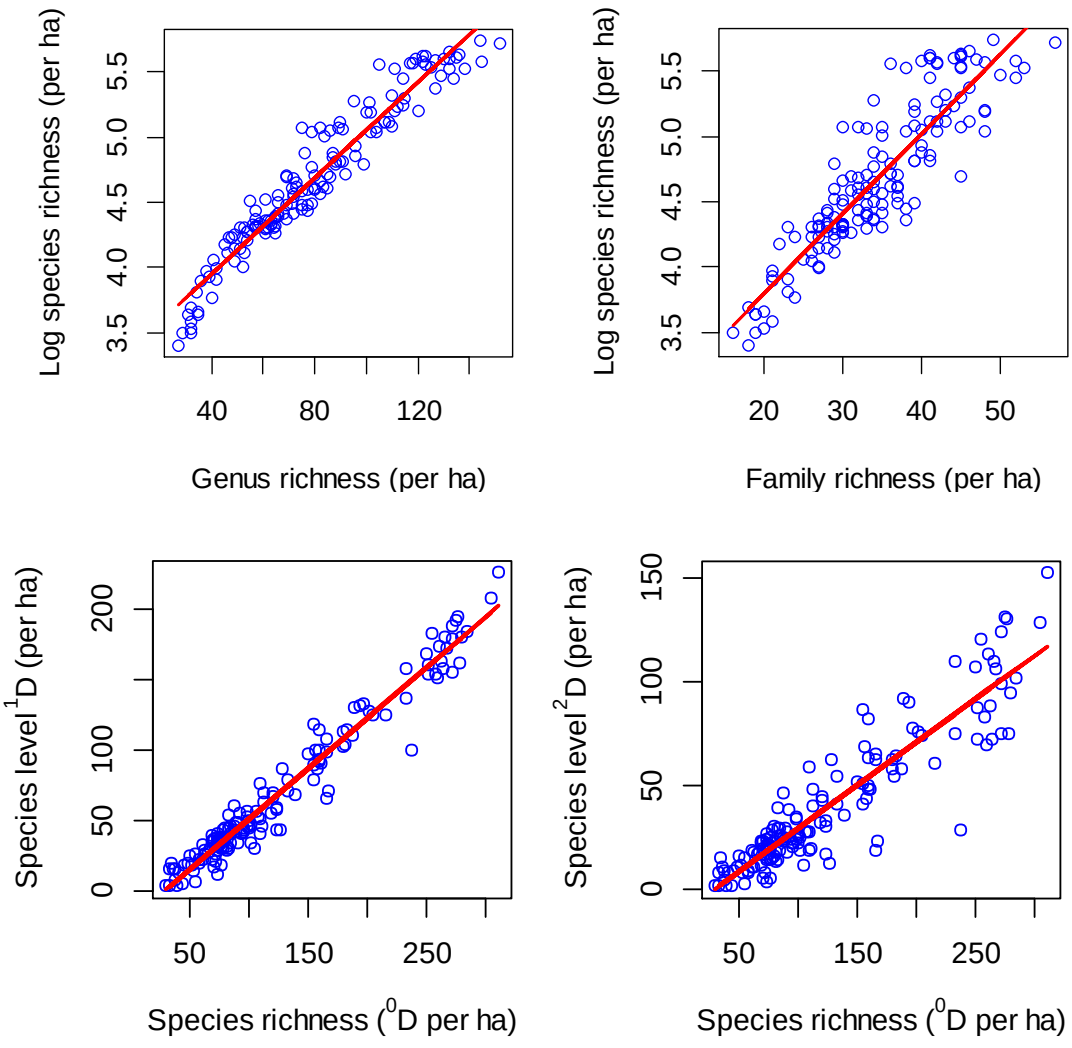


Figure 3.6: Comparisons of diversity estimates at the plot level. Red lines show significant relationships. These relationships are exponential for species richness as a function of genus and family richness, and linear for ^{1}D and ^{2}D as a function of species richness.

The use of preferred richness estimates may inflate evenness slightly, since when multiple additional taxa are assigned to a group of unidentified stems with particular available taxonomic information, these additional taxa are assumed to have equal abundance. However, the mean ratio of ^{2}D: ^{0}D using the preferred species richness estimates is 0.29 ± 0.11, which is almost identical to the mean ^{2}D: ^{0}D ratio using fully identified stems only, of 0.29 ± 0.13.

3.4.2.3 Diversity metrics at the subplot level

At the subplot level, again Min_s and $Best_s$ are strongly correlated (r = 0.99) (Figure 3.7). At this scale, there is very little difference between $Best_s$ and Max_s, because there are very few unidentified stems per subplot, and most of these are assumed to belong to new species when estimating $Best_s$. The correlation between Min_s and Max_s is also stronger (r = 0.97) than at the plot level. The one outlier is again plot ALP-40, where there are large numbers of unidentified stems even at the subplot level.

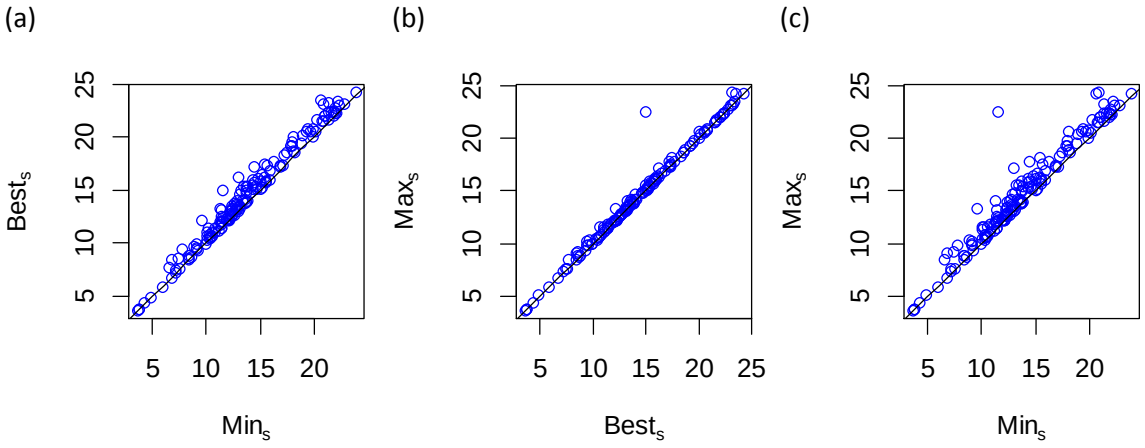


Figure 3.7: Comparing species richness estimates at the subplot level. Each point shows the mean value for all subplots within a single plot. The line y=x is shown in black. (a) Comparing minimum and preferred richness estimates, (b) comparing preferred and maximum richness estimates (c) comparing minimum and maximum richness estimates.

At the subplot level, species richness (using the preferred estimate) is linearly related to genus (r = 0.97) and family (r = 0.92) richness, and also to species-level ^1D (r = 0.98) and ^2D (r = 0.96) diversity (Figure 3.8). The correlations between these measures are even stronger than the equivalent correlations at the plot level.

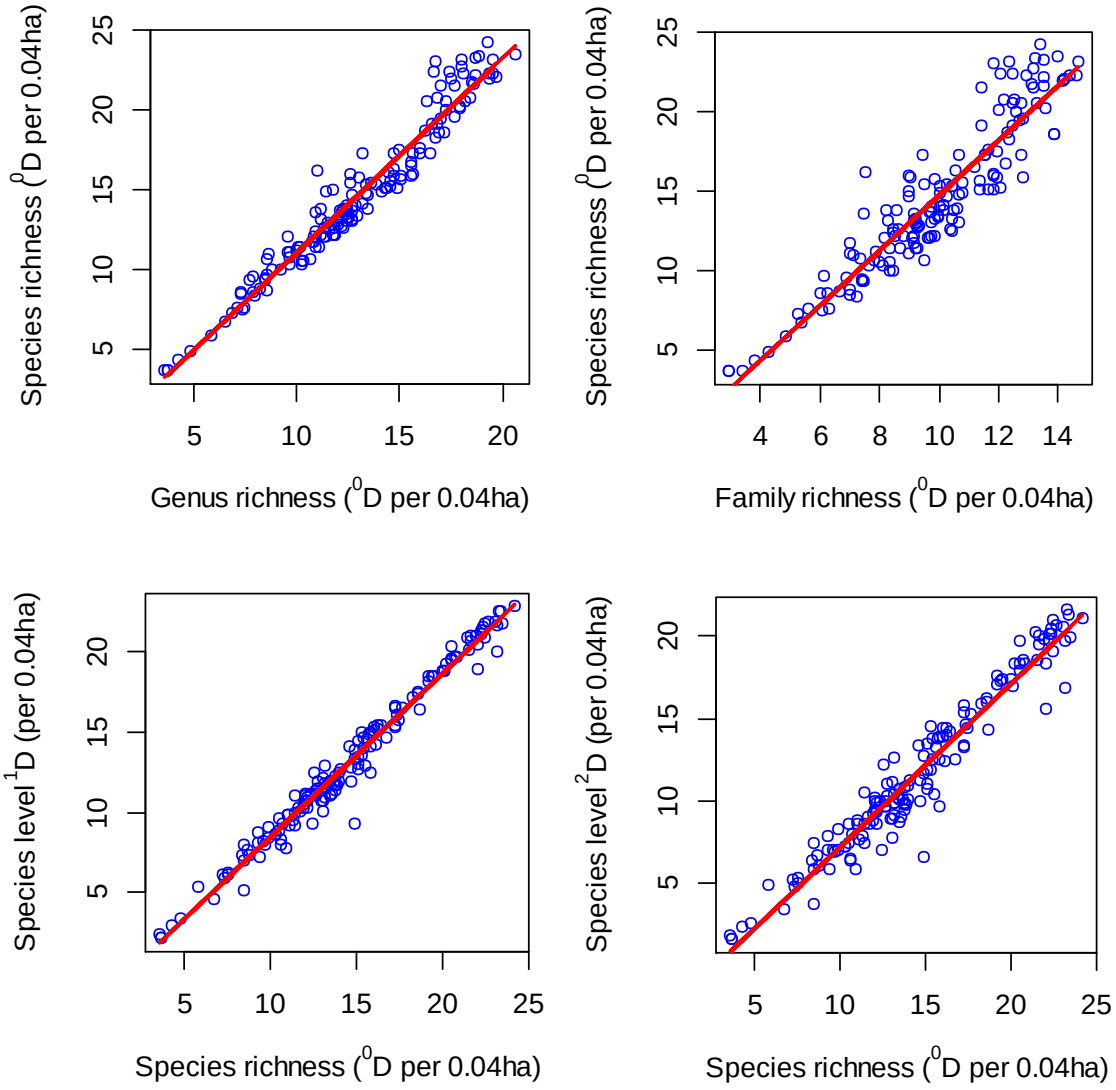


Figure 3.8: Comparisons of diversity estimates at the subplot level. Each point shows the mean value for all subplots within a single plot. Red lines show significant relationships, all of which are linear.

3.4.3 Tree diversity of African and South American tropical forests

At a 1-ha scale, diversity is considerably greater in South America than in Africa. This pattern holds across all diversity metrics, including both area-based (Figure 3.9) and stem-based (Figure 3.10) measures. Many diversity metrics also have greater variance in South America than in Africa, especially Fisher's α and the species level metrics. Mean species richness per hectare in South America, at 158.2 ± 77.9, is double the mean 78.2 ± 22.1 species per ha in Africa. Mean Fisher's α is 87.9 ± 63.9 in South America, which is triple the mean Fisher's α of 28.6 ± 10.9 in Africa. Showing less difference between the continents, mean family richness is 37.5 ± 8.7 in South America and 29.7 ± 5.0 in Africa.

Diversity measures at the family level have low means and low variance in both Africa and South America. For example, family level ^{2}D is 9.0 ± 4.2 in Africa and 11.4 ± 3.6 in South America. The standard deviation of these measures is around one-third to one-half of the magnitude of the mean. At the species level, ^{2}D has a mean of 22.2 ± 13.5 in Africa and 52.1 ± 37.0 in South America, showing greater variance in proportion to the mean.

Excluding monodominant forests, mean species richness per hectare in Africa rises to 82.0 ± 19.9 and mean Fisher's α per hectare rises to 30.2 ± 10.3. This shows that significant differences in diversity between these continents exist even within mixed forests. Stem density is also higher in South America (558.3 ± 120.8) than in Africa (435.2 ± 81.4), but species richness per 300 stems in Africa (67.1 ± 16.7) is still only 60% (or 63% excluding monodominant forests) of that in South America (112.3 ± 47.0).

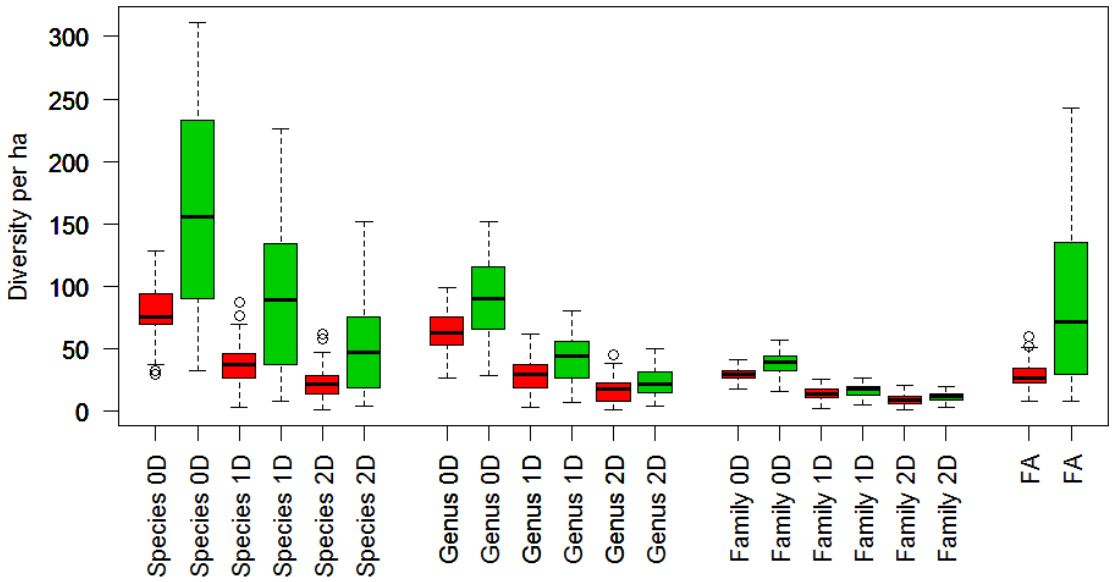


Figure 3.9: Mean values per ha for various measures of diversity. Red boxes represent African forest plots; green boxes represent South American plots. FA represents Fisher's α; ^{0}D, ^{1}D and ^{2}D represent richness, Shannon and Simpson diversity respectively.

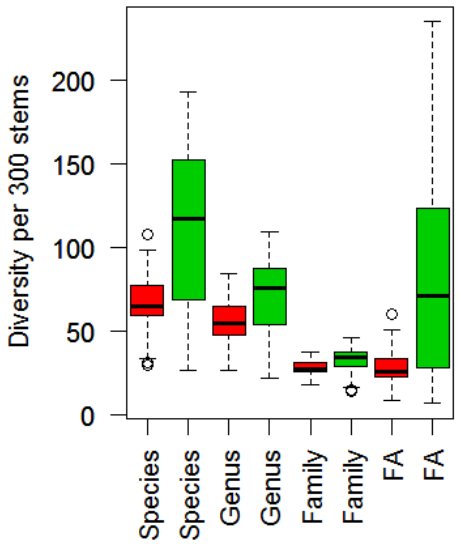


Figure 3.10: Mean values per 300 stems for richness at three taxonomic levels and Fisher's α (FA). Red boxes represent African forest plots; green boxes represent South American plots.

At the subplot level, again diversity is greater in South American than in African forests (Figure 3.11 and Figure 3.12), although the two continents show less difference in their diversity at this scale than at the 1-ha scale. African species richness (11.6 ± 4.5) is 70% of South American species richness (16.6 ± 5.7), and excluding monodominant forests makes this 75%. Stem density per 0.04-ha is higher in South America (22.3 ± 5.2) than in Africa (17.4 ± 6.7). When this is accounted for by using species richness per 10 stems, richness in African forests (7.5 ± 1.9) is 89% (or 94% excluding monodominant plots) of that in South American forests (8.5 ± 1.3). The variances of diversity measures are similar in both continents at this scale.

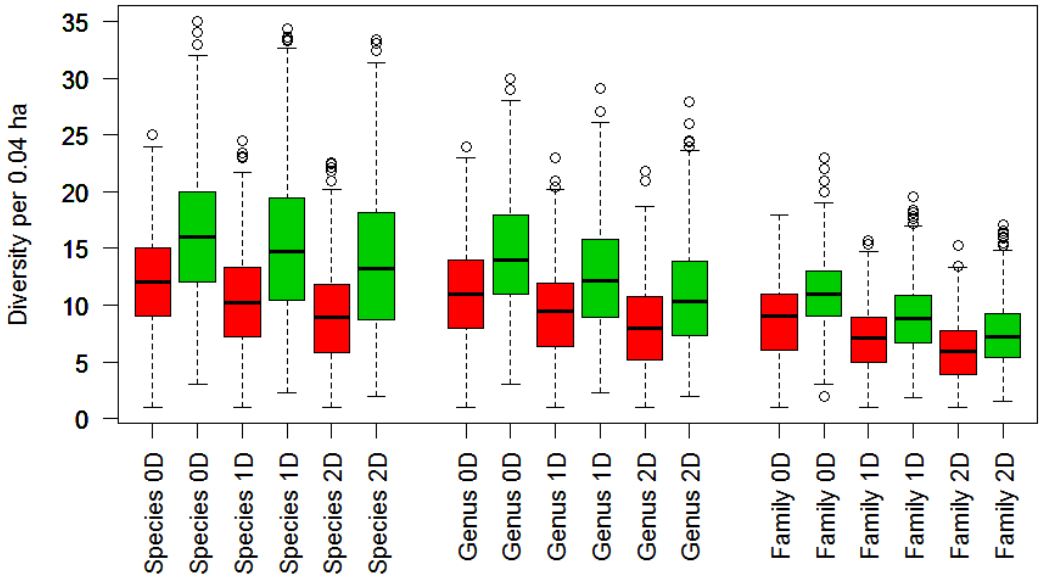


Figure 3.11: Mean values per 0.04-ha for various measures of diversity. Red boxes represent African forest plots; green boxes represent South American plots. ^{0}D, ^{1}D and ^{2}D represent richness, Shannon and Simpson diversity respectively.

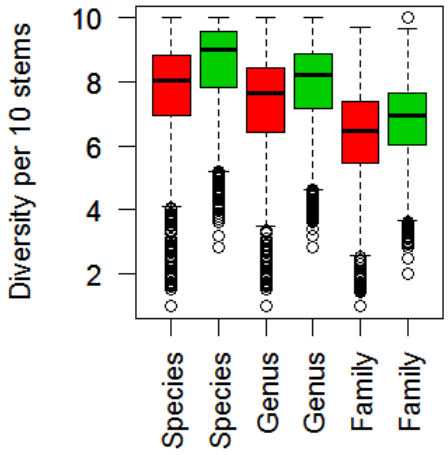


Figure 3.12: Mean values per 10 stems for richness at three taxonomic levels. Red boxes represent African forest plots; green boxes represent South American plots.

3.5 Discussion

By developing techniques to fully account for all of the trees within a given area, reliable estimates of richness and diversity can be produced. Using these diversity estimates to compare tropical forests in Africa and South America, I find major differences between the forests of these two continents. The magnitude of these differences depends on the aspect of diversity and the spatial scale being considered. Differences between African and South

American forests are greater at a scale of 1-ha than at a scale of 0.04-ha. Mean species richness per hectare of African forests (78.2 ± 22.1) is just 50% of that of South American forests (158.2 ± 77.9), while mean species richness per 0.04-ha in Africa is 70% of that in South American forests.

3.5.1 Producing reliable richness estimates

The methods described above for the estimation of taxonomic richness in forest plots allow richness and diversity estimates to be made that account for all trees ≥100 mm diameter, even in plots that contain a small proportion of trees that cannot be fully identified. Where unidentified trees remain after accounting for stems belonging to morphospecies or to other additional taxa, this technique establishes the minimum and maximum bounds for richness values, and provides a preferred estimate of richness, based on the technique of Martinez and Phillips (2000), that accounts for these unidentified stems. Techniques such as these, which account for unidentified trees, are not always used in the analysis of tropical forest diversity (Parmentier et al., 2007).

Uncertainty in richness estimates is related to the proportion of fully identified trees. To limit mean uncertainty in species richness per hectare to 20 species, 95% of trees should be identified to species level in the field or at herbaria, alongside sufficient identification to genus and family level and sufficient assignment to morphospecies. In terms of the absolute number of stems that are identified in the field or at herbaria, uncertainty in species richness per hectare is limited on average to 20 species when 27 trees have not been identified to species level, or 7 trees have not been identified to genus level, or 5 trees have not been identified to family level. When identification to species level is problematic, greater effort to identify trees to genus and family level could yield equivalent robustness of species richness values.

Most of the richness estimates produced here are tightly constrained, as evidenced by the difference between the mean minimum (Min_s) and maximum (Max_s) richness values. At the 0.04-ha scale, mean richness estimates for all taxonomic levels are constrained within 7% at most (Table 3.2). At the 1-ha scale, mean richness estimates for family and genus are constrained within less than 15%, but at the species level more unidentified stems exist so estimates are less constrained. Mean Min_s at the 1-ha scale is 28% less than mean Max_s. This appears to reveal a degree of uncertainty in richness and diversity estimates. However, it is clear that many of the Max_s values are simple not feasible. Extreme outliers exist, especially one highly unusual Podzol plot (ALP-40) which contains 1207 stems. The great majority of plots

have around 350-650 stems, and a spatial model of tree density per hectare across Amazonia estimates density to always be <750 (Ter Steege et al., 2003).

While Max_s does not always provide sensible estimates of richness, the difference between the preferred richness estimate ($Best_s$) and Min_s is smaller and these two variables have a strong correlation (r = 0.99) at the 1-ha scale. An extended morphospecies definition further constrains these estimates so that mean Min_s is only 22% less than mean Max_s (Table 3.3). This is a less repeatable approach, but $Best_s$ obtained using the extended morphospecies definition is only 1% greater than $Best_s$ obtained using the core morphospecies definition, suggesting that the core approach provides a reliable estimate of species richness.

There exist two potential sources of bias in the preferred richness estimates. First, equal abundances are assumed when multiple additional taxa are assigned to the unidentified stems belonging to a particular taxonomic group. However, this has minimal effect on the estimated evenness of diversity, since the mean ^2D: ^0D ratio using the preferred species richness estimates is almost identical to the mean ^2D: ^0D ratio when only stems that are fully identified at species level are considered. Second, those stems that cannot be identified may be more likely to belong to rare taxa than the stems that can be identified, since botanists normally find it easier to identify common species (Martinez and Phillips, 2000). This means that in some cases the preferred richness estimates may be slightly conservative. However, unidentified stems are first organised using any available taxonomic information at the genus or family level, before they are assigned to additional or existing taxa. Since a mean 99% of stems are identified at the family level, and a mean 98% are identified at the genus level, the magnitude of any such bias must necessarily be small.

Another persistent problem that impacts the analysis of diversity in the tropics is the prevalence of synonyms, many of which may not yet be recognised, or are placed differently according to such databases as Tropicos (http://www.tropicos.org) and The Plant List (http://www.theplantlist.org/). Further, many taxa remain unresolved. However, this is a problem which typically affects the comparison of β-diversity across plots visited by different botanists. Focusing on quantifying the α-diversity of individual plots in their initial censuses reduces the impact of such concerns, as all identifications within any given census have always been made by the same botanist.

3.5.2 Comparing richness and diversity metrics

3.5.2.1 The effects of spatial scale

Both spatial scale and sample size affect diversity estimates, and it is helpful to produce both area-based and stem-based diversity measures in order to control for these factors. The diversity measures used may need to differ between scales. In the selected plots, I find that variation between different diversity metrics is greater at the 1-ha scale. A 0.04-ha scale approaches the smallest grain size at which meaningful estimates of tree diversity can be made in diverse forests, and at this scale mean family richness is 67.8% of mean species richness, and mean species level ^{2}D is 80.1% of mean species richness. In comparison, at a 1-ha scale mean family richness is 27.3% of mean species richness, and mean species level ^{2}D is 31.8% of mean species richness. This shows that different aspects of diversity increasingly diverge at larger spatial scales, allowing distinct effects relating to these aspects to be more easily picked apart. At scales of 1-ha, Fisher's α provides a useful measure of diversity, although, unlike the other indices described, it cannot be used to make inferences about the relative importance of richness versus evenness. It is not appropriate for use at the subplot scale and shows extremely skewed distributions at this scale (Figure 3.4), due to the low stem: species ratio.

3.5.2.2 Comparisons across the richness–evenness spectrum

Taxonomic richness (^{0}D), Shannon diversity (^{1}D) and Simpson diversity (^{2}D) comprise a spectrum that can be used as a framework in which the forms of diversity that are the most relevant to any given question can be identified. For example, if correlations between aspects of forest function and taxonomic richness are strongest, this would suggest a disproportionately large role for rare taxa in influencing these correlations. Conversely if correlations between function and ^{2}D are strongest, a disproportionately large role for dominant taxa is revealed. If correlations between ^{1}D and function are strongest, the effect of each species is expected to be in direct proportion to its abundance. In African and South American forests, these measures are positively and linearly correlated (most having $r > 0.90$), with ^{1}D and richness being more strongly correlated than ^{2}D and richness, as expected. At a 1-ha scale, species level ^{2}D is 31.8% of ^{0}D and ^{1}D is 55.2% of ^{0}D. At a 0.04-ha scale, ^{2}D is 80.1% of ^{0}D and ^{1}D is 89.7% of ^{0}D.

3.5.2.3 Comparisons by taxonomic level

The use of a range of diversity measures from different taxonomic levels can aid in elucidating how diversity is structured, and may be used as a means to approximate phylogenetic diversity, for example to reveal the taxonomic level at which the variation in a given trait corresponds most strongly with diversity. For all eukaryote kingdoms, Mora et al. (2011) find exponential functions best fit the relationship between the number of individuals and taxonomic rank, for ranks below kingdom. I also find species richness to be exponentially related to genus and family richness at a plot scale, although linear relations exist at the subplot scale. At both scales, strong correlations (most of $r > 0.90$) between species, generic and family richness exist.

3.5.3 Comparing African and South American forests

All of the diversity indices explored show that South American forests are more diverse than African forests. The differences between forests in these two continents exist at scales of both 1-ha and 0.04-ha, but are much greater at 1-ha scales. The South American forests have mean species richness per hectare double that of the African forests, and mean Fisher's α per hectare three times that of the African forests. When monodominant forests are excluded and the higher stem density in South America is accounted for, species richness of African forests is still only 63% of that of South America forests. The low diversity of African forests cannot be attributed simply to their relatively low stem density.

The estimated mean Fisher's α per hectare of 28.6 ± 10.9 in Africa (30.2 ± 10.3 without monodominant plots) and 87.9 ± 63.9 in South America suggests even greater differences between Africa and South America than those reported by Parmentier et al. (2007), who found Fisher's α of 40.4 ± 13.8 in Africa for plots with a mean size of 1.023 ha, and 74.6 ± 45 in South America for plots with a mean size of 1.021 ha. The cause of the disparity in Africa may be related to the use of plots from relatively low diversity forests in Liberia and Tanzania, which Parmentier et al. (2007) mostly lack, while the higher Fisher's α I find in South America may be due to the effects of accounting for unidentified trees in diversity estimates.

It is the high diversity South American forests that provide the greatest contrast with African forests. At a 1-ha scale, the diversity of South American forests shows greater variance than that of African forests. African forests may be similar to the less diverse South American forests, but more diverse forests here have no analogue. This is most notable for diversity

measures that make use of species level data, including Fisher's α. The variance of diversity does not vary between continents at the 0.04-ha scale.

3.6 Conclusion

I have developed methods for estimating richness and diversity in diverse systems, dealing with unidentified individuals to produce richness estimates that take account of every single individual. These methods have been applied to tree diversity in tropical forest plots. The use of these methods considerably reduces uncertainty in diversity values, especially for species richness. Different aspects of diversity are strongly correlated, with measures across the richness–evenness spectrum being linearly related, while species richness is an exponential function of genus or family richness at scales of 1-ha. The spatial scale being used has major effects on the behaviour of diversity measures. Using these techniques, the tree diversity of African forests is found to be 2-3 times lower than that of South American forests.

4 Does tree diversity predict carbon storage and productivity across tropical forests?

4.1 Abstract

Two reasons are commonly put forward for the protection of tropical forests – (1) biodiversity conservation, and (2) avoiding carbon emissions. One key question is whether these objectives are complementary or whether trade-offs exist between them? Positive biodiversity–ecosystem function relations have been found in many other ecosystems, but in tropical forests it is largely unknown whether any such relations exist. When comparing multiple forests, many environmental variables can differ, and this must be accounted for when investigating diversity–function associations across many sites. I investigate whether relationships exist between tree diversity and aboveground biomass (AGB) or aboveground wood production (AGWP) in tropical Africa and South America, the two continents containing the most extensive areas of remaining tropical forests. Using 295 permanent 1-ha sample plots distributed across both continents, and using multiple area- and stem-based alpha-diversity indices, I explore first the bivariate diversity–function correlations, and then develop linear models having AGB or AGWP as the response variable, and including climate and soil variables plus diversity indices as predictor variables. I construct both ordinary least squares (OLS) models and models in which I select spatial filters using a Spatial Eigenvector Mapping (SEVM) approach to account for spatial autocorrelation. In all cases corrected Akaike Information Criterion values are used to choose the most parsimonious model. Whether analysed by the bivariate correlations or by linear models that account for soil, climate, and geographic distance, I find no evidence of positive associations between diversity and AGB. For AGWP, in African forests there is no significant diversity–AGWP relationship for any of the diversity metrics explored. In South American forests, bivariate diversity–AGWP correlations are not significant, but measures of diversity at the family and genus (but not species) levels are present in the linear models of AGWP. Thus, an additional 10 families per hectare are associated with a 27% increase in AGWP in South America. This suggests that once environmental variations have been taken into account, some aspects of diversity and productivity are related in these forests. It also emphasises the importance of considering diversity at multiple taxonomic levels, and suggests that at the finest grain of diversity usually

measured (species) there is little extra functional effect. The lack of any relationship between AGB and diversity means care must be taken to conserve both the biodiversity of tropical forests and their function as carbon stores.

4.2 Introduction

4.2.1 Two contrasting objectives of tropical forest conservation

The protection of tropical forests is one of the major goals of international conservation policy. An important reason for conserving these forests is their exceptionally high biodiversity. For example, up to 329 tree species per hectare have been recorded in central Amazonia (Laurance et al., 2010), a uniquely high value across all terrestrial biomes. Furthermore, many tropical forest regions are recognised as 'hot-spots' in particular need of conservation, due to their exceptional concentration of endemic plant species and threat levels (Myers et al., 2000). Protected areas have been widely used as a conservation strategy.

More recently, arguments used to justify conservation efforts have increasingly focused on the ecosystem services provided by tropical forests. These include provision of timber and non-timber forest products, provision of genetic material used for medicinal purposes, local hydrological regulation, and regulation of global carbon cycling. Many of these ecosystem services are underlain by biodiversity, and their continued provision depends on the existence of species able to tolerate changing environmental conditions and anthropogenic pressures (Malhi et al., 2008; Miles et al., 2004). Yet it is the contribution of tropical forests to global carbon cycling that has become a major focus of international efforts for climate change mitigation. The increase in atmospheric CO_2 concentrations due to the burning of fossil fuels and land use change has been mediated by carbon uptake by both land and ocean sinks (Le Quéré et al., 2013), with intact tropical forests thought to provide a significant proportion of the current land sink (Pan et al., 2011). In addition to providing a carbon sink, tropical forests store around 40% of the carbon found in terrestrial vegetation (Malhi and Grace, 2000; Malhi et al., 2002b), and are responsible for 34% of global terrestrial gross primary productivity (Beer et al., 2010). For these important contributions to the global carbon cycle to continue unabated, it is essential that existing tropical forests remain, as far as possible, intact.

An important tool for the conservation of tropical forests as carbon stores is the REDD+ mechanism, which has developed from United Nations Framework Convention on Climate Change (UNFCCC) negotiations in recent years (Angelson et al., 2009). Under the Warsaw

Agreements reached in 2013, developing countries could be paid to conserve or sustainably manage existing forests. There have been extensive efforts to develop tools and methodologies to monitor carbon stocks and enable REDD+ compliance, and to produce maps of both carbon and biodiversity (UNEP-WCMC, 2008). Although the instigation of compliance-based national REDD+ schemes has yet to come to fruition, many voluntary REDD+ schemes serving the corporate sector are already in existence.

A crucial question for tropical forest conservation is therefore whether there is any complementarity between the twin aims of conservation of biodiversity and preservation of the forests' role as carbon stores and sinks. Do the most diverse forests store and uptake the most carbon? Absolute levels of diversity are only one of many aspects that may require conservation efforts, with other factors including endemism, threat levels, and the need to retain examples of all ecosystems, not just the most diverse ones. Nevertheless, if diversity and carbon storage can be shown to be complementary, this could boost conservation efforts, with REDD+ schemes providing important biodiversity co-benefits. If the most diverse forests are not the most carbon-rich or productive, then this could point to difficult trade-offs between forest conservation for biodiversity and carbon. Thus, in an ecosystem service-led approach, the displacement of land-use change could occur as a result of efforts to preserve particular sites (Miles and Kapos, 2008), and the magnitude of the potential impacts of this leakage on tropical forest biodiversity depends on the degree of overlap between diverse and carbon-rich forests.

4.2.2 Biodiversity and ecosystem functioning relations

The relationship between biodiversity and ecosystem functioning has recently become a focus of much ecological research (Cardinale et al., 2012). The effects of species loss have been assessed in meta-analyses (Balvanera et al., 2006; Cardinale et al., 2007) and experimental studies from ecosystems as varied as temperate grasslands (Hector and Bagchi, 2007; Tilman et al., 2001) and benthic diatom biofilms (Vanelslander et al., 2009), all of which have found at least some positive diversity effects in existence. Positive diversity effects do not always predominate though, and others have found compositional effects related to the traits of individual species to show the greatest influence on the particular function of interest (Duarte et al., 2006), or have not found significant diversity effects to remain after other environmental variables are taken into account (Vila et al., 2003).

Forests have been the focus of observational studies which have shown a variety of diversity–function relationships, including a weak negative diversity–biomass correlation in Eastern European forests (Szwagrzyk and Gazda, 2007), a positive hump-shaped relationship between species richness and productivity in Swedish temperate and boreal forests (Gamfeldt et al., 2013), a positive species richness–productivity relationship in successional forests in the Midwest USA (Caspersen and Pacala, 2001), and both non-significant (Vila et al., 2003) and weak positive (Vila et al., 2007) associations between biodiversity and productivity in Mediterranean woodlands. Positive relations could indicate various mechanisms, as described in section 4.2.4. Unimodal relations may be found more commonly when the extent of studies crosses community boundaries, for example including sites with a wide range in annual rainfall (Mittelbach et al., 2001). Most research focuses on species richness as a simple measure of diversity, but a global meta-analysis finds that both evenness and richness have positive relationships with forest productivity (Zhang et al., 2012). Yet, among this extensive research, there has been remarkably little effort applied to exploring diversity–function relationships within the most diverse and productive terrestrial ecosystems of all, tropical forests.

4.2.3 Current knowledge of biodiversity and ecosystem functioning in tropical forests

The high diversity of tropical forests makes them particularly important for biodiversity–ecosystem functioning research, because it is not known whether increased diversity will continue to promote increased function in such diverse ecosystems. The alternative is redundancy, whereby above a certain threshold, greater diversity is no longer associated with greater function. Redundancy has been shown to diminish when multiple ecosystem functions and multiple years are considered (Hector and Bagchi, 2007; Isbell et al., 2011). Further, in a meta-analysis of 103 publications the size of observed diversity effects in a given study has been found to be positively related to the maximum number of species in that study (Balvanera et al., 2006, although the highest category considered was >20 species), but redundancy may still occur in extremely diverse tropical rainforests.

Local-scale positive relationships between species richness and aboveground biomass (AGB) have been found in a mature tropical (Ruiz-Jaen and Potvin, 2010) and a mature subtropical forest (Vance-Chalcraft et al., 2010). Some positive associations between species richness and ecosystem function have been reported – doubling species richness corresponded to a 7% or 53% mean increase in biomass, when effects potentially related to stem density were or were not excluded, respectively – within 25 tropical forest sites at small scales (20 x 20 m; Chisholm

et al., 2013). This same doubling of species richness corresponded to a 5% or 48% mean increase in wood production when 12 tropical forest sites were examined at the same scales (Chisholm et al., 2013). However, the same study failed to detect consistent richness–function relations at the 1-ha scale, and furthermore included only one Amazonian and one African site, thus the generality of the results are unclear. Across the world's two most extensive tropical forests, diversity–ecosystem functioning relations remain essentially unknown.

4.2.4 Potential mechanisms underlying diversity–function relations in tropical forests

There are many ecological mechanisms by which community-level (alpha) diversity and productivity could potentially be related. Under complementarity, more diverse stands are more productive as a direct result of their greater diversity. Complementarity processes can include niche partitioning (Paoli et al., 2006) and facilitation (Cardinale et al., 2002). Alternatively, selection effects could exist, by which more diverse stands are more likely to contain highly productive species, and these species are sufficiently dominant to ensure high productivity in these stands (Huston, 1997). According to the insurance hypothesis, biodiversity insures against declining ecosystem function in changing environmental conditions, since diverse assemblages are more likely to contain species that are adapted to a wide range of environmental conditions (Yachi and Loreau, 1999). Other potential mechanisms could see links between diversity and productivity via the effects of stem turnover. Turnover has been suggested as a predictor of species richness (Phillips et al., 1994) because it is associated with frequent small-scale disturbances which maintain non-equilibrium conditions (Connell, 1978).

Biomass might be expected to have a less direct relationship with diversity than productivity does, since biomass is a function of wood production and turnover rates (Baker et al., 2004), while productivity is itself a process that may directly affect or be affected by diversity. Biomass and productivity do not share a simple positive correlation, and in Amazonia, the forests with the highest productivity tend not to be those with the highest biomass (Keeling and Phillips 2007). However, it is possible that processes affecting mortality rates, such as the prevalence of pests and pathogens, could be related to diversity (Wills et al., 1997). These effects may relate mostly to the mortality of seedlings (Harms et al., 2000), which make little contribution to forest biomass, but the effects do suggest a potential means by which biomass could show a more direct association with diversity.

4.2.5 The role of other environmental variables and their potential as covariates that may obscure diversity–function relations

In forests composed of very long-lived individuals, it is not feasible to experimentally manipulate diversity in a similar fashion to that achieved in studies undertaken in grassland ecosystems (Hector and Bagchi, 2007; Tilman et al., 2001). Instead, it is necessary to conduct observational studies. In these circumstances, the possibility of observing diversity–ecosystem function relationships will be complicated by the presence of multiple covarying environmental and forest structural factors (Huston, 1997). These or other factors could be the true drivers of any observed correlation between diversity and function. Many of these factors may also be spatially autocorrelated, and this needs to be assessed as a possible cause of any observed relationships (Dormann, 2007). Factors that may potentially affect diversity or carbon dynamics in tropical forests include the absolute amount and seasonality of precipitation, temperature, soil fertility and its physical structure, topography, and local forest structure (Ferry et al., 2010a).

Differences in stem density are a potential 'hidden treatment' because they render uncertain whether any observed changes in forest function are due to diversity effects or simply due to differing numbers of individuals. Large trees are particularly important in driving variation in aboveground biomass in tropical forests (Slik et al., 2013). Processes of gap dynamics can also have a major influence on forest structure at small scales, creating patchy structures with high variability of biomass and productivity, which may in part be related to differences in stem density. To control for the varying number of stems between plots, individual-based rarefaction can be used to produce richness measures that estimate the number of taxa for a given number of stems. The use of stem-based diversity metrics, in addition to area-based metrics, can allow effects driven by stem density to be distinguished from those driven by diversity.

Moisture availability can limit biomass and productivity as proposed by the hydraulic limitation hypothesis (Ryan et al., 2006). Annual rainfall and dry season length may also be positively correlated with AGB (Baraloto et al., 2011; Malhi et al., 2006; Slik et al., 2013). Outside high latitudes, variables related to moisture availability are often the strongest predictors of species richness (Hawkins et al., 2003). Both mean annual rainfall and seasonal moisture availability are known to be correlated with tree species richness (Clinebell et al., 1995) and alpha-diversity (Parmentier et al., 2007) across the Neotropics. Dry season length has been reported to be a strong predictor of maximum Fisher's α in Amazonia (Ter Steege et al., 2003). In Africa

the relationship, if it exists, appears much weaker (Parmentier et al., 2007), and OLS models using a set of climate variables have been shown to predict alpha-diversity less well than a kriging model with no climate components (Parmentier et al., 2011).

Mean annual temperature has been observed to be positively correlated with total net primary productivity in a meta-analysis of studies from moist tropical forests (Raich et al., 2006), however this study included montane forests. Conversely, Slik et al. (2013) found temperatures in the warmest and coldest months to be negatively correlated with AGB, and in lowland Amazonia a small negative correlation between mean annual temperature and aboveground coarse woody productivity (AGWP) has been observed (Malhi et al., 2004), but this may be related to the coincidence that more fertile soils tend to occur in the slightly higher altitude plots of western Amazonia. It has also been suggested that higher temperatures could also be a driver of greater biodiversity, through the promotion of faster speciation rates (Currie et al., 2004).

Soil fertility is positively correlated with AGB in Borneo (Slik et al., 2010), and is thought to be an important driver of forest productivity across Amazonia (Quesada et al., 2012). Soil fertility may also influence turnover (Phillips et al., 2004; Stephenson and van Mantgem, 2005), although turnover may be more closely linked to soil physical properties such as depth and structure. Soil waterlogging and topographic position can influence treefall rates, thus affecting biomass and productivity (Ferry et al., 2010b), while soil water retention and its availability to trees could mediate the impacts of drought (Phillips et al., 2009a). Other factors such as underlying geology (Irion, 1978), fluvial dynamics and water chemistry could also be of relevance to soil formation and soil properties. Thus, many environmental factors may interact with diversity or carbon dynamics in tropical forests, and these must be taken into account in order to explore diversity–function relations.

4.2.6 Aims of the study

This study develops a major dataset of diversity and function to explore the fundamental theoretical and practical concern of whether one drives the other in tropical forests –the most diverse of the terrestrial ecosystems which perform globally important ecosystem functions. I explore diversity–function relations by addressing four specific questions:

(1) Is there a positive correlation between tree diversity and aboveground biomass in tropical forests?

(2) Is there a positive correlation between tree diversity and aboveground coarse wood production in tropical forests?
(3) Does biomass vary with tree diversity, after accounting for differences in climate and soil variables?
(4) Does wood production vary with tree diversity, after accounting for differences in climate or soil variables?

I address these questions, using 295 tropical forest inventory plots taken from a pan-global dataset (Lopez-Gonzalez et al., 2011), all of which have been measured and analysed according to a standardised protocol (Phillips et al., 2009b). These permanent plots span the full environmental range of moist forest conditions in South America and in Africa, which together hold the majority of the world's remaining tropical forests.

First, I investigate bivariate correlations between tree diversity, AGB and AGWP, plus correlations of these factors with soil and climate variables and with the turnover of aboveground biomass. Then, I explore whether any relationships emerge (or diminish) once additional environmental and/or spatial factors are considered. Models will be used with both AGB and AGWP as the response variables. These models will include mean annual temperature and variables representing precipitation, plus variables that represent soil nutrient capacity and texture. Possible spatial autocorrelation is accounted for using eigenvector-based spatial filters (Griffith and Peres-Neto, 2006), in addition to analyses involving ordinary least squares (OLS) models. To explore whether any relationship between diversity and these key ecosystem functions is likely to be general or if they differ by continent, I will repeat all tests separately for South American and African forests. To ensure that any observed diversity–function relations are not caused by diversity being a proxy for stem density, I use both area-based and stem-based diversity measures. To gain a broader understanding of the role of alpha-diversity, I use multiple indices that characterise various aspects of the complex nature of alpha-diversity, spanning the spectrum of richness and evenness and characterising diversity at species, genus and family levels.

In any large-scale observational study where there is great variation between plots and a large number of potential drivers may be acting, I do not necessarily expect any single set of processes to maintain a particular functional role across multiple forests. Nevertheless, the great value of the macroecological lens is that it can help us to understand the importance of biodiversity–ecosystem functioning relationships in multiple real-world forests. The purpose of

this study is to elucidate diversity–function relations across the most species-rich and carbon-rich ecosystems on Earth.

4.3 Methods

4.3.1 Plot selection

I selected tropical forest permanent plots from a global dataset (Lopez-Gonzalez et al., 2011), based on the contributions of research groups that use standardised field methods (Phillips et al., 2009b). I only used plots of 1-ha size representing old-growth, closed-canopy tropical forests, which have a high standard of taxonomic identification. All selected plots were visited by a professional botanist and scientific names were used to identify species. These plots have ≥80% of trees identified at least to genus level and ≥60% of trees identified to species level. The diversity, biomass, and productivity measures are based on all stems ≥100 mm diameter (*D*). In 16 plots, Arecaceae or other monocotyledonous taxa (*Phenakospermum sp.*) had not been measured following the same protocol in earlier censuses (see attached CD, Table A4.1); I therefore excluded these taxa from diversity, productivity and biomass measures for all censuses of these plots.

Non-contiguous plots and transects >500 m in length or <20 m in width were excluded, since habitat heterogeneity associated with topographic, edaphic, and microclimatic factors is likely to rise in accordance with the distance between the opposite corners of a plot. This would increase the chances of β-diversity existing within a plot and inflate the plot-level diversity estimates (Condit et al., 1996), which I aim to avoid. For the same reason, plots known to contain more than one soil type were avoided. I also excluded swamp and Histosol forests, those subject to anthropogenic disturbance, and forest classified as montane or plots with mean annual temperature <20°C.

In total, 295 plots were selected, of which 191 had repeat censuses spanning ≥3 years and were thus also suitable for analysis of productivity (Table 4.1). Of these, the mean length of the sampling period was 11.5 years, maximum 31.8 years. The full dataset comprises 139 African and 156 South American plots. For area-based diversity measures, I use all available plots, but only plots with ≥300 stems are used for stem-based diversity measures. Fifteen of the African plots are from monodominant forests, dominated by the same species, *Gilbertiodendron dewevrei*, with low diversity. Plots are often located in clusters, within a few kilometres of one

another and tend to be surveyed at similar times. There are 112 clusters of plots across the two continents.

Table 4.1: The number of plots used for each section of the analysis.

Plot selection criteria		*Number of African plots*	*Number of South American plots*	*Total number of plots*
Biomass	All	139	156	295
	≥300 stems	128	154	282
Productivity	All	75	116	191
	≥300 stems	71	116	187

4.3.2 Estimating Aboveground Biomass

Aboveground biomass (AGB) for all trees ≥100 mm diameter (*D*) was computed using the Chave moist forest equation (Model 1.5 in Chave et al., 2005). This requires estimates of diameter, wood density and height for each tree. Diameter measurements were taken in each plot census with the point of measurement (POM) at a standard height of 1.3 m, except when buttresses or other stem deformities were present at this height, in which case diameter above the buttress or deformity was used. In plots with multiple censuses, POM changes were necessary for some trees, in anticipation of future buttress creep. In all cases, AGB was calculated using the field measurement at the correct POM for that census, clear of all buttresses.

For wood density, I used continent-specific values taken from a reference database (Chave et al., 2009; Zanne et al., 2009), taking the values for the lowest available taxonomic resolution following the method of Lewis et al. (2009). Stem heights were estimated using the Feldpausch regional Weibull equation (Feldpausch et al., 2012). Aboveground biomass was calculated in the first and final census for plots with more than one census, with the mean of these used as the best AGB estimate in the subsequent statistical models. This allows biomass estimates to correspond as closely as possible to the time period across which productivity is measured.

4.3.3 Estimating Aboveground Wood Production and Turnover

To derive aboveground wood productivity (AGWP), I used a methodological approach as described in Chapter 2. In brief, it involves estimating AGWP for each census interval as the gain in AGB of all stems present at both the start and end of the interval, plus the AGB of stems that are newly recruited during the interval. I divide the resulting totals by the time elapsed to obtain productivity estimates on an annual basis, and apply correction factors to account for census interval effects. I then estimate mean annual plot-level AGWP across the

entire period through which a plot has been sampled, as the time-weighted mean of the annual productivity in each interval.

Changes in the point of measurement of diameter are sometimes necessary in anticipation of future buttress creep. When POM changes occurred, I used a method to prevent stem taper from causing bias in the growth estimates, as outlined in Chapter 2. Thus in POM change censuses, diameter was measured at both the new POM and the old POM, and for these trees I calculated estimates of D at the old POM (D_{old}) in all censuses after the POM change, and D at the new POM (D_{new}) in all censuses before the POM change, using the ratio of D_{old}: D_{new} in the POM change census. To estimate productivity, I used the original field measurements in all intervals that did not end in a POM change, but for those intervals ending in a POM change, I used the mean of D_{old} and D_{new}.

The method by which the growth of recruits was included in the stand-level productivity measure entailed applying only their growth above an initial diameter of 100 mm. This method was chosen because it ensures the population of stems from which productivity is estimated is equivalent to the population of stems from which diversity is estimated (see Chapter 2). Corrections for census interval length are made to take into account the growth of known trees that subsequently die within an interval, plus the growth of trees that both recruit and die unobserved within an interval (see Chapter 2). Corrections for known trees that die are made by assuming death occurs at the interval mid-point, and estimating diameter growth until this point using the median growth rate of dicotyledonous trees from the same plot and diameter size class ($100 \leq D < 200$ mm; $200 \leq D < 400$ mm; $D \geq 400$ mm). The number of unobserved recruits in each census is estimated using plot level mortality and recruitment rates, their growth is assumed to follow median growth rates for dicotyledonous trees in the 100-199mm size class, and they are assumed to recruit on average after one-third of the interval and die after two-thirds of the interval.

The mean annual turnover of aboveground biomass is estimated as the sum of the biomass of trees that die within a census and the biomass of newly recruited trees. Following the same approach as used to quantify AGWP, the 100 mm ‘core’ is subtracted from the estimates of biomass for both recruits and dead trees. Corrections for census interval length are also made, to include the recruitment and mortality of trees that recruit and die unseen within a census, and to account in mortality estimates for the full size of trees that grow a certain amount before subsequently dying within an interval. These corrections follow the same methods as do the equivalent corrections for AGWP.

4.3.4 Estimating Diversity

To ensure that all stems could be accounted for in richness and diversity measures, I developed an approach to account for those stems that could not be fully identified to species, neither in the field nor at herbaria. This approach is fully described in Chapter 3. Most stems were identified in the field by botanists, while the collection of voucher specimens and their storage in herbaria enabled further identification and cross-referencing. The inspection of these specimens in herbaria reduces the risk of multiple synonyms being used for the same species, although this remains possible when comparing between plots. However, my focus on the α-diversity of plots in their initial census avoids these problems, since all identifications in a single plot census were always made by the same botanist.

Since 100% of stems could not always be identified, I used further methods to improve the accuracy of the richness and diversity measures. The first of these was the classification of morphospecies, which I identified from botanists' comments. I assigned morphospecies when comments indicated scientific names or affinity to scientific names not accepted by the ForestPlots.net database (i.e. does not conform to an accepted name in the African Flowering Plants database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php), or The Plant List (http://www.theplantlist.org/) for South American species names), or when the botanist had assigned the stem to a numbered morphospecies. Secondly, after the assignment of morphospecies, I collated all remaining stems which were unidentified at species level but belonged to a genus not otherwise represented within the plot, or unidentified at genus level but belonged to a family not otherwise represented within the plot. I assumed that these stems must represent new taxa at the relevant taxonomic levels. After using these two methods, a small number of stems still remained unidentified. I organised these remaining stems using all of the information that was available for them at higher taxonomic ranks, and assumed that the number of additional taxa within a given plot that were represented by each group of stems was equal to the rounded product of the number of stems in the group and the taxon: stem ratio for fully identified stems within the same plot (based on Martinez and Phillips, 2000).

I used a range of diversity metrics, including both area-based and stem-based measures, estimated from the stems present during the initial plot census. For all measures I used only plots of 1-ha size to ensure strict comparability amongst plots. The area-based measures used are species, genus, and family richness per hectare, Shannon diversity (exponential Shannon entropy) and Simpson diversity (Simpson's Reciprocal Index) at species, genus and family

levels, and Fisher's α (*FA*). For the stem-based measures, I used species, genus, and family richness, derived as estimated values per 300 stems in each plot using individual-based rarefaction, plus *FA* per 300 stems.

Species, genus, and family richness provide contrast in terms of taxonomic level, which may enable assessment of which taxonomic level has the greatest variability in the traits affecting or affected by biomass and productivity. Shannon and Simpson diversity are used together with richness to provide a spectrum of diversity measures, in which progressively greater weight is placed on species abundances, and where all of the indices are comparable since they provide measures of the 'effective number of species' (see Chapter 3). Within this spectrum, richness, Shannon and Simpson diversity correspond respectively to the Hill numbers ${}^{0}D$ (diversity of order 0), ${}^{1}D$ (diversity of order 1) and ${}^{2}D$ (diversity of order 2; Hill, 1973), with Simpson diversity (${}^{2}D$) reflecting dominance (and being the most closely related to evenness) since this measure gives greater weighting to individuals from more abundant species. Fisher's α is also included since this is frequently used to characterise tropical tree diversity (Ter Steege et al., 2003), and thus is useful for comparative purposes. Given sufficient sample size, variations in *n* do not strongly affect this measure.

4.3.5 Climate and soil data

Environmental variation must be statistically accounted for in order to better understand biodiversity–ecosystem functioning relations. The following climate data from the WorldClim database (Hijmans et al., 2005) using interpolations of observed data representing mean conditions 1950-2000 and a 30 arc-second resolution (~ 1km) were extracted: mean annual temperature (*MAT*), mean annual precipitation (*MAP*), seasonality of precipitation (P_S) measured as the coefficient of variation in monthly means, precipitation in the driest month (P_{DM}), and precipitation in the driest quarter (P_{DQ}).

For each plot, a reference soil group was identified (see attached CD, Table A4.2) following the World Reference Base soil classification system (IUSS Working Group WRB, 2006). These data were obtained from published sources where possible. These data were largely from Quesada et al. (2010) for South America, and from Lewis et al. (2013) for Africa. When a published reference soil group could not be found for a particular plot, I used those as mapped in the Harmonised World Soil Database (FAO/IIASA/ISRIC/ISS-CAS/JRC, 2012), or for the Democratic Republic of the Congo, SOTER (Batjes, 2007).

Estimates for the Total Extractable Bases (*TEB*), % sand, % silt and % clay at depths of 0 - 30 cm were obtained using data from within the plot where possible. The sum of bases represents the cations available as nutrients to trees; while the other variables represent soil texture and provide a measure of soil physical characteristics. I used data from Quesada et al. (2010) for the plots listed within, and for any other plots located within the same plot clusters and of the same soil type. I also obtained mean soil data across one central Amazonian cluster from Laurance et al. (1999) and *TEB* for some Ghanaian plots from Sophie Fauset (personal communication). For the remaining plots, I extracted data from the Harmonised World Soil Database for the same reference soil group at the nearest possible location to the plot location. While this is not as accurate as data collected *in situ*, it allows an approximation of soil parameters for all plots.

Finally, I conducted Principal Components Analysis (PCA) on the soil textural data. The first two principal components represent a proportional 0.74 and 0.26 respectively of the variation, cumulatively representing >0.99 of the variation (Table 4.2). The first principal component (*PCA1*) represents the proportion of sand in the soil, while the second principal component (*PCA2*) forms an axis of silt versus clay (Table 4.3).

Table 4.2: The proportion of variability in the soil textural variables represented by the first two Principal Components.

	Eigenvalues	*Proportion*	*Cumulative Proportion*
PCA1	2.209	0.736	0.736
PCA2	0.791	0.264	1

Table 4.3: The contributions of the individual variables to the first two Principal Components.

	PCA1	*PCA2*
Sand	-1	-0.005
Silt	0.770	-0.639
Clay	0.786	0.619

4.3.6 Statistical analysis

To answer my first two questions, I initially examine linear correlations between the diversity metrics and AGB or AGWP. Correlations of diversity, AGB, and AGWP with soil and climate variables and with turnover of aboveground biomass, collinearity among the environmental and diversity variables, and correlations between AGB and AGWP, are also explored. All of these correlations are computed using Kendall's τ, as this can be used with data that are not

bivariate normal, and it is able to deal with ties (i.e. individual plots having identical values). The *p*-values are corrected for multiple tests using the false discovery rate (Benjamini and Yekutieli, 2001). This correction is computed separately for ten groups of tests: diversity–AGB correlations, diversity–AGWP correlations, correlations of diversity, AGB and AGWP with turnover, correlations of soil variables with AGB, correlations of soil variables with AGWP, correlations of precipitation variables with AGB, correlations of precipitation variables with AGWP, correlations of *MAT* with AGB, correlations of *MAT* with AGWP, and AGB–AGWP correlations, and independence of tests is assumed only for the final three groups. The division into these groups reflects where the results of multiple tests will be synthesised into a single conclusion (Bender and Lange, 2001).

For my final two questions, I develop linear models of biomass and productivity, with separate models for Africa and South America. The response variables both needed to be log-transformed to normalise their distributions. Each model combination contains a single diversity metric plus a set of soil and climate variables as candidate predictor variables. Interaction terms between the predictor variables were not included in the analysis.

To prevent collinearity and reduce the number of predictor variables, correlations among the three variables representing seasonality of precipitation, and correlations of these variables with log(AGB) and log(AGWP), were investigated. In both Africa and South America, these three variables were collinear, and P_S had the strongest correlations with log(AGB) so was chosen as a candidate predictor variable for the models having log(AGB) as the response variable, while P_{DQ} had the strongest correlations with log(AGWP) and was chosen for the models having log(AGWP) as the response variable.

Instead of testing for ‘significance’ and ‘non-significance’ of terms, with an arbitrary cut-off point such as the classic $p < 0.05$, my approach follows information theory to discover the most parsimonious model to represent the given data (Dayton, 2003). I therefore use the corrected Akaike’s Information Criterion (AICc), an estimator of the Kullback-Leibler distance based on Fisher’s maximised log-likelihood (Burnham and Anderson, 1998), which has been corrected for finite sample sizes.

I investigate spatial autocorrelation of the response variables using correlograms. To account for the effects of this spatial autocorrelation when constructing linear models, my approach is based on spatial eigenvector mapping (SEVM; Borcard and Legendre, 2002) as used by Quesada et al. (2012) and Lewis et al. (2013). The OLS model with the lowest AICc value is identified, and only spatial filters that are significantly correlated with the residuals from this

OLS model are selected (similar to the approach of Griffith and Peres-Neto, 2006), and identical to the SEVM-3 approach of Quesada et al. (2012). The regression is then re-run including these spatial filters as parameters.

The standardised (β) coefficients and *p*-values for each predictor variable in the best OLS and SEVM models are reported. The β coefficients show how many standard deviations the response variable will change given an increase of one standard deviation in the predictor variable. The *p*-values of parameters present in the lowest AICc models are not always necessarily < 0.05, since the information-theory philosophy followed does not rely on multiple significance testing for model selection. The OLS and SEVM models are run using Spatial Analysis in Macroecology version 4.0 (Rangel et al., 2010), and other analyses are carried out using R version 3.0.2 (R Core Team, 2013).

4.4 Results

4.4.1 General overview

Diversity estimates for 295 plots reveal extensive variation between and among African and South American forests, with the differences by continent remaining even when African monodominant forest plots are excluded (Table 4.4). Whether measured by area or by stem, tree diversity is considerably greater in South America than in Africa, and is also more variable. In both continents, species richness per hectare is more variable than family richness per hectare, in terms of both the absolute range of values and the relative variance expressed as the coefficient of variation (Table 4.5).

Across the whole dataset, species richness per ha varies by an order of magnitude, from the monodominant forests of Central Africa to extremely diverse plots with up to 311 species per hectare in Brazilian central Amazonia. Fisher's α closely follows species richness in its distribution, and the mean area-based *FA* of South American forests is triple that of African forests. By contrast, the plots with the highest family richness per ha are mostly located in western Amazonia – in Peru, Colombia and Ecuador – rather than in central Amazonia. The stem-based diversity metrics behave similarly to the area-based measures, with family richness tending to be greatest in western Amazonia and species richness and *FA* greatest in central Amazonia. There are 13 plots containing less than 300 stems which are excluded from these stem-based measures, 11 of which are in Africa.

As with diversity, major differences in function and environmental conditions are also revealed between African and South American forests (Table 4.4). Aboveground biomass varies by more than a magnitude, from 70 to 736 Mg ha^{-1}, with the very highest values found in Guyana, where trees are known to be tall and have high wood density (Ter Steege et al., 2006), and the lowest in eastern Bolivia. In general, African plots, especially monodominant forests, have higher AGB than South American plots. Aboveground coarse woody productivity varies four-fold, from 2.5 to 10.2 Mg ha^{-1} a^{-1}, with only one plot, located in Gabon, having AGWP in excess of 9 Mg ha^{-1} a^{-1}. In general, African plots have slightly higher AGWP than South American plots. Mean annual precipitation and rainfall seasonality are also more variable in South America, with plots ranging from very wet, aseasonal sites in northwestern Amazonia to drier, more seasonal locations on the fringes of the tropical forest zone in eastern Bolivia.

Table 4.4: Mean plot level variables by continent. All variables except aboveground wood production (AGWP) and the stem-based diversity metrics are calculated using the full set of 295 plots. I estimate AGWP using all plots with multiple censuses. The stem-based diversity metrics are estimated in all plots with ≥300 stems. In Africa, variables are also calculated excluding 15 monodominant plots. For comparative purposes, mean annual AGWP is estimated in two ways; 1) by treating recruits as having grown only from 100 mm diameter (see Chapter 2), as used in the rest of the analyses in this chapter; 2) using the commonly used alternative method in which the growth of recruits is assumed to begin from 0 mm at the time of the census prior to recruitment.

Variable	*Africa*	*Africa excluding 15 monodominant forests*	*South America*
Mean aboveground biomass (Mg dry mass ha^{-1})	395 ± 104	387 ± 100	282 ± 102
Mean annual AGWP (Mg dry mass ha^{-1} a^{-1})	5.74 ± 1.35	5.83 ± 1.39	5.08 ± 1.14
Mean annual AGWP (recruits from 0 mm) (Mg dry mass ha^{-1} a^{-1})	5.92 ± 1.35	6.02 ± 1.39	5.44 ± 1.17
Stem density (per ha)	420 ± 88	429 ± 88	545 ± 112
^0D (species richness per ha)	73.8 ± 26.4	77.6 ± 24.4	147.9 ± 72.3
^0D (genus richness per ha)	58.6 ± 18.8	61.3 ± 17.3	88.3 ± 31.4
^0D (family richness (per ha)	27.5 ± 6.2	28.4 ± 5.4	37.0 ± 8.8
^1D (Shannon effective species per ha)	36.6 ± 18.4	39.9 ± 16.4	84.0 ± 53.7
^2D (Simpson effective species per ha)	22.1 ± 12.4	24.3 ± 11.2	47.3 ± 33.7
^1D (Shannon effective genera per ha)	27.9 ± 13.0	30.3 ± 11.4	42.5 ± 18.9
^2D (Simpson effective genera per ha)	17.3 ± 9.2	18.9 ± 8.2	24.3 ± 11.7
^1D (Shannon effective families per ha)	13.1 ± 4.7	14.1 ± 3.8	17.2 ± 5.2
^2D (Simpson effective families per ha)	9.0 ± 3.8	9.8 ± 3.2	11.5 ± 3.9
Fisher's α (per ha)	27.5 ± 13.2	29.2 ± 12.7	79.1 ± 57.9
^0D (species richness per 300 stems)	64.7 ± 20.5	67.2 ± 19.6	107.1 ± 44.9
^0D (genus richness per 300 stems)	53.3 ± 15.0	55.0 ± 14.3	70.2 ± 22.5
^0D (family richness per 300 stems)	26.3 ± 5.1	26.9 ± 4.7	32.4 ± 7.2
Fisher's α (per 300 stems)	27.0 ± 12.7	28.4 ± 12.3	74.1 ± 54.5
Mean Annual Temperature (°C)	24.6 ± 1.3	24.6 ± 1.4	25.6 ± 1.4
Mean Annual Precipitation (mm)	1923 ± 393	1957 ± 404	2316 ± 735
Precipitation seasonality (coefficient of variation of precipitation monthly means)	57.0 ± 13.2	57.9 ± 13.1	48.5 ± 18.0
Precipitation in the Driest Month (mm)	25.6 ± 20.3	24.7 ± 20.2	76.0 ± 59.8
Precipitation in the Driest Quarter (mm)	121 ± 72	120 ± 74	264 ± 196
Mean sum of bases (cmol+ kg^{-1})	2.86 ± 2.15	3.03 ± 2.21	3.15 ± 4.88
Mean sand content (%)	64.2 ± 17.8	64.3 ± 17.9	46.0 ± 25.2
Mean silt content (%)	16.0 ± 9.2	16.6 ± 9.4	23.8 ± 17.9
Mean clay content (%)	19.8 ± 11.7	19.1 ± 10.9	30.2 ± 17.0
Mean value on PCA Axis 1 (sand)	-0.60 ± 1.11	-0.61 ± 1.12	0.54 ± 1.58
Mean value on PCA Axis 2 (silt to clay)	-0.05 ± 0.51	-0.11 ± 0.45	0.04 ± 1.12

Table 4.5: The absolute and relative variance of richness values per hectare, for 169 tropical forest plots. CV is the coefficient of variation, measured as the standard deviation divided by the mean.

	Species richness per hectare			*Genus richness per hectare*			*Family richness per hectare*		
	Mean	*Range*	*CV*	*Mean*	*Range*	*CV*	*Mean*	*Range*	*CV*
Africa	73.8	119	0.36	58.6	90	0.32	27.5	35	0.23
South America	147.9	279	0.49	88.3	131	0.36	37.0	43	0.24
All plots	113.0	302	0.59	74.3	149	0.40	32.5	51	0.28

4.4.2 Question 1: Is tropical forest biomass related to tropical forest tree diversity?

There is no clear linear relationship between biomass and area-based measures of tree diversity (Figure 4.1). Aboveground biomass is not significantly associated ($p < 0.05$) with any richness or diversity measures in either African or South American forests using Kendall's τ, although species richness per hectare in South America, after correcting for multiple tests, does come close to having a significant positive relationship with AGB ($\tau = 0.15$, $p = 0.082$). When African monodominant forest plots are removed, correlations are still not significant. When data from both continents are treated together, a significant negative relationship between biomass and family richness per hectare is observed, but this is driven by the general property of African forests to have higher biomass and lower diversity than South American forests.

With stem-based measures of diversity, again no biomass-diversity relationship is significant in Africa or South America (Figure 4.2), although species richness per 300 stems in South America comes close to having a significant positive relationship with AGB ($\tau = 0.16$, $p = 0.082$). Again, if data from the two continents are treated together, a negative correlation between AGB and family richness is present, reflecting the higher biomass and lower family richness of African forests compared to South American forests. Additionally, removing monodominant plots does not reveal any correlations when analysing the remaining African forests.

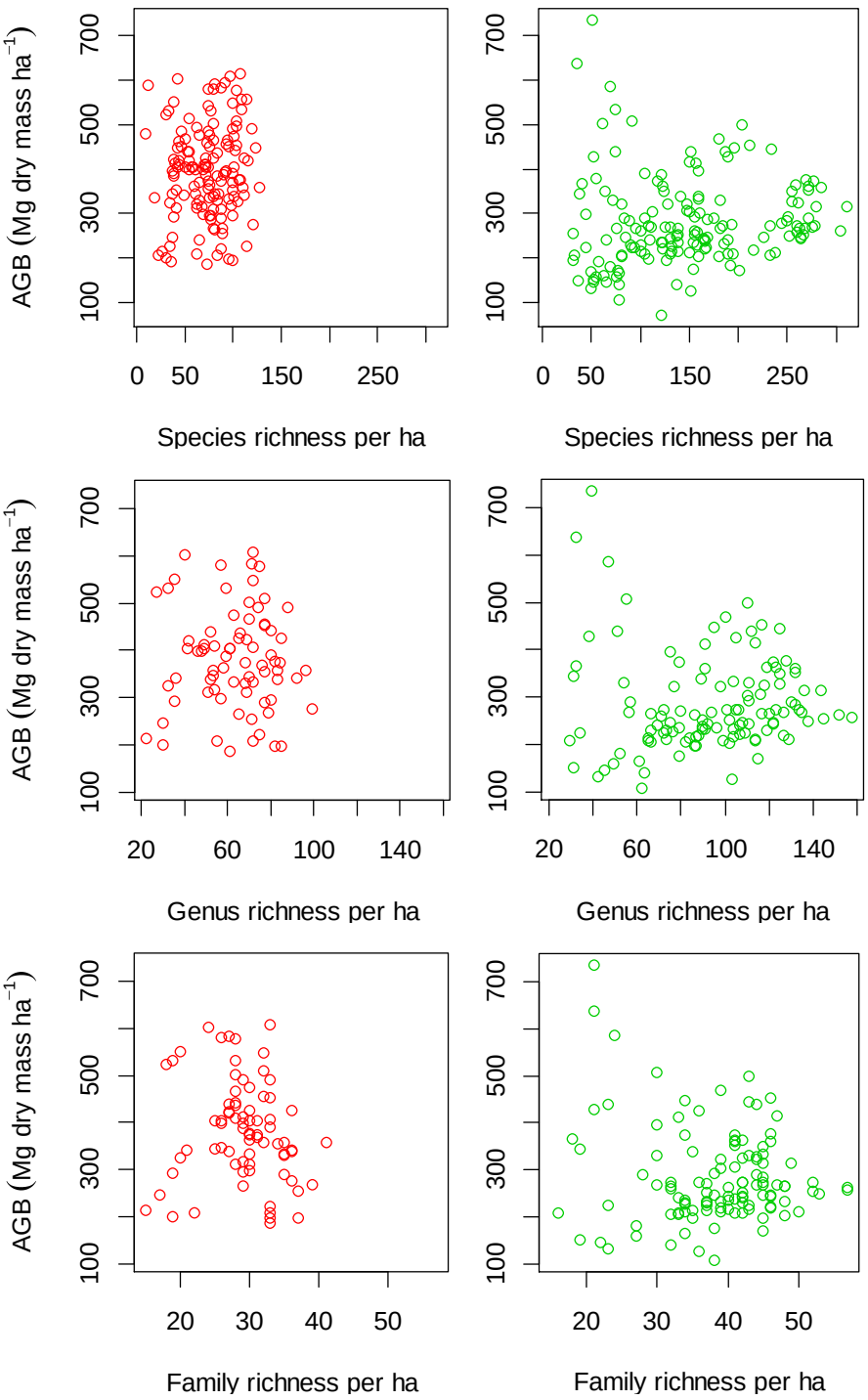


Figure 4.1: Associations between tropical forest aboveground biomass and area-based diversity metrics. Red circles represent African forest plots, green circles South American plots (top: tree species richness, middle: genus richness, bottom: family richness).

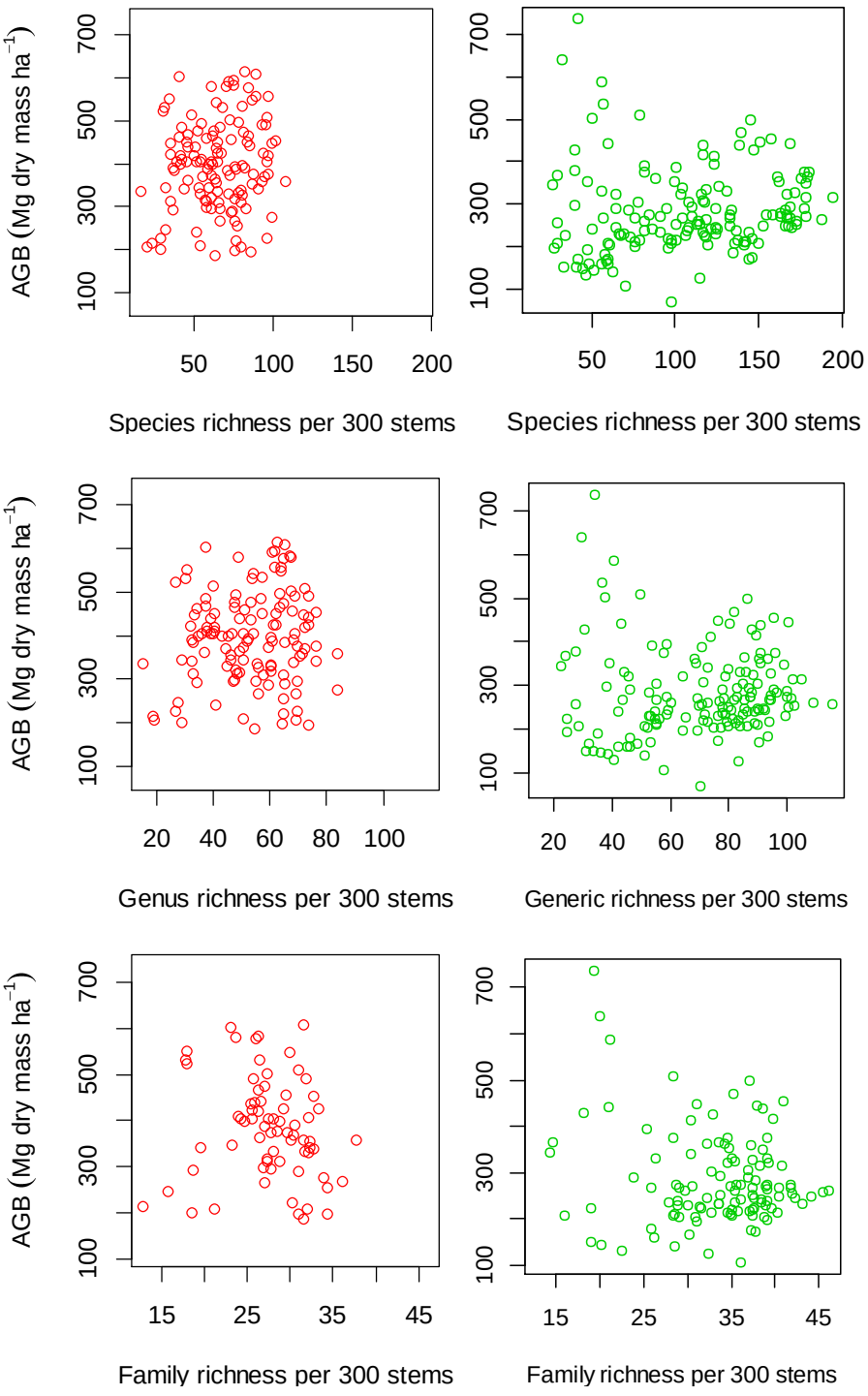


Figure 4.2: Associations between tropical forest aboveground biomass and stem-based diversity metrics, for plots with ≥300 stems. Red circles represent African forest plots, green circles South American plots (top: tree species richness, middle: genus richness, bottom: family richness).

4.4.3 Question 2: Is tropical forest productivity related to tropical forest tree diversity?

There are no significant correlations ($p < 0.05$) between AGWP and tree diversity in Africa or South America (Figure 4.3). The same is true if we consider only South American plots with <150 species, to match with the African diversity levels, or combine data from the two continents, or when African monodominant plots are excluded. There is also no significant quadratic (unimodal) relationship between species richness and AGWP. Using diversity metrics that control for stem density (Figure 4.4), again there are no significant correlations in Africa or South America between AGWP and measures of diversity. This remains the case when monodominant forests in Africa are excluded.

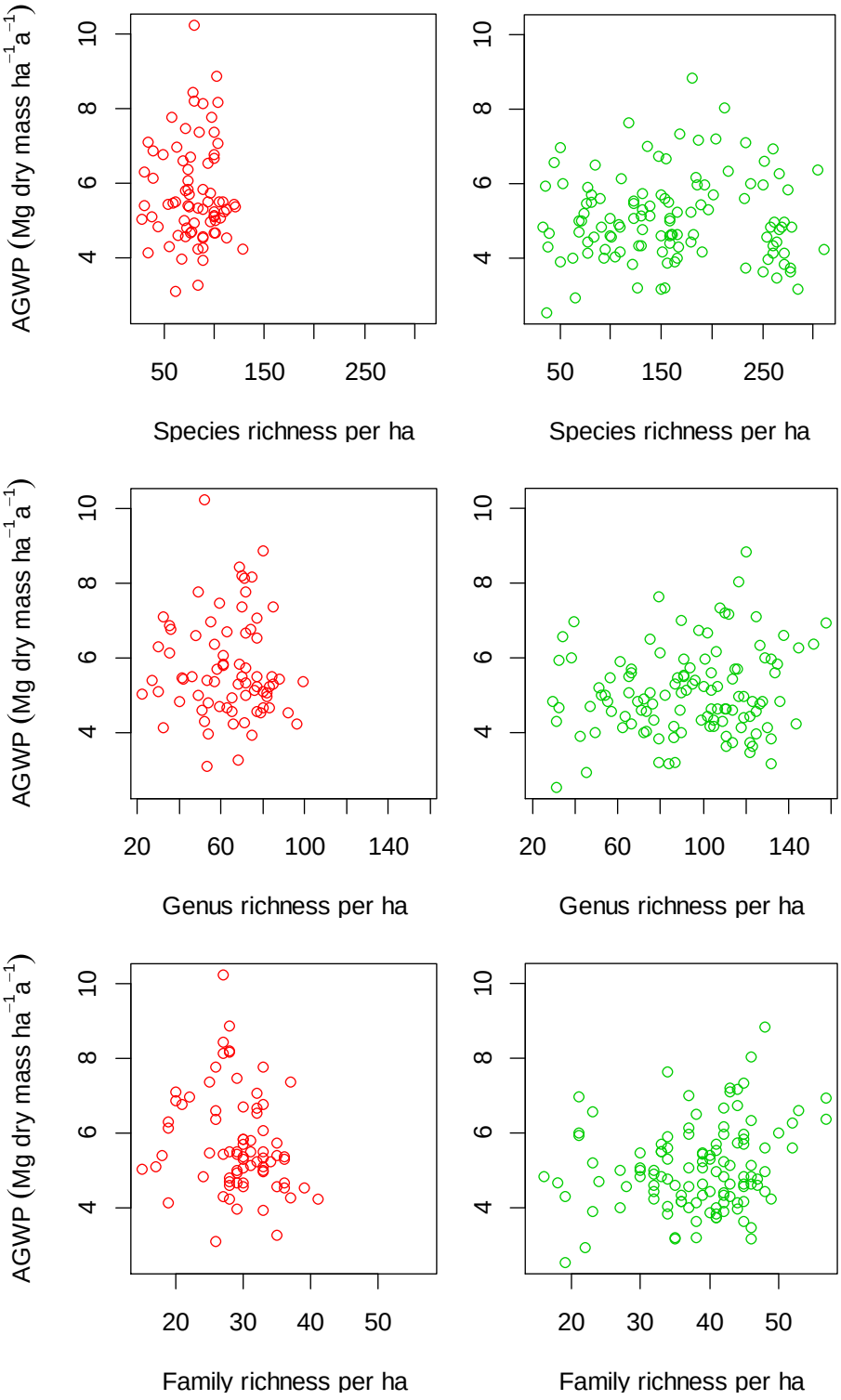


Figure 4.3: Association between tropical forest aboveground coarse woody productivity and area-based diversity metrics. Red circles represent African forest plots, green circles South American plots (top: tree species richness, middle: genus richness, bottom: family richness).

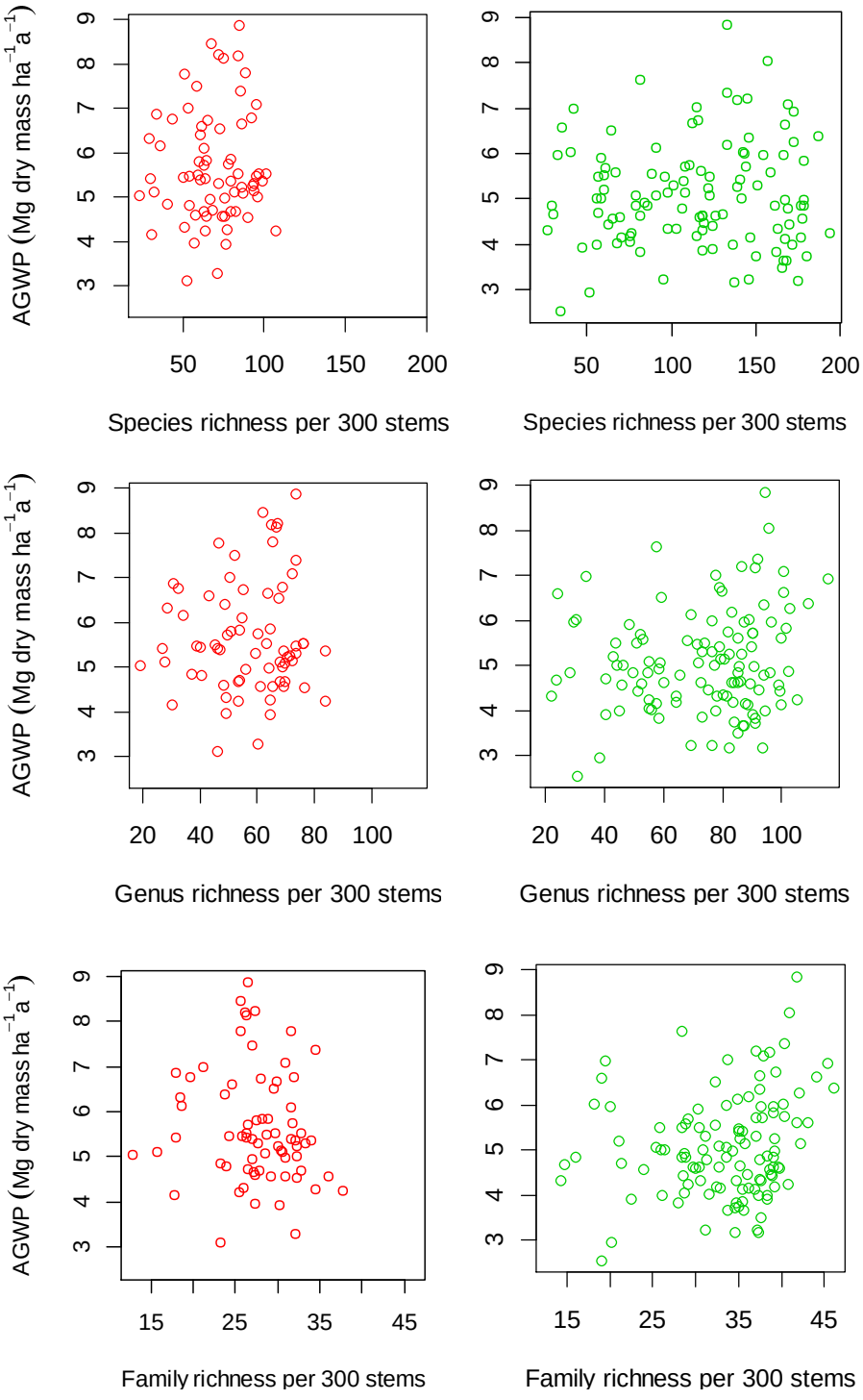


Figure 4.4: Associations between tropical forest aboveground coarse woody productivity and stem-based diversity metrics, for tropical forest plots with ≥300 stems. Red circles represent African forest plots, green circles South American plots (top: tree species richness, middle: genus richness, bottom: family richness).

4.4.4 Correlations of other predictor variables with productivity and biomass

In Africa, no environmental variables have significant correlations ($p < 0.05$) with aboveground biomass, and this remains the case when fifteen monodominant forest plots are excluded. In South America, mean annual temperature ($\tau = 0.29$, $p < 0.001$) and mean annual precipitation ($\tau = 0.23$, $p < 0.001$) are positively correlated with AGB, and precipitation seasonality is negatively correlated with AGB ($\tau = -0.21$, $p = 0.001$) using Kendall's τ (Figure 4.5).

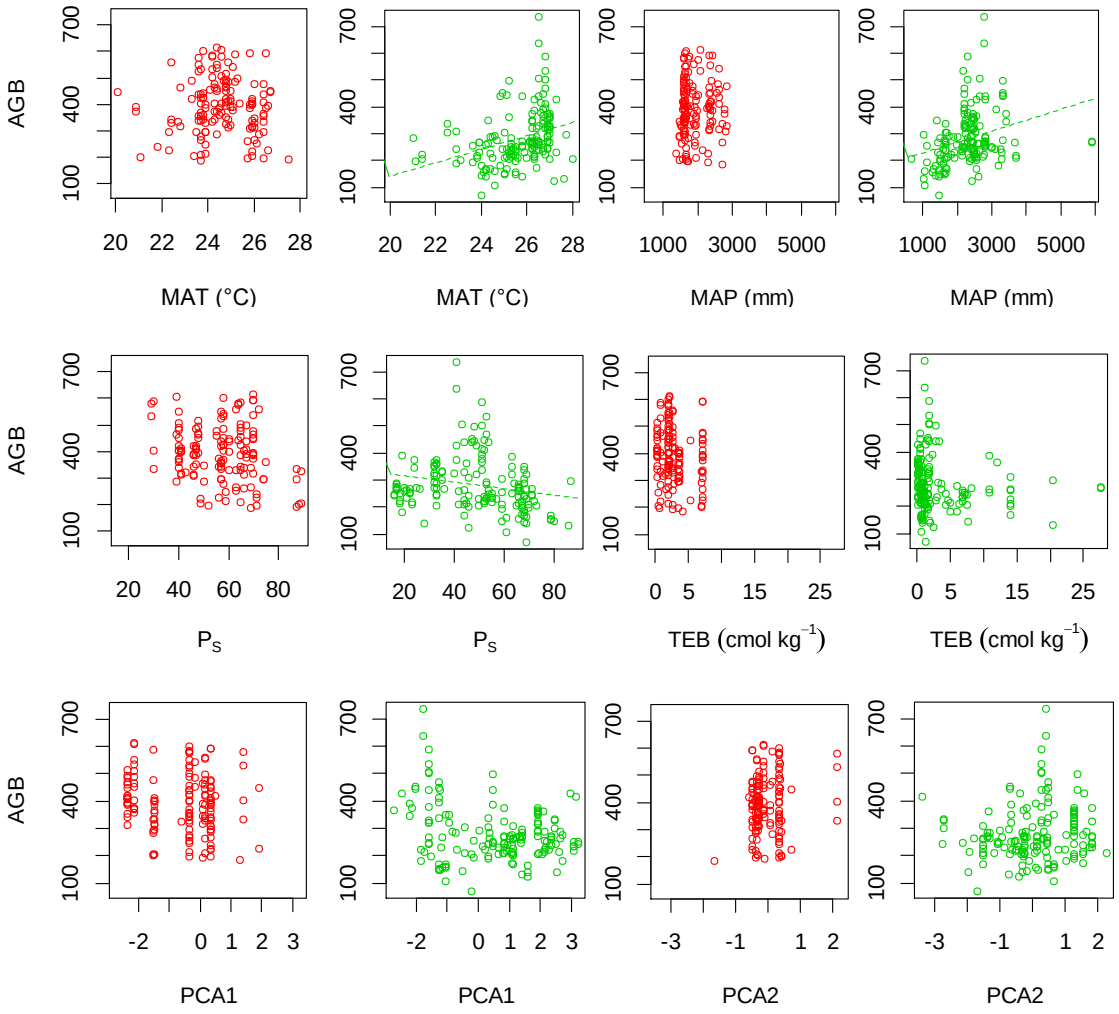


Figure 4.5: Tropical forest tropical forest aboveground biomass (Mg dry mass ha^{-1}) as a function of climate and soils. Red circles represent African forest plots, green circles South American plots. Dashed lines are drawn when correlations using Kendall's τ are significant ($p < 0.05$) after correcting for multiple tests by controlling the false discovery rate. MAT is mean annual temperature, MAP is mean annual precipitation, P_S is seasonality of precipitation, TEB is total extractable bases, PCA1 is the first principal component of soil texture, PCA2 is the second principal component of soil texture.

In Africa, the only environmental variable to be significantly correlated with productivity is mean annual temperature ($\tau = -0.17$, $p = 0.040$). This remains the case when monodominant

forest plots are excluded. In South America, AGWP has a strong positive correlation with mean annual precipitation ($\tau = 0.33$, $p < 0.001$) and weaker negative correlations with mean annual temperature ($\tau = -0.21$, $p = 0.002$) and *PCA2* ($\tau = -0.21$, $p = 0.014$; Figure 4.6). Other variables do not show any significant correlations with AGWP.

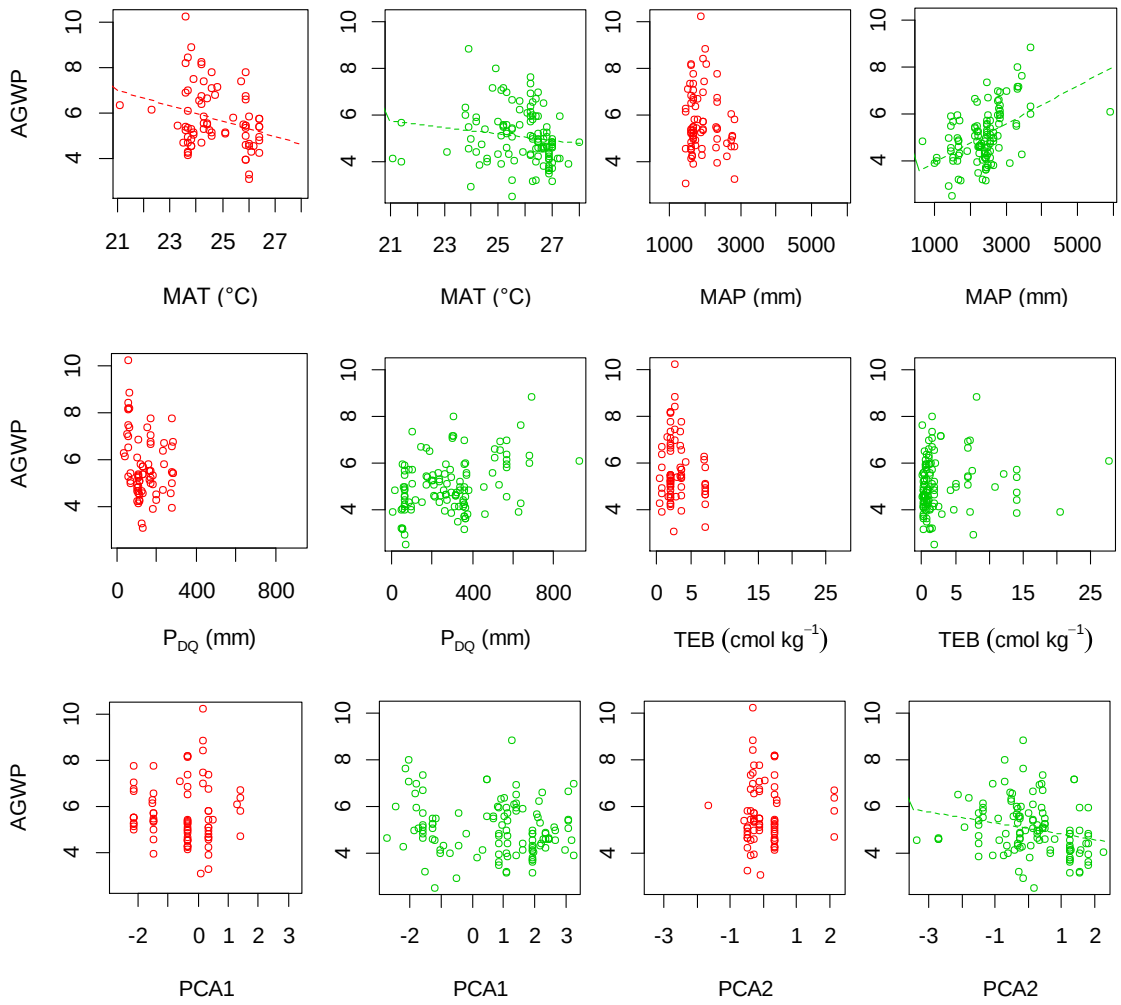


Figure 4.6: Tropical forest aboveground wood production (Mg dry mass ha^{-1} a^{-1}) as a function of climate and soils. Red circles represent African forest plots, green circles South American plots. Dashed lines are drawn when correlations using Kendall's τ are significant ($p < 0.05$) after correcting for multiple tests by controlling the false discovery rate. MAT is mean annual temperature, MAP is mean annual precipitation, P_{DQ} is precipitation in the driest quarter, TEB is total extractable bases, PCA1 is the first principal component of soil texture, PCA2 is the second principal component of soil texture.

4.4.5 Relationships between productivity, biomass and turnover

Productivity and biomass are significantly correlated in both Africa ($\tau = 0.16$, $p = 0.049$) and South America ($\tau = 0.15$, $p = 0.031$) using Kendall's τ (Figure 4.7). In Africa, no significant correlations ($p < 0.05$) involving the turnover of aboveground biomass are found, but in South

America turnover is significantly correlated with species richness per hectare ($\tau = 0.19$, $p = 0.015$), family richness per hectare ($\tau = 0.29$, $p < 0.001$), and AGWP ($\tau = 0.20$, $p = 0.015$), of which the strongest correlation is with family richness per hectare (Figure 4.8).

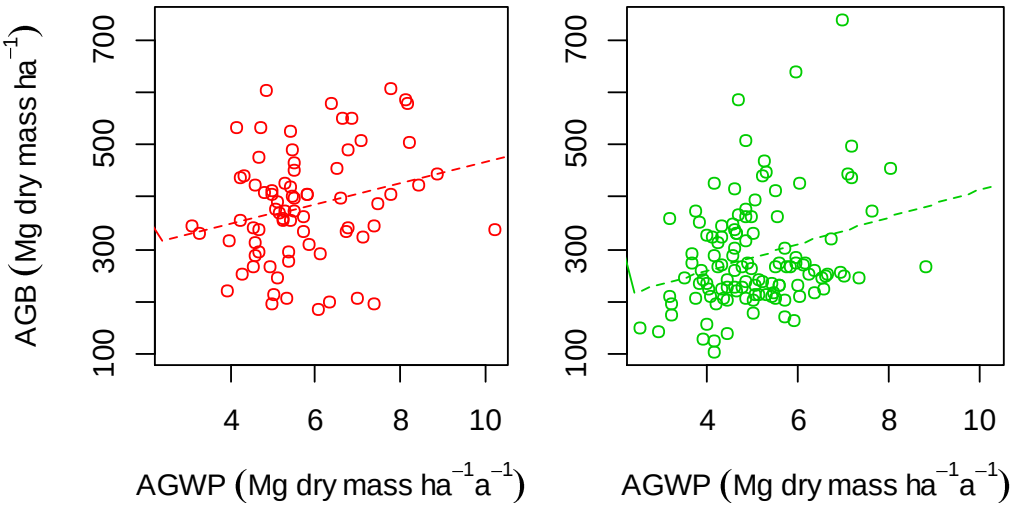


Figure 4.7: Relationship between aboveground coarse wood production and aboveground biomass in tropical forests. Red circles represent African forest plots, green circles South American plots. Dashed lines are drawn when correlations using Kendall's τ are significant ($p < 0.05$) after correcting for multiple tests by controlling the false discovery rate.

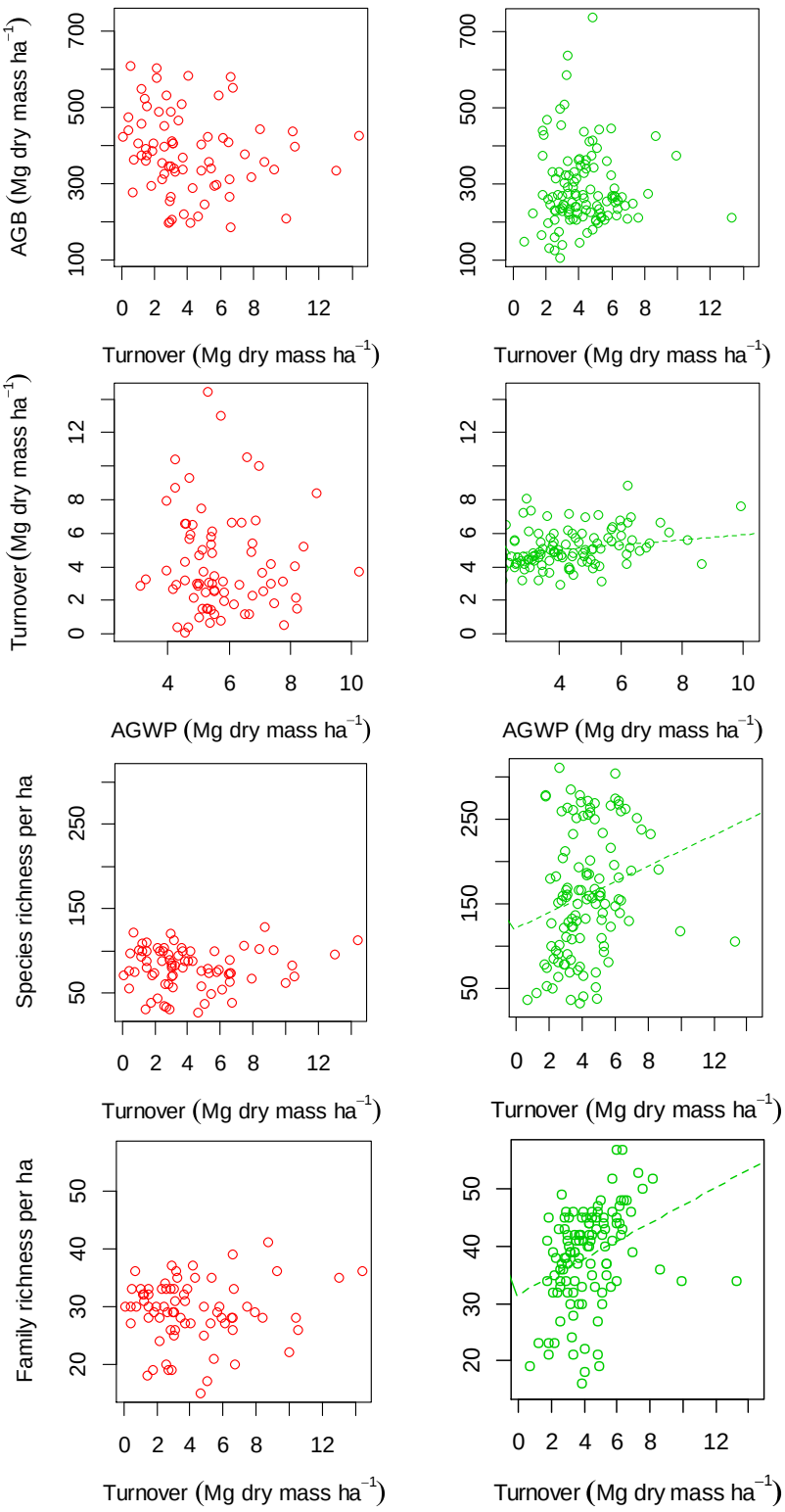


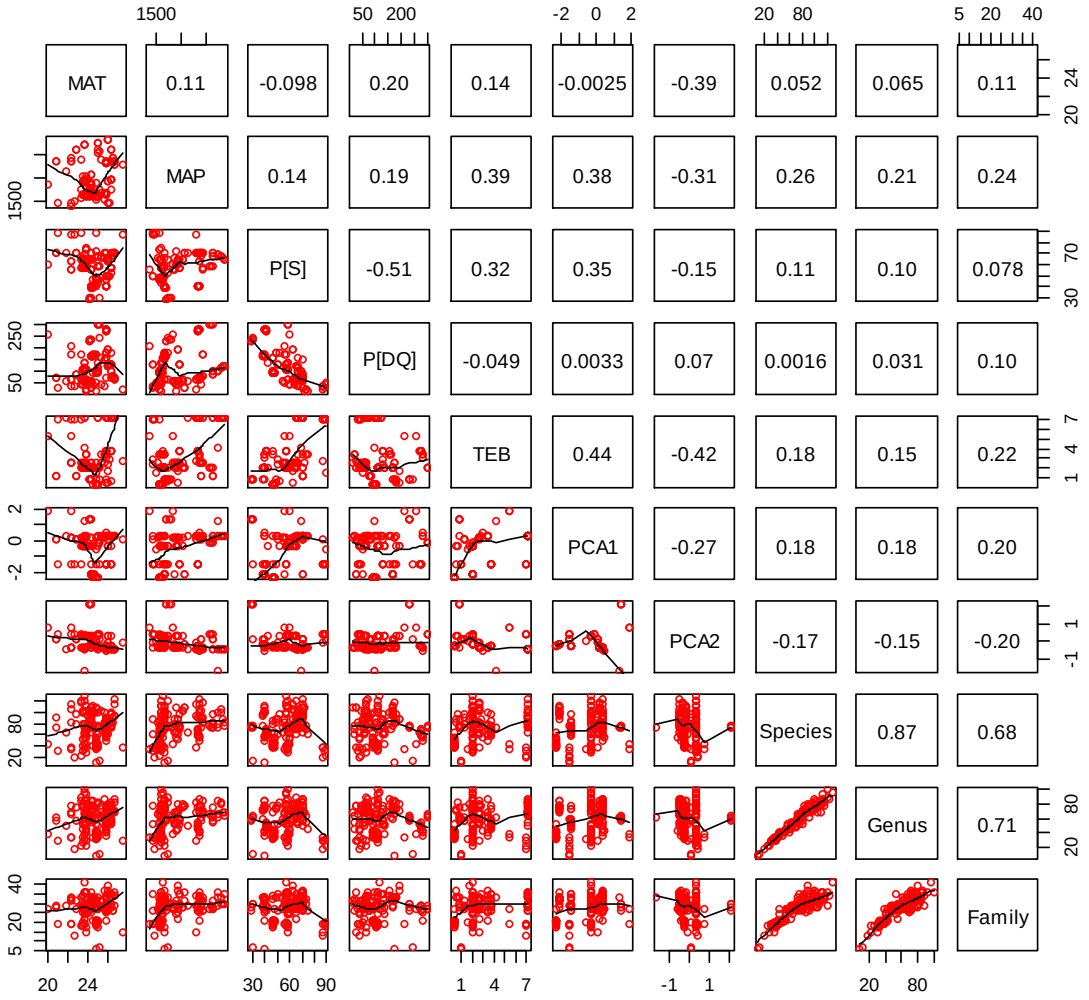
Figure 4.8: Correlations of turnover with AGB, AGWP and richness. Red circles represent African forest plots, green circles South American plots. Dashed lines are drawn when correlations using Kendall's τ are significant ($p < 0.05$) after correcting for multiple tests by controlling the false discovery rate.

4.4.6 Collinearity among predictor variables

Varying degrees of collinearity exist among the variables used in the diversity–function models. Correlations using Kendall's τ are shown in Figure 4.9. Within both continents, the strongest correlations are those among the diversity metrics and among measures of precipitation seasonality. In both continents, species and genus richness are slightly more closely correlated than are genus and family richness. Family richness begins to diverge from species richness at higher levels of diversity.

Relatively strong correlations also exist between other environmental variables, but the richness measures lack strong correlations with any environmental variables. In Africa, *MAP* is positively correlated with *TEB* and *PCA1*, while *TEB* has a positive correlation with *PCA1* and a negative correlation with *PCA2*. In South America, the strongest relationship between any two variables that occur within the same model combination is a positive correlation between *MAP* and P_{DQ} ($\tau = 0.69$). The richness measures have somewhat stronger correlations with environmental variables in South America than they do in Africa, including positive correlations with *MAP*, P_{DQ}, and *PCA1* and a negative correlation with P_S.

(a)


MAT
MAP
P[S]
P[DQ]
TEB
PCA1
PCA2
Species
Genus
Family
0.11
-0.098
0.20
0.14
-0.0025
-0.39
0.052
0.065
0.11
0.14
0.19
0.39
0.38
-0.31
0.26
0.21
0.24
-0.51
0.32
0.35
-0.15
0.11
0.10
0.078
-0.049
0.0033
0.07
0.0016
0.031
0.10
0.44
-0.42
0.18
0.15
0.22
0.18
0.18
0.20
-0.17
-0.15
-0.20
0.87
0.68
0.71

(b)

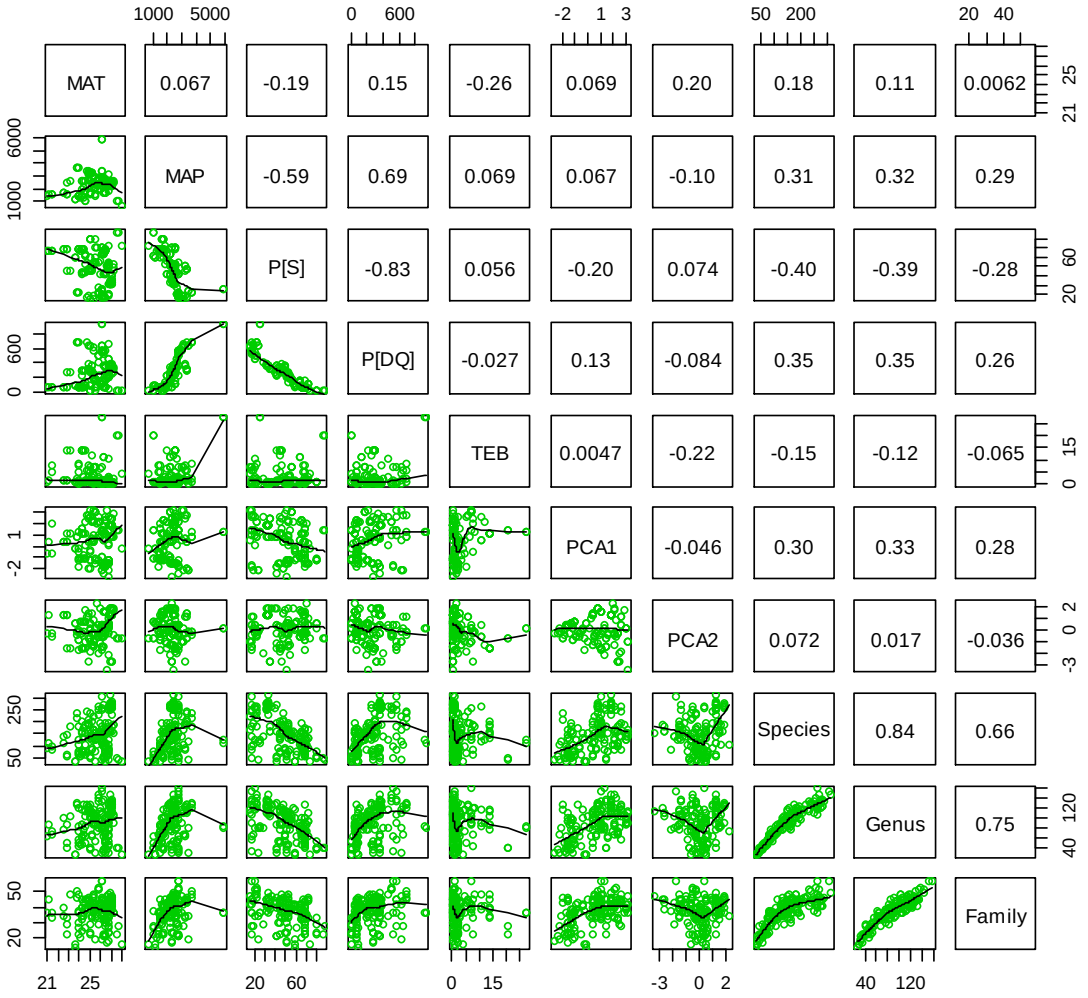


Figure 4.9: Correlations amongst candidate model parameters in (a) African, and (b) South American plots. The upper panels show Kendall's τ. Lowess smoothers are used in the lower panels to illustrate apparent trends; no statistical significance is implied. MAT is mean annual temperature; MAP is mean annual precipitation; P[S] is seasonality of precipitation; P[DQ] is precipitation in the driest quarter; TEB is total extractable bases; PCA1 is the first soil principal component (sand content); PCA2 is the second soil principal component (silt-clay axis); species is species richness per hectare, genus is genus richness per hectare; family is family richness per hectare.

4.4.7 Question 3: Do environmental variables mediate relationships between tropical forest biomass and tree diversity?

Testing continents separately, linear models that include environmental variables show little evidence of associations between biomass and tree diversity (Table 4.7 and Table 4.9). In none of the model combinations is any diversity metric present in the lowest AICc model. In both Africa and South America, some of the diversity metrics are present in OLS models within 2 AICc units of the lowest AICc model, but these diversity metrics are never present in the majority of these low AICc models. Moreover, where diversity metrics are present, both positive and negative diversity–AGB relationships exist, and the mean *p*-values for these diversity parameters are always >0.1. Since I use an information-theoretic approach to model selection, non-significant *p*-values may legitimately occur in low AICc models, but the combination of non-significant *p*-values and a mixture of positive and negative effects gives no support for the existence of tree diversity–AGB relationships in the world's most extensive tropical forests.

When plots from the two continents are treated together, relationships between tree diversity and AGB are inconsistent (Table 4.10 and Table 4.11). Most of the diversity metrics are negatively related to AGB in the lowest AICc OLS models, but diversity is rarely found in the lowest AICc SEVM models, and when diversity metrics occur in models with Δ AICc <2, both positive and negative effects exist.

In Africa, *PCA1, PCA2,* and *MAP* appear to be the most important environmental variables, present in all the lowest AICc models (Table 4.6). Aboveground biomass has positive correlations with *PCA2* and *MAP*, suggesting biomass is greater when mean annual precipitation is greater and when soils are clay-rich and low in silt, and a negative correlation with *PCA1*, suggesting that biomass increases with soil sand content. Other environmental variables found in some of the lowest AICc models include *TEB*, which is negatively correlated with log(AGB) in the set of plots used with stem-based diversity metrics, and P_S, which is negatively correlated with log(AGB) in the set of plots used with area-based diversity metrics. A spatial filter is present only in the area-based SEVM models. In most models, *MAP* has the greatest standardised (β) coefficients, so that an increase in *MAP* corresponding to one standard deviation is associated with a greater increase in biomass than a change of equivalent magnitude in any other environmental variable. In the area-based SEVM models the spatial filter has a greatest β values, suggesting spatial proximity has a greater effect on biomass than

any single environmental variable. The adjusted R^2 values for the African models are low (Table 4.7).

In South America, *TEB*, *MAT,* and *MAP* are present in the lowest AICc models for all model combinations (Table 4.8). Aboveground biomass is positively correlated with *MAT* and *MAP* and negatively correlated with *TEB*, suggesting biomass is higher in soils with lower cation availability. In addition, *PCA1* appears in the OLS models but not in the SEVM models. There are three spatial filters present in the SEVM models, and one of these has the greatest β values of any parameter in these models. In the OLS models, *MAP* has the greatest β values. This shows that an increase in *MAP* corresponding to one standard deviation is associated with a greater increase in biomass than a change of equivalent magnitude in any other environmental variable.

Table 4.6: Results of OLS and SEVM models for African plots with log(AGB) as the response variable. The parameters given are from the lowest AICc models, among a total of 127 models. The SEVM models are run using only the variables found in the lowest AICc OLS model, and are only shown when at least one spatial filter is selected as being correlated with the OLS model residuals. The standardised coefficients are given as β, except for the intercept, for which the non-standardised version is given. Predictor variables not found in the OLS model with lowest AICc are denoted as '-'. Analyses are performed using (a) species richness per ha (to provide an example of an area-based diversity metric where diversity is not present in the lowest AICc model), and (b) species richness per 300 stems (to provide an example of a stem-based diversity metric where diversity is not present in the lowest AICc model). None of the other diversity metrics are present in the lowest AICc models, so they are not shown (they would identical to the ones presented). *TEB* is total extractable bases; *PCA1* is the first principal component of soil texture; PCA2 is the second principal component of soil texture; *MAT* is mean annual temperature; *MAP* is mean annual precipitation; P_S is precipitation seasonality.

(a)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.779	0	5.851	0
TEB	-	-	-	-
PCA1	-0.241	0.023	-0.162	0.091
PCA2	0.221	0.028	0.208	0.022
MAT	-	-	-	-
MAP	0.256	0.012	0.277	0.003
P_S	-0.184	0.046	-0.256	0.003
^{0}D (species richness per ha)	-	-	-	-
Filter 1	NA	NA	-0.421	<.001

(b)

	OLS - by stem density	
	β	*p*
Intercept	5.548	<.001
TEB	-0.168	0.124
PCA1	-0.237	0.031
PCA2	0.226	0.035
MAT	-	-
MAP	0.314	0.006
P_S	-	-
^{0}D (species richness per 300 stems)	-	-

Table 4.7: Mean standardised coefficients and their significance, for a set of diversity metrics in OLS models for African plots with log(AGB) as the response variable. Among a total of 127 models, the number of these with Δ AICc < 2 is shown, as well as the number of these low AICc models in which each diversity metric is present. The mean standardised coefficients (β) and p-values for each diversity metric are calculated using only those low AICc models in which the metric is present. Analyses are performed using both (a) area-based (per ha) and (b) stem-based (per 300 stems) diversity metrics. SEVM models are not shown because the diversity variables were never present in the lowest AICc OLS models. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

Area-based diversity metric	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	7	3	0.122	0.160	0.101
^{0}D (genus level)	5	1	0.074	0.386	0.101
^{0}D (family level)	4	0	-	-	0.101
^{1}D (species level)	5	1	0.068	0.417	0.101
^{1}D (genus level)	4	0	-	-	0.101
^{1}D (family level)	7	3	-0.125	0.157	0.101
^{2}D (species level)	5	1	0.081	0.333	0.101
^{2}D (genus level)	4	0	-	-	0.101
^{2}D (family level)	5	1	-0.086	0.320	0.101
Fisher's α	6	2	0.110	0.190	0.101

(b)

Stem-based diversity metric	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	7	3	0.124	0.165	0.079
^{0}D (genus level)	6	2	0.094	0.291	0.079
^{0}D (family level)	4	0	-	-	0.079
Fisher's α	7	3	0.110	0.213	0.079

Table 4.8: Results of OLS and SEVM models for South American plots with log(AGB) as the response variable. The parameters given are from the lowest AICc models, among a total of 127 models. The SEVM models are run using only the variables found in the lowest AICc OLS model, and spatial filters are only selected when they are correlated with the OLS model residuals. The standardised coefficients are given as β, except for the intercept, for which the non-standardised version is given. Predictor variables not found in the OLS model with lowest AICc are denoted as '-'.Analyses are performed using (a) species richness per ha (to provide an example of an area-based diversity metric where diversity is not present in the lowest AICc model), and (b) species richness per 300 stems (to provide an example of a stem -based diversity metric where diversity is not present in the lowest AICc model). None of the other diversity metrics are present in the lowest AICc models, so they are not shown. *TEB* is total extractable bases; *PCA1* is the first principal component of soil texture; PCA2 is the second principal component of soil texture; *MAT* is mean annual temperature; *MAP* is mean annual precipitation; P_S is precipitation seasonality.

(a)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	3.452	<.001	3.713	0
TEB	-0.153	0.047	-0.124	0.047
PCA1	-0.221	0.002	-	-
PCA2	-	-	-	-
MAT	0.272	<.001	0.235	<.001
MAP	0.360	<.001	0.315	<.001
P_S	-	-	-	-
^{0}D (species richness per ha)	-	-	-	-
Filter 4	NA	NA	0.386	<.001
Filter 5	NA	NA	0.232	<.001
Filter 7	NA	NA	-0.314	<.001

(b)

	OLS - by stem density		*SEVM - by stem density*	
	β	*p*	β	*p*
Intercept	3.411	<.001	3.774	<.001
TEB	-0.118	0.111	-0.118	0.048
PCA1	-0.213	0.003	-	-
PCA2	-	-	-	-
MAT	0.275	<.001	0.223	<.001
MAP	0.367	<.001	0.327	<.001
P_S	-	-	-	-
^{0}D (species richness per 300 stems)	-	-	-	-
Filter 4	NA	NA	0.381	<.001
Filter 5	NA	NA	0.234	<.001
Filter 7	NA	NA	-0.292	<.001

Table 4.9: Mean standardised coefficients and their significance, for a set of diversity metrics in OLS models for South American plots with log(AGB) as the response variable. Among a total of 127 models, the number of these with Δ AICc < 2 is shown, as well as the number of these low AICc models in which each diversity metric is present. The mean standardised coefficients (β) and p-values for each diversity metric are calculated using only those low AICc models in which the metric is present. Analyses are performed using both (a) area-based (per ha) and (b) stem-based (per 300 stems) diversity metrics. SEVM models are not shown because the diversity variables were never present in the lowest AICc OLS models. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

Area-based diversity metric	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	6	2	0.127	0.168	0.261
^{0}D (genus level)	5	1	0.074	0.428	0.261
^{0}D (family level)	4	0	-	-	0.261
^{1}D (species level)	6	2	0.103	0.246	0.261
^{1}D (genus level)	4	0	-	-	0.261
^{1}D (family level)	5	1	-0.105	0.197	0.261
^{2}D (species level)	5	1	0.070	0.401	0.261
^{2}D (genus level)	4	0	-	-	0.261
^{2}D (family level)	5	1	-0.071	0.366	0.261
Fisher's α	5	1	0.066	0.460	0.261

(b)

Stem-based diversity metric	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	6	2	0.092	0.313	0.273
^{0}D (genus level)	4	0	-	-	0.273
^{0}D (family level)	5	1	-0.075	0.380	0.273
Fisher's α	6	2	0.095	0.280	0.273

Table 4.10: Results of OLS and SEVM models for both Africa and South America combined, with log(AGB) as the response variable. The parameters given are from the lowest AICc models, among a total of 127 models. The SEVM models are run using only the variables found in the lowest AICc OLS model, and are only shown when at least one spatial filter is selected as being correlated with the OLS model residuals. The standardised coefficients are given as β, except for the intercept, for which the non-standardised version is given. Predictor variables not found in the OLS model with lowest AICc are denoted as '-'. Analyses are performed using both area-based (per ha) and stem-based (per 300 stems) diversity metrics. The diversity metrics used are as follows: (a) species richness per ha; (b) genus richness per ha; (c) family richness per ha; (d) ^{1}D per ha (at species level); (e) ^{1}D per ha (at genus level); (f) ^{1}D per ha (at family level); (g) ^{2}D per ha (at species level); (h) ^{2}D per ha (at genus level); (i) ^{2}D per ha (at family level); (j) Fisher's α per ha; (k) species richness per 300 stems; (l) genus richness per 300 stems; (m) family richness per 300 stems; and (n) Fisher's α per 300 stems. *TEB* is total extractable bases; *PCA1* is the first principal component of soil texture; PCA2 is the second principal component of soil texture; *MAT* is mean annual temperature; *MAP* is mean annual precipitation; P_S is precipitation seasonality; ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.807	0	5.620	0
TEB	-0.095	0.146	-0.112	0.042
PCA1	-0.295	<.001	-0.195	<.001
PCA2	0.088	0.123	0.098	0.045
MAT	-	-	-	-
MAP	0.192	0.008	0.258	<.001
P_S	-0.136	0.046	-0.136	0.017
^{0}D (species richness per ha)	-0.175	0.022	-	-
Filter 1	NA	NA	0.535	<.001

(b)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.806	0	5.627	<.001
TEB	-0.110	0.082	-0.142	0.009
PCA1	-0.302	<.001	-0.189	<.001
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.184	0.012	0.256	<.001
P_S	-0.110	0.099	-0.131	0.022
^{0}D (genus richness per ha)	-0.136	0.065	-	-
Filter 1	NA	NA	0.529	<.001

(c)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.975	<.001	5.627	<.001
TEB	-0.120	0.050	-0.142	0.009
PCA1	-0.250	<.001	-0.189	<.001
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.222	0.002	0.256	<.001
P_S	-0.110	0.088	-0.131	0.022
^{0}D (family richness per ha)	-0.255	<.001	-	-
Filter 1	NA	NA	0.529	<.001

(d)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.862	0	5.691	<.001
TEB	-	-	-	-
PCA1	-0.336	<.001	-0.219	<.001
PCA2	0.106	0.059	0.124	0.009
MAT	-	-	-	-
MAP	0.136	0.037	0.209	<.001
P_S	-0.156	0.021	-0.171	0.002
^{1}D (species level, per ha)	-0.129	0.071	-	-
Filter 1	NA	NA	0.526	<.001

Table 4.10 (continued)

(e)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.793	0	5.627	<.001
TEB	-0.099	0.111	-0.142	0.009
PCA1	-0.312	<.001	-0.189	<.001
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.178	0.013	0.256	<.001
P_S	-0.112	0.091	-0.131	0.022
^{1}D (genus level, per ha)	-0.143	0.031	-	-
Filter 1	NA	NA	0.529	<.001

(f)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.916	0	5.756	0
TEB	-0.088	0.144	-0.140	0.008
PCA1	-0.285	<.001	-0.152	0.005
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.197	0.005	0.279	<.001
P_S	-0.105	0.100	-0.139	0.014
^{1}D (family level, per ha)	-0.251	<.001	-0.144	0.008
Filter 1	NA	NA	0.499	<.001

(g)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.732	0	5.691	0
TEB	-	-	-	-
PCA1	-0.384	<.001	-0.219	<.001
PCA2	0.084	0.126	0.124	0.009
MAT	-	-	-	-
MAP	0.118	0.068	0.209	<.001
P_S	-0.110	0.078	-0.171	0.002
^{2}D (species level, per ha)	-	-	-	-
Filter 1	NA	NA	0.526	<.001

(h)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.834	<.001	5.724	0
TEB	-	-	-	-
PCA1	-0.384	<.001	-0.218	<.001
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.125	0.054	0.187	<.001
P_S	-0.135	0.033	-0.177	0.001
^{2}D (genus level, per ha)	-0.117	0.057	-	-
Filter 1	NA	NA	0.514	<.001

(i)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.936	0	5.838	0
TEB	-	-	-	-
PCA1	-0.328	<.001	-0.192	<.001
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.136	0.033	0.203	<.001
P_S	-0.136	0.028	-0.187	<.001
^{2}D (family level, per ha)	-0.207	<.001	-0.128	0.013
Filter 1	NA	NA	0.493	<.001

(j)

	OLS - by area		*SEVM – by area*	
	β	*p*	β	*p*
Intercept	5.825	0	5.691	<.001
TEB	-	-	-	-
PCA1	-0.330	<.001	-0.219	<.001
PCA2	0.114	0.045	0.124	0.009
MAT	-	-	-	-
MAP	0.139	0.034	0.209	<.001
P_S	-0.162	0.017	-0.171	0.002
FA (per ha)	-0.142	0.053	-	-
Filter 1	NA	NA	0.526	<.001

Table 4.10 (continued)

(k)

	OLS - by stem density		*SEVM – by stem density*	
	β	*p*	β	*p*
Intercept	5.513	0	5.368	<.001
TEB	-0.095	0.103	-0.162	0.002
PCA1	-0.341	<.001	-0.167	0.002
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.203	<.001	0.327	<.001
P_S	-	-	-	-
^{0}D (species richness per 300 stems)	-	-	-	-
Filter 1	NA	NA	-0.529	0

(l)

	OLS - by stem density		*SEVM – by stem density*	
	β	*p*	β	*p*
Intercept	5.513	0	5.368	<.001
TEB	-0.095	0.103	-0.162	0.002
PCA1	-0.341	<.001	-0.167	0.002
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.203	<.001	0.327	<.001
P_S	-	-	-	-
^{0}D (genus richness per 300 stems)	-	-	-	-
Filter 1	NA	NA	-0.529	0

(m)

	OLS - by stem density		*SEVM – by stem density*	
	β	*p*	β	*p*
Intercept	5.768	<.001	5.368	<.001
TEB	-0.122	0.036	-0.162	0.002
PCA1	-0.247	<.001	-0.167	0.002
PCA2	-		-	-
MAT	-		-	-
MAP	0.270	<.001	0.327	<.001
P_S	-		-	-
^{0}D (family richness per 300 stems)	-0.217	0.001	-	-
Filter 1	NA	NA	-0.529	0

(n)

	OLS - by stem density		*SEVM – by stem density*	
	β	*p*	β	*p*
Intercept	5.513	0	5.368	<.001
TEB	-0.095	0.103	-0.162	0.002
PCA1	-0.341	<.001	-0.167	0.002
PCA2	-	-	-	-
MAT	-	-	-	-
MAP	0.203	<.001	0.327	<.001
P_S	-	-	-	-
FA (per 300 stems)	-	-	-	-
Filter 1	NA	NA	-0.529	0

Table 4.11: Mean standardised coefficients and their significance, for a set of diversity metrics in OLS and SEVM models for both Africa and South America combined, with log(AGB) as the response variable. Among a total of 127 models, the number of these with Δ AICc < 2 is shown, as well as the number of these low AICc models in which each diversity metric is present. The mean standardised coefficients (β) and p-values for each diversity metric are calculated using only those low AICc models in which the metric is present. Analyses are performed using (a) OLS models with area-based (per ha) diversity metrics; (b) OLS models with stem-based (per 300 stems) diversity metrics; (c) SEVM models with area-based (per ha) diversity metrics; and (d) SEVM models with stem-based (per 300 stems) diversity metrics. The SEVM models are run using only the variables found in the lowest AICc corresponding OLS model, and are only shown when at least one spatial filter is selected as being correlated with the OLS model residuals, and the appropriate diversity metric is present in the lowest AICc corresponding OLS model. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

Area-based diversity metric (OLS models)	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	6	6	-0.142	0.063	0.154
^{0}D (genus level)	15	7	-0.122	0.099	0.147
^{0}D (family level)	6	6	-0.245	<.001	0.177
^{1}D (species level)	9	5	-0.116	0.114	0.148
^{1}D (genus level)	7	7	-0.128	0.059	0.151
^{1}D (family level)	7	7	-0.246	<.001	0.187
^{2}D (species level)	16	5	-0.073	0.298	0.143
^{2}D (genus level)	14	10	-0.108	0.083	0.145
^{2}D (family level)	7	7	-0.201	0.001	0.171
Fisher's α	5	3	-0.146	0.050	0.150

(b)

Stem-based diversity metric (OLS models)	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	15	7	-0.108	0.151	0.129
^{0}D (genus level)	10	2	-0.063	0.374	0.129
^{0}D (family level)	6	6	-0.216	0.001	0.158
Fisher's α	15	7	-0.105	0.168	0.129

(c)

Area-based diversity metric (SEVM models)	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	5	3	0.100	0.159	0.368
^{0}D (genus level)	2	1	0.042	0.526	0.361
^{0}D (family level)	2	1	-0.056	0.381	0.361
^{1}D (species level)	2	1	0.074	0.260	0.361
^{1}D (genus level)	2	1	-0.032	0.583	0.361
^{1}D (family level)	1	1	-0.144	0.008	0.375
^{2}D (genus level)	2	1	-0.051	0.344	0.348
^{2}D (family level)	1	1	-0.128	0.013	0.360
Fisher's α	2	1	0.081	0.233	0.361

Table 4.11 (continued)

(d)

Stem-based diversity metric (SEVM models)	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (family level)	2	1	-0.076	0.209	0.356

The degree of spatial autocorrelation of aboveground biomass, as measured by Moran's *I* (Moran, 1950), is clearly greater in South America than in Africa (Figure 4.10). This is reflected by the fact that three spatial filters are retained as being significantly correlated with the OLS model residuals in the South American models, while only one is retained in the African area-based models, and none in the African stem-based models. Spatial autocorrelation of AGB appears weak and limited to distances <1000 km in African forests, while autocorrelation is much stronger and exists at up to ~1250 km in South American forests. There is also dissimilarity at distances of ~ 1500-3000 km in South American forests.

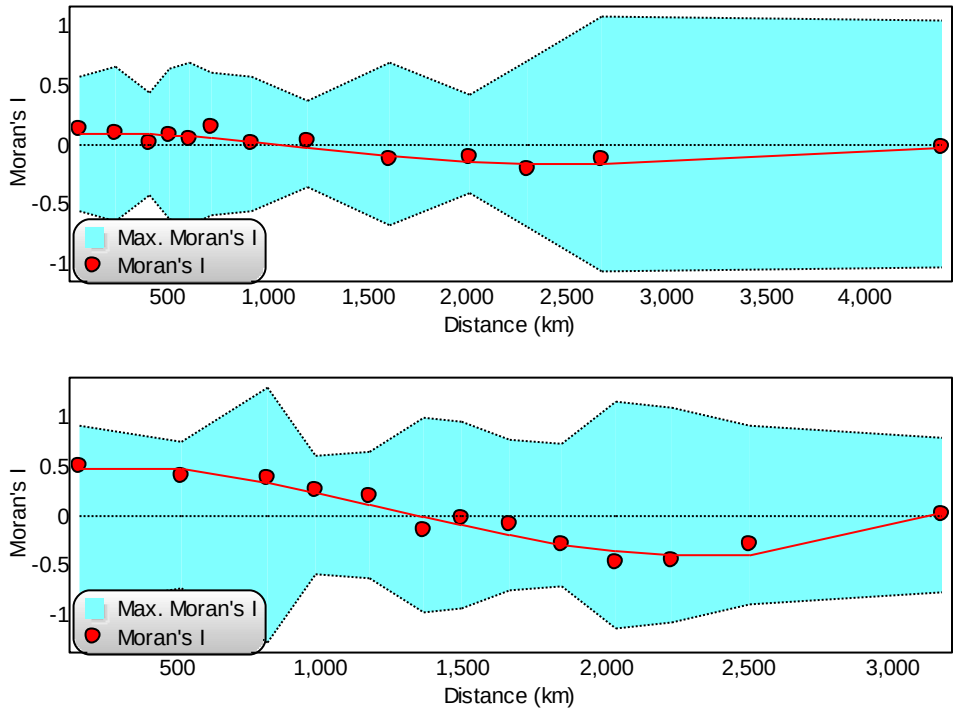


Figure 4.10: Spatial correlograms of Moran's *I* for log(AGB) in African (top) and South American (bottom) plots.

4.4.8 Question 4: Do environmental variables mediate relationships between tropical forest productivity and tree diversity?

There are major differences between linear models of AGWP in Africa and South America. In Africa, diversity metrics are absent from all of the lowest AICc models with log(AGWP) as the response variable. Some of the diversity metrics can be found in models with Δ AICc < 2, but only ever in a minority of these models (Table 4.13). Where diversity metrics are present, both positive and negative diversity–AGB relationships exist. The mean *p*-values for these diversity parameters are always >0.2, which suggests that the data provide little evidence for diversity–AGWP relationships in Africa.

In South America, for species level metrics, including *FA*, diversity is absent from all of the lowest AICc models. However, for the genus and family level metrics, diversity is present in all of the lowest AICc models (Table 4.14). These diversity metrics are present in many of the models with Δ AICc < 2, and mean *p*-values of these parameters across the low AICc models in which they are present range from 0.151 to 0.016 (Table 4.15). This suggests that associations between diversity and log(AGWP) do exist in South America. These associations are maintained across both the area- and stem-based models, and in both the OLS and SEVM models, with no consistent trend from ^{0}D to ^{2}D (Table 4.15). Using the β values in the area-based SEVM models, this indicates that an additional 10 families per 1-ha plot are associated with a 27% increase in AGWP, and an additional 30 genera per 1-ha plot are associated with a 21% increase in AGWP. Using the β values in the stem-based SEVM models, the effects are slightly stronger. An additional 10 families per 300 stems are associated with a 36% increase in AGWP, and an additional 30 genera per 300 stems are associated with a 30% increase in AGWP.

When plots from the two continents are treated together, tree diversity and productivity appear unrelated (.16 and Table 4.17). Diversity metrics are present in only a small proportion of the low AICc models, with some metrics showing positive associations with AGWP and others negative associations in these models. Only for genus level ^{1}D and ^{2}D are more consistent positive associations of diversity and AGWP found.

There are also large differences between Africa and South America in terms of the soil and climate parameters present in the lowest AICc models. In Africa, *MAT* is the only environmental variable found in the OLS and SEVM models with lowest AICc (Table 4.12). The negative correlation of *MAT* with log(AGWP) suggests that productivity is lower when

temperatures are higher. In the African SEVM models, no spatial filters are selected. The R^2 values for all the African models are extremely low (Table 4.13), suggesting that the great majority of the variation in AGWP between African forests is related to factors other than spatial autocorrelation, diversity, and the environmental variables tested here.

In South America *PCA1*, *PCA2* and *MAP* consistently occur as parameters in the OLS and SEVM models with the lowest AICc values (Table 4.14). Both *PCA1* and *PCA2* have negative correlations with log(AGWP). This suggests productivity is higher in forests with soils that are silt-rich and low in clay (this is the opposite of the effect of *PCA2* on AGB), and in forests with sandy soils. Mean annual precipitation is positively correlated with log(AGWP). In all models, *MAP* has the greatest β values, showing that an increase in mean annual precipitation corresponding to one standard deviation is associated with a greater increase in productivity than a change of equivalent magnitude in any other environmental variable or diversity measure. A single spatial filter is present in some but not all of the SEVM models.

Table 4.12: Results of OLS and SEVM models in African plots with log(AGWP) as the response variable. The parameters given are from the lowest AICc models, among a total of 127 models. The SEVM models are run using only the variables found in the lowest AICc OLS model, and are not shown because no spatial filters are selected as being correlated with the OLS model residuals. The standardised coefficients are given as β, except for the intercept, for which the non-standardised version is given. Predictor variables not found in the OLS model with lowest AICc are denoted as '-'. Analyses are performed using (a) species richness per ha (to provide an example of an area-based diversity metric where diversity is not present in the lowest AICc model), and (b) species richness per 300 stems (to provide an example of a stem -based diversity metric where diversity is not present in the lowest AICc model). None of the other diversity metrics are present in the lowest AICc models, so they are not shown. *TEB* is total extractable bases; *PCA1* is the first principal component of soil texture; PCA2 is the second principal component of soil texture; *MAT* is mean annual temperature; *MAP* is mean annual precipitation; P_S is precipitation seasonality.

(a)

	OLS - by area	
	β	*p*
Intercept	3.171	<.001
TEB	-	-
PCA1	-	-
PCA2	-	-
MAT	-0.294	0.011
MAP	-	-
P_{DQ}	-	-
^{0}D (species richness per ha)	-	-

(b)

	OLS - by stem density	
	β	*p*
Intercept	2.962	<.001
TEB	-	-
PCA1	-	-
PCA2	-	-
MAT	-0.270	0.023
MAP	-	-
P_{DQ}	-	-
^{0}D (species richness per 300 stems)	-	-

Table 4.13: Mean standardised coefficients and their significance, for a set of diversity metrics in OLS models for African plots with log(AGWP) as the response variable. Among a total of 127 models, the number of these with Δ AICc < 2 is shown, as well as the number of low AICc models in which each diversity metric is present. The mean standardised coefficients (β) and p-values for each diversity metric are calculated using only those low AICc models in which the metric is present. Analyses are performed using both (a) area-based (per ha) and (b) stem-based (per 300 stems) diversity metrics. SEVM models are not shown because the diversity variables were never present in the lowest AICc OLS models. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

Area-based diversity metric	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	5	0	-	-	0.086
^{0}D (genus level)	5	0	-	-	0.086
^{0}D (family level)	8	3	-0.155	0.218	0.086
^{1}D (species level)	6	1	0.112	0.320	0.086
^{1}D (genus level)	6	1	0.084	0.458	0.086
^{1}D (family level)	5	0	-	-	0.086
^{2}D (species level)	6	1	0.127	0.260	0.086
^{2}D (genus level)	6	1	0.098	0.390	0.086
^{2}D (family level)	5	0	-	-	0.086
Fisher's α	6	1	0.071	0.529	0.086

(b)

Stem-based diversity metric	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	5	1	0.065	0.577	0.073
^{0}D (genus level)	4	0	-	-	0.073
^{0}D (family level)	4	0	-	-	0.073
Fisher's α	4	0	-	-	0.073

Table 4.14: Results of OLS and SEVM models in South American plots with log(AGWP) as the response variable. The parameters given are from the lowest AICc models, among a total of 127 models. The SEVM models are run using only the variables found in the lowest AICc OLS model, and are only shown when at least one spatial filter is selected as being correlated with the OLS model residuals. The standardised coefficients are given as β, except for the intercept, for which the non-standardised version is given. Predictor variables not found in the OLS model with lowest AICc are denoted as '-'. Analyses are performed using both area-based (per ha) and stem-based (per 300 stems) diversity metrics. The diversity metrics used are as follows: (a) species richness per ha; (b) genus richness per ha; (c) family richness per ha; (d) ^{1}D per ha (at species level); (e) ^{1}D per ha (at genus level); (f) ^{1}D per ha (at family level); (g) ^{2}D per ha (at species level); (h) ^{2}D per ha (at genus level); (i) ^{2}D per ha (at family level); (j) Fisher's α per ha; (k) species richness per 300 stems; (l) genus richness per 300 stems; (m) family richness per 300 stems; and (n) Fisher's α per 300 stems. *TEB* is total extractable bases; *PCA1* is the first principal component of soil texture; PCA2 is the second principal component of soil texture; *MAT* is mean annual temperature; *MAP* is mean annual precipitation; P_S is precipitation seasonality. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

	OLS - by area		*SEVM - by area*	
	β	*p*	β	*p*
Intercept	1.267	0	1.467	<.001
TEB	-	-	-	-
PCA1	-0.151	0.061	-0.172	0.033
PCA2	-0.230	0.005	-0.179	0.034
MAT	-	-	-	-
MAP	0.443	<.001	0.497	<.001
P_{DQ}	-	-	-	-
^{0}D (species richness per ha)	-	-	-	-
Filter 1	NA	NA	-0.175	0.048

(b)

	OLS - by area		*SEVM - by area*	
	β	*p*	β	*p*
Intercept	1.21	<.001	1.441	<.001
TEB	-	-	-	-
PCA1	-0.224	0.017	-0.272	0.004
PCA2	-0.254	0.002	-0.200	0.018
MAT	-	-	-	-
MAP	0.395	<.001	0.444	<.001
P_{DQ}	-	-	-	-
^{0}D (genus richness per ha)	0.150	0.130	0.198	0.047
Filter 1	NA	NA	-0.210	0.018

(c)

	OLS - by area	
	β	*p*
Intercept	1.109	<.001
TEB	-	-
PCA1	-0.247	0.006
PCA2	-0.241	0.003
MAT	-	-
MAP	0.381	<.001
P_{DQ}	-	-
^{0}D (family richness per ha)	0.214	0.023

(d)

	OLS - by area		*SEVM - by area*	
	β	*p*	β	*p*
Intercept	1.267	0	1.467	<.001
TEB	-	-	-	-
PCA1	-0.151	0.061	-0.172	0.033
PCA2	-0.230	0.005	-0.179	0.034
MAT	-	-	-	-
MAP	0.443	<.001	0.497	<.001
P_{DQ}	-	-	-	-
^{1}D (species level, per ha)	-	-	-	-
Filter 1	NA	NA	-0.175	0.048

Table 4.14 (continued)

(e)

	OLS - by area		*SEVM - by area*	
	β	*p*	β	*p*
Intercept	1.218	0	1.166	0
TEB	-	-	-	-
PCA1	-0.227	0.011	-0.258	0.004
PCA2	-0.239	0.003	-0.183	0.027
MAT	-	-	-	-
MAP	0.392	<.001	0.445	<.001
P_{DQ}	-	-	-	-
^{1}D (genus level, per ha)	0.182	0.048	0.203	0.026
Filter 1	NA	NA	-0.195	0.026

(f)

	OLS - by area	
	β	*p*
Intercept	1.161	<.001
TEB	-	-
PCA1	-0.213	0.015
PCA2	-0.226	0.005
MAT	-	-
MAP	0.415	<.001
P_{DQ}	-	-
^{1}D (family level, per ha)	0.163	0.064

(g)

	OLS - by area		*SEVM - by area*	
	β	*p*	β	*p*
Intercept	1.267	0	1.467	<.001
TEB	-	-	-	-
PCA1	-0.151	0.061	-0.172	0.033
PCA2	-0.230	0.005	-0.179	0.034
MAT	-	-	-	-
MAP	0.443	<.001	0.497	<.001
P_{DQ}	-	-	-	-
^{2}D (species level, per ha)	-	-	-	-
Filter 1	NA	NA	-0.175	0.048

(h)

	OLS - by area	
	β	*p*
Intercept	1.214	<.001
TEB	-	-
PCA1	-0.213	0.012
PCA2	-0.214	0.008
MAT	-	-
MAP	0.398	<.001
P_{DQ}	-	-
^{2}D (genus level, per ha)	0.195	0.025

(i)

	OLS - by area		*SEVM - by area*	
	β	*p*	β	*p*
Intercept	1.19	<.001	1.146	0
TEB	-	-	-	-
PCA1	-0.193	0.024	-0.215	0.012
PCA2	-0.223	0.006	-0.170	0.043
MAT	-	-	-	-
MAP	0.427	<.001	0.481	<.001
P_{DQ}	-	-	-	-
^{2}D (family level, per ha)	0.128	0.136	0.131	0.121
Filter 1	NA	NA	-0.177	0.043

(j)

	OLS - by area		*SEVM - by area*	
	β	*p*	β	*p*
Intercept	1.267	0	1.467	<.001
TEB	-	-	-	-
PCA1	-0.151	0.061	-0.172	0.033
PCA2	-0.230	0.005	-0.179	0.034
MAT	-	-	-	-
MAP	0.443	<.001	0.497	<.001
P_{DQ}	-	-	-	-
FA (per ha)	-	-	-	-
Filter 1	NA	NA	-0.175	0.048

Table 4.14 (continued)

(k)

	OLS - by stem density		*SEVM - by stem density*	
	β	*p*	β	*p*
Intercept	1.267	<.001	1.226	<.001
TEB	-	-	-	-
PCA1	-0.151	0.061	-0.172	0.033
PCA2	-0.230	0.005	-0.179	0.034
MAT	-	-	-	-
MAP	0.443	<.001	0.497	<.001
P_{DQ}	-	-	-	-
^{0}D (species richness per 300 stems)	-	-	-	-
Filter 1	NA	NA	-0.175	0.048

(l)

	OLS - by stem density		*SEVM - by stem density*	
	β	*p*	β	*p*
Intercept	1.182	<.001	1.123	0
TEB	-	-	-	-
PCA1	-0.236	0.012	-0.272	0.004
PCA2	-0.260	0.002	-0.207	0.014
MAT	-	-	-	-
MAP	0.393	<.001	0.446	<.001
P_{DQ}	-	-	-	-
^{0}D (genus richness per 300 stems)	0.175	0.072	0.202	0.037
Filter 1	NA	NA	-0.197	0.025

(m)

	OLS - by stem density	
	β	*p*
Intercept	1.066	<.001
TEB	-	-
PCA1	-0.251	0.005
PCA2	-0.248	0.002
MAT	-	-
MAP	0.389	<.001
P_{DQ}	-	-
^{0}D (family richness per 300 stems)	0.229	0.012

(n)

	OLS – by stem density		*SEVM – by stem density*	
	β	*p*	β	*p*
Intercept	1.267	<.001	1.226	<.001
TEB	-	-	-	-
PCA1	-0.151	0.061	-0.172	0.033
PCA2	-0.230	0.005	-0.179	0.034
MAT	-	-	-	-
MAP	0.443	<.001	0.497	<.001
P_{DQ}	-	-	-	-
FA (per 300 stems)	-	-	-	-
Filter 1	NA	NA	-0.175	0.048

Table 4.15: Mean standardised coefficients and their significance, for a set of diversity metrics in OLS and SEVM models for South American plots with log(AGWP) as the response variable. Among a total of 127 OLS and 31 SEVM models, the number of these with Δ AICc < 2 is shown, as well as the number of low AICc models in which each diversity metric is present. The mean standardised coefficients (β) and p-values for each diversity metric are calculated using only those low AICc models in which the metric is present. Analyses are performed using (a) OLS models with area-based (per ha) diversity metrics; (b) OLS models with stem-based (per 300 stems) diversity metrics; (c) SEVM models with area-based (per ha) diversity metrics; and (d) SEVM models with stem-based (per 300 stems) diversity metrics. The SEVM models are run using only the variables found in the lowest AICc corresponding OLS model, and are only shown when at least one spatial filter is selected as being correlated with the OLS model residuals, and the appropriate diversity metric is present in the lowest AICc corresponding OLS model. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

Area-based diversity metric (OLS models)	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	9	0	-	-	0.272
^{0}D (genus level)	11	3	0.155	0.119	0.281
^{0}D (family level)	3	3	0.208	0.028	0.299
^{1}D (species level)	9	0	-	-	0.272
^{1}D (genus level)	4	3	0.184	0.046	0.291
^{1}D (family level)	5	4	0.157	0.077	0.288
^{2}D (species level)	9	0	-	-	0.272
^{2}D (genus level)	4	4	0.193	0.027	0.298
^{2}D (family level)	13	4	0.125	0.151	0.280
Fisher's α	9	0	-	-	0.272

(b)

Stem-based diversity metric (OLS models)	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	11	2	0.086	0.393	0.272
^{0}D (genus level)	5	3	0.176	0.071	0.287
^{0}D (family level)	3	3	0.222	0.016	0.306
Fisher's α	9	0	-	-	0.272

(c)

Area-based diversity metric (SEVM models)	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (genus level)	2	1	0.198	0.047	0.310
^{1}D (genus level)	1	1	0.203	0.026	0.316
^{2}D (family level)	2	1	0.131	0.121	0.300

Table 4.15 (continued)

(d)

Stem-based diversity metric (SEVM models)	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (genus level)	1	1	0.202	0.037	0.313

Table 4.16: Results of OLS and SEVM models for both Africa and South America combined, with log(AGWP) as the response variable. The parameters given are from the lowest AICc models, among a total of 127 models. The SEVM models are run using only the variables found in the lowest AICc OLS model, and are not shown because no spatial filters are selected as being correlated with the OLS model residuals. The standardised coefficients are given as β, except for the intercept, for which the non-standardised version is given. Predictor variables not found in the OLS model with lowest AICc are denoted as '-'. Analyses are performed using (a) species richness per ha (to provide an example of an area-based diversity metric where diversity is not present in the lowest AICc model), (b) genus level ^2D per hectare, and (c) species richness per 300 stems (to provide an example of a stem -based diversity metric where diversity is not present in the lowest AICc model) diversity metrics. None of the other diversity metrics are present in the lowest AICc models, so they are not shown. *TEB* is total extractable bases; *PCA1* is the first principal component of soil texture; PCA2 is the second principal component of soil texture; *MAT* is mean annual temperature; *MAP* is mean annual precipitation; P_S is precipitation seasonality. ^0D is taxonomic richness; ^2D is Simpson diversity.

(a)

	OLS - by area	
	β	*p*
Intercept	2.936	0
TEB	-0.124	0.096
PCA1	-0.172	0.013
PCA2	-0.136	0.052
MAT	-0.339	<.001
MAP	0.306	<.001
P_{DQ}	-	-
^0D (species richness per ha)	-	-

(b)

	OLS - by area	
	β	*p*
Intercept	2.862	0
TEB	-0.109	0.145
PCA1	-0.204	0.004
PCA2	-0.124	0.075
MAT	-0.331	<.001
MAP	0.281	<.001
P_{DQ}	-	-
^2D (genus level, per ha)	0.120	0.088

(c)

	OLS - by stem density	
	β	*p*
Intercept	2.795	0
TEB	-0.120	0.112
PCA1	-0.181	0.010
PCA2	-0.136	0.054
MAT	-0.321	<.001
MAP	0.331	<.001
P_{DQ}	-	-
^0D (species richness per 300 stems)	-	-

Table 4.17: Mean standardised coefficients and their significance, for a set of diversity metrics in OLS models for both Africa and South America combined, with log(AGWP) as the response variable. Among a total of 127 models, the number of these with Δ AICc < 2 is shown, as well as the number of low AICc models in which each diversity metric is present. The mean standardised coefficients (β) and p-values for each diversity metric are calculated using only those low AICc models in which the metric is present. Analyses are performed using both (a) area-based (per ha) and (b) stem-based (per 300 stems) diversity metrics. SEVM models are not shown because no spatial filters are selected as being correlated with the OLS model residuals. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

Area-based diversity metric	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	5	1	-0.046	0.608	0.176
^{0}D (genus level)	4	0	-	-	0.176
^{0}D (family level)	5	1	-0.038	0.640	0.176
^{1}D (species level)	4	0	-	-	0.176
^{1}D (genus level)	7	3	0.110	0.144	0.176
^{1}D (family level)	4	0	-	-	0.176
^{2}D (species level)	5	1	0.034	0.664	0.176
^{2}D (genus level)	7	4	0.131	0.064	0.176
^{2}D (family level)	4	0	-	-	0.176
Fisher's α	4	0	-	-	0.176

(b)

Stem-based diversity metric	*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean β value for diversity metric*	*Mean p-value for diversity metric*	*Adjusted R^2 of lowest AICc model*
^{0}D (species level)	4	0	-	-	0.178
^{0}D (genus level)	7	3	0.027	0.754	0.178
^{0}D (family level)	4	0	-	-	0.178
Fisher's α	4	0	-	-	0.178

Similarly to AGB, the spatial autocorrelation of log(AGWP) extends to greater distances in South American than in African forests. Spatial autocorrelation appears to exist only at very small distances in Africa, while it can be found for over 500 km in South America, with some dissimilarity at greater distances (Figure 4.11). This is borne out in the SEVM models; in the African models, no spatial filters are selected as being significantly correlated with the OLS model residuals, while in some of the South American models a single spatial filter is selected. Overall, spatial autocorrelation of AGWP is limited to shorter distances than spatial autocorrelation of AGB is.

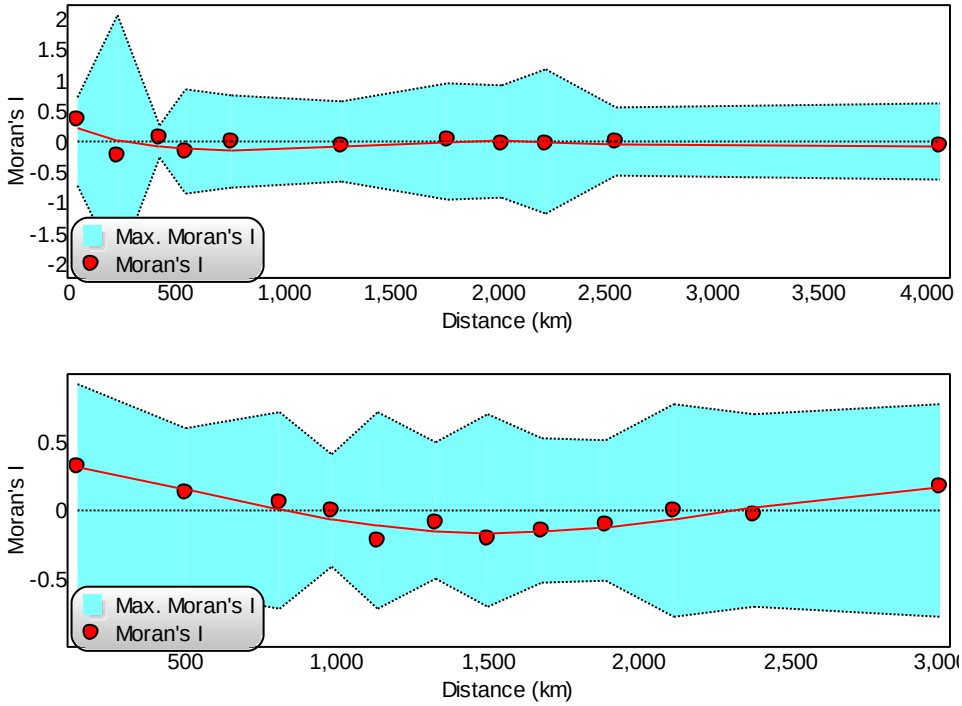


Figure 4.11: Spatial correlograms of Moran's *I* for log(AGWP) in African (top) and South American (bottom) plots. Note the different y-axis scales.

4.5 Discussion

The hypothesis that higher biodiversity drives greater ecosystem biomass or productivity has been a focus of much ecological study, but few have studied these relationships within the two most extensive tropical forests of the world in Amazonia and Africa. I have found positive relationships between family and genus diversity and productivity in South American forests, such that an additional 10 families per hectare are associated with a 27% increase in AGWP, or alternatively, an additional 30 genera per hectare are associated with a 21% increase in AGWP. However, these relationships do not extend to species-level diversity, and are not documented in African forests. Moreover, these associations are found only in linear models that also include climate and soil variables; bivariate correlations between diversity and productivity are never significant. Furthermore, I find no evidence for any relationships between diversity and aboveground biomass, whether in terms of bivariate correlations or in linear models that include soil and climate variables.

4.5.1 Differences between African and South American forests

I find great variation between the characteristics of lowland tropical forests in Africa and South America. The differences between these continents are not simply due to the presence of

monodominant forests in Africa (Torti et al., 2001), but extend also to non-monodominant forests. Aboveground biomass is found to be much greater in Africa (395 ± 104 Mg dry mass ha^{-1}) than in South America (282 ± 102 Mg dry mass ha^{-1}); this is similar to the findings of Slik et al. (2013) and Lewis et al. (2013). In contrast, mean Fisher's α is three times greater in South America than in Africa. Both the diversity metrics and some soil and climate variables such as *MAP* and *PCA2* have noticeably lower ranges in African forests than in South American forests. Under these circumstances, in which the flora of African forests is distinctly impoverished relative to South America, but biomass and productivity are on average greater in Africa, a positive effect of diversity on carbon storage and productivity would seem unlikely to exist. However, when relationships are examined separately within each continent, it appears that contrasting processes take place in African and South American forests.

4.5.2 Bivariate correlations between biomass, wood production, diversity, turnover, and environmental variables

My first two key questions regard whether or not correlations exist between AGB and diversity and between AGWP and diversity in tropical forests. I find no significant bivariate correlations between aboveground biomass and any diversity metrics in either Africa or South America (Figure 4.1 and Figure 4.2). This may reflect the fact that much of the variation in AGB is explained by the density of relatively few large trees (Slik et al., 2013). The negative correlation observed between AGB and diversity when using data from both continents appears to be an artefact of the comparatively higher biomass and lower diversity in African than South American forests.

Regarding correlations of other environmental variables with biomass, these differ between the two continents. In Africa, no variables are observed to have significant correlations with AGB. This contrasts with Lewis et al. (2013), who found, albeit using a dataset twice as large, that AGB was negatively correlated with precipitation seasonality and soil *TEB*, and positively correlated with soil clay content, in African forests. The lack of observed correlations of AGB with any of the soil variables in Africa may in part be related to the limitations of the soil data. In 95% of African plots it was not possible to utilise soil samples collected from the plots themselves. Instead, values from the Harmonised World Soil Database (FAO/IIASA/ISRIC/ISS-CAS/JRC, 2012) were used. However, Lewis et al. (2013) also made use of HWSD data rather than *in situ* soil data, so the number of African plots included (139 here, compared to 260 by Lewis et al. (2013)) must also be an important factor.

In South America, several climatic variables (*MAT*, *MAP* and P_S) have significant correlations with AGB (Figure 4.5). Weak positive correlations of AGB with *MAP* and *MAT* were also found by Quesada et al. (2012) using a smaller Amazon dataset, while Baraloto et al. (2011) found AGB in 74 Amazonian plots to be positively correlated with *MAP* and negatively correlated with dry season length. Reduced basal area in regions with longer dry seasons may account for the association between AGB and rainfall (Malhi et al., 2006).

No significant correlation between diversity and aboveground wood production exists in Africa or South America (Figure 4.3 and Figure 4.4). However, AGWP is found to be significantly correlated with the turnover of aboveground biomass in South America, and species and family richness are also significantly correlated with AGB turnover in this continent (Figure 4.8). This suggests that turnover could play a key role in AGWP–diversity relations.

In Africa, of the soil and climate variables, only mean annual temperature is significantly correlated with AGWP. The lack of observed correlations involving the soil variables may again be related in part to the limitations of the African soil data. In South America, mean annual precipitation has a significant positive correlation with AGWP, and *MAT* and *PCA2* have weak significant negative correlations with AGWP (Figure 4.6). This somewhat contrasts with Quesada et al. (2012) who found that dry season rainfall was more consistently positively related with AGWP than was mean annual precipitation, although neither correlation was significant, again using a smaller Amazon dataset.

The finding that AGWP tends to be higher in silt-rich / clay-poor South American soils may be due to the relatively high silt content of more fertile fluvial and alluvial soils, in comparison to the heavily weathered, clay-rich and infertile older Ferralsols (Malhi et al., 2004). No significant correlations between AGWP and soil silt or clay fractions were found by Quesada et al. (2012). However, Quesada et al. (2012) also developed a soil structure score based in part on particle size distribution data, plus two indices of soil physical conditions that were calculated using the soil structure scores along with other variables such as soil depth and topography. The soil structure score was found to have a significant positive relationship with stand-level turnover rates, while the soil physical conditions indices were significantly related to AGWP, turnover, and wood density (but not AGB; Quesada et al., 2012).

Since productivity is an immediate driver of changes in biomass, it is possible that productivity may act as an unseen covarying factor in models with biomass as the response variable. Positive correlations between biomass and productivity were found in both Africa and South America (Figure 4.7). However, in Amazonia, the highest biomass occurs in the Guiana Shield

(Baker et al., 2004), but some of the most productive forests are in western Amazonia (Malhi et al., 2004).

4.5.3 Linear models of biomass with tree diversity, including environmental variables and spatial filters

When I run linear models that include climate and soil variables as well as diversity metrics as predictor variables, and log(AGB) as the response variable, I find little evidence for a relationship between diversity and biomass. When treating African and South American forests separately, no diversity metrics appeared in any of the models with the lowest AICc values, although they did appear in some models with Δ AICc < 2. This includes model combinations having both area- and stem-based diversity metrics in the list of candidate predictor variables. When combining data from the two continents, negative associations with biomass existed in the OLS models for most diversity metrics. In the SEVM models, which include spatial filters, the relations were less consistent. It seems likely that the negative relations are an artefact of the higher biodiversity and lower biomass of South American forests in comparison to African forests.

There is likely to be a complex web of environmental and ecological factors that interact to determine the carbon dynamics of tropical forests. While biomass is driven proximately by ecosystem properties including tree turnover rates, productivity, and wood density (Baker et al., 2004), these may each respond to multiple drivers. In Africa, environmental variables associated with AGB appear to include *PCA1*, *PCA2,* and *MAP*. The positive associations of AGB with mean annual precipitation and clay-rich soils concur with previous findings from Africa, but the positive relation between AGB and soil sand content does not (Lewis et al., 2013; Slik et al., 2013). Moreover, in a Bornean forest, AGB and soil sand content have been found to be significantly negatively correlated (Paoli et al., 2008).

In South America, *TEB* and *PCA1* are negatively associated with AGB, and *MAT* and *MAP* are positively associated with AGB, although the absence of *PCA1* from the SEVM models suggests that it is spatially autocorrelated, and may not be a true driver of changes in biomass. Exchangeable soil potassium was found by Quesada et al. (2012) to be negatively related to AGB in South America, due to the abundance of low wood density species in stands with high soil potassium levels; a similar effect of exchangeable potassium could drive the negative association between *TEB* and AGB which I have found. Previously, Slik et al. (2013) have found AGB in South America to be significantly positively related with the temperature of the

warmest month in a linear multiple regression analysis, but not significantly related to the rainfall in the wettest month; Quesada et al. (2012) found no significant relationships between AGB and *MAP* or *MAT*.

Spatial autocorrelation of biomass extends to greater distances in South America than in Africa. Biogeographically and geomorphologically, Amazonia comprises a more coherent region across which important, large-scale environmental gradients occur, promoting spatial autocorrelation at long distances of up to 1000 km or more. The Andes run the length of South America dominating regional precipitation patterns. On the Andean foreplain to the east, relatively young and fertile soils derived from mountain weathering and the former Lake Pebas cover much of western Amazonia, while further east by contrast the heavily weathered Ferralsols of the ancient Brazilian and Guiana Shields dominate (Irion, 1978). In Africa, the plots I have used are located in a number of disparate regions, from Liberia and Sierra Leone in the west, through Ghana, Cameroon, Gabon, and the Congo Basin to Tanzania in the east. However, conditions across the African tropics appear relatively constant in comparison to the plots in South America, as expressed through the tighter ranges of diversity and most environmental variables in my African forest plots than in the South American plots.

In South America, spatial autocorrelation of AGB is stronger than the effect of any other single variable in these models. In addition to the points related above, this could denote phylogenetically-mediated processes such as differences in the mean wood density of local species pools. Wood density is thought to be the major proximate driver explaining patterns of biomass in Amazonian forests (Baker et al., 2004). Wood density tends to follow a gradient from NE to SW, with the highest values in the Guianas.

4.5.4 Linear models of wood production with tree diversity, including environmental variables and spatial filters

Family and genus level diversity metrics were retained in all of the South American lowest AICc models of aboveground wood production. This includes both OLS and SEVM models, and both area- and stem-based diversity metrics. This suggests that positive biodiversity–ecosystem function relations may exist in South American forests. Diversity metrics were not retained in any of the lowest AICc models for Africa. When data from both continents were combined, no diversity metrics except ^{2}D were present in the lowest AICc models. The general lack of diversity–AGWP relations when combining data from the two continents may be due to the

overriding effect of the great differences between African and South American forests, especially in their diversity (see Chapter 3) and floristic composition.

Wood production is proximately controlled by photosynthetic rates, carbon use efficiency, and allocation of photosynthates (Malhi et al., 2009, 2011), but these are ultimately affected by properties of the physical environment and, perhaps, of the species present. However, it is salient to note that focussing on coarse wood production excludes the approximately 60% of net primary productivity (NPP) that is allocated to belowground growth and the production of leaves and reproductive materials (Malhi et al., 2011), and the proportional allocation of NPP to AGWP may vary (Galbraith et al., 2013).

4.5.4.1 AGWP models for African forests

In Africa, mean annual temperature is the only predictor variable present in any of the lowest AICc models of wood production. Temperature is an important (positive) driver of global patterns of productivity, including patterns within tropical forests if montane forests are included (Raich et al. 2006), but in this case, higher temperatures appear to limit productivity. Compared to South America, Africa may have fewer species adapted to warm, wet conditions (Parmentier et al., 2007). The African forests sampled currently are mostly in more marginal rainfall conditions for tropical forests, with precipitation in the driest quarter always below 300 mm. Moreover, the range of variation of *MA*P and P_{DQ} in these forests is small compared to the range of variation of temperature. In moisture-limited dry season conditions, high midday temperatures may increase the leaf-to-air vapour pressure difference sufficiently to cause reduced stomatal conductance, similar to the effects of temperature on *Eperua grandiflora* saplings in simulated forest gap conditions (Pons and Welschen, 2003) in Guyana. As well as reducing photosynthesis, higher temperatures could also increase respiration costs. This could act to reduce net primary productivity.

It is also the case that the sample size used here for African forests is smaller than that for South American forests, and the range of diversity values found in Africa is lower than that found in South America. This may be responsible for the lack of diversity effects. The low R^2 values found in the African AGWP models also suggest that other factors not investigated here are likely to represent important influences in these forests. These could include the impacts of bushmeat hunting, which has been suggested to lead to the decline of large-seeded species, potentially affecting forest biomass since these species tend to have high wood density (Brodie and Gibbs, 2009), or other biotic interactions such as the effects of lianas (Schnitzer and Bongers, 2002). In addition, soils may be more poorly characterised in Africa than in South

America, since in 95% of the African plots Harmonised World Soil Database (FAO/IIASA/ISRIC/ISS-CAS/JRC, 2012) values from the nearest soil unit of the same soil reference group were used, while in 30% of South American plots soil data from the plots themselves was available.

4.5.4.2 AGWP models for South America forests

Many diversity metrics were present in the lowest AICc South American models. These did not include any of the species-level diversity metrics or Fishers α, but did include all of the genus- and family-level metrics. Family richness in South America showed positive relations with AGWP, such that an additional 10 families per hectare are associated with an increase of 27% in AGWP. This suggests that the lack of observed bivariate correlations between diversity and AGWP, as discussed in section 4.5.2, does not imply that these variables are unrelated. It is necessary to take into account any covarying soil or climate variables.

There is remarkable consistency between the models using stem-based and area-based diversity metrics, showing for the first time that observed relations between tropical forest diversity and productivity cannot be simply an artefact of correlations between diversity and stem density, because it is impossible for stem-based diversity metrics to act as proxies for stem density. Positive effects of diversity on AGWP in forests have been found previously at small (0.04-ha) scales (Chisholm et al., 2013), but the magnitude of these effects was highly uncertain, with a doubling of species richness causing an increase in AGWP of anywhere between 5% and 48%, an unknown portion within this range being due to differences in stem density rather than diversity *per se*.

In South America, diversity covaries with *MAP*, P_S, P_{DQ} and *PCA1* (Figure 4.9). Of these, *MAP* and *PCA1* are consistently represented in the lowest AICc models, along with *PCA2*. Mean annual precipitation appears strongly associated with wood production in South America, since it has the greatest β values of any of the parameters in these models. For example, in the SEVM model that includes family richness per hectare, an additional 500 mm of mean annual rainfall is associated with a 32% increase in AGWP. This contrasts with Malhi et al. (2004), who found no evidence of a relationship between mean annual rainfall and AGWP in Amazonia, although they did find that wet sites in Ecuador and northern Peru are some of the most productive tropical forests. The presence of *PCA1* in the lowest AICc models, suggesting an association between high soil sand content and high AGWP, is surprising. White sand plots often have much lower AGWP than *terra firme* plots (Aragao et al., 2009), but most of the plots with low *PCA1* scores were not classified as Arenosols, despite their high sand content.

The fact that not all of the diversity metrics are present in the lowest AICc South American models underlines the importance of using a range of measures rather than simply substituting species richness for diversity as is commonly practised. However, the greatest differences are apparent when comparing diversity at different taxonomic levels, rather than when comparing diversity measures across the richness–evenness spectrum at the same taxonomic level. The measurement of diversity at multiple taxonomic levels provides a simplified representation of phylogenetic diversity, and this appears to be more important than differences between richness and evenness.

The finding that measures of diversity at the family and genus levels are included in the lowest AICc models, but diversity measures at the species level are not, could have several potential explanations. Species richness is more variable from plot to plot than genus and family richness are, as shown by its higher coefficient of variation (Table 4.5). This may be because neutral processes such as stochasticity and dispersal limitation (Hubbell, 2001) affect species richness to a greater extent than they do genus and family richness, and this conceals the impacts of AGWP on species richness. Uncertainty in richness values also remains greatest at the species level (see Chapter 3), and this could contribute to the lack of observed relations of species richness with AGWP.

The positive relations between family and genus diversity and AGWP may be due to their associations with AGB turnover, which could signal a causal mechanism linking diversity and AGWP. Residence times and AGWP appear to be linked by a power function (Galbraith et al., 2013). High turnover could promote high diversity by maintaining a heterogeneous range of conditions, as predicted by the intermediate disturbance hypothesis (IDH, Connell, 1978). The IDH has been validated in Guianan forest affected by a 10-year-old silvicultural experiment, with nearby natural forests falling within the rising limb in which increasing disturbance, measured as the percentage of heliophilic stems, is associated with increased species richness, while richness eventually decreases in some of the plots that have suffered even greater disturbance as part of the silvicultural experiment (Molino and Sabatier, 2001). In Barro Colorado Island, Panama, 20 x 20 m quadrats containing gaps were not found to have higher species richness than non-gap quadrats, after accounting for differences in stem density, but this may be due to the past disturbance history of the site or the small grain size used. At a larger spatial scale, the patchiness of disturbed forests may be one of the features that contribute to their diversity (Sheil and Burslem, 2003).

The positive correlation with turnover is stronger for family richness than for species richness, reflecting the fact that the highest family richness values are mainly found in western Amazonia, which tends to also have the highest turnover (Phillips et al., 2004), while many of the highest values of species richness come from a set of plots close to Manaus in central Amazonia. Genus richness occupies an intermediate position, with high values in both western and central Amazonia. The high species richness of the Manaus plots is well-known (Laurance et al., 2010), and may be caused by mid-domain effects due to their location in the centre of the South American tropical forest zone (Colwell and Lees, 2000), although it is also possible that it could in part be influenced by the greater floristic knowledge of these well-studied forests compared to other regions.

The association of AGWP and diversity at higher taxonomic levels could also mean that it is at these levels that complementarity effects related to niche partitioning occur. These may be the levels at which variation of traits related to productivity are greatest. The selected plots have been sampled for a mean of 11.5 years; over these long sampling periods biodiversity may be acting to insure the forest against environmental change or extreme events such as the 2005 Amazon drought (Phillips et al., 2009a), reducing the impact of these events on forest function (Fauset et al., 2012).

4.5.5 Policy implications

I have found no compelling evidence of relationships between diversity and aboveground biomass in African or South American forests. This is the case both for bivariate diversity–AGB correlations and for linear models of AGB that also include soil and climate variables and spatial autocorrelation. The lack of an observed relationship between diversity and AGB shows that careful consideration must be made to ensure that conservation efforts are beneficial for both carbon storage and biodiversity (Grainger et al., 2009). Trade-offs between these competing conservation goals may exist in some regions.

For the implementation of REDD+ projects to substantially benefit biodiversity and prevent future extinctions (Strassburg et al., 2012), it is vital to ensure biodiversity conservation is an explicit goal of national initiatives and individual projects, rather than assuming that REDD+ will necessarily provide positive diversity co-benefits. In the Cancún Agreements it is noted that REDD+ should be used to promote biodiversity conservation. There are many opportunities to achieve positive diversity co-benefits (Harvey et al., 2010), but a strong regulatory framework is required (Paoli et al., 2010). If strategies based on carbon mitigation

make available extra funds for tropical forest protection (Ring et al., 2010), it is critical to ensure that any additional funding is directed in such a way to benefit biodiversity. This could entail the setting of priorities to facilitate a funding allocation strategy that maximises benefits to biodiversity while minimising carbon emissions (Venter et al., 2009). While biomass and diversity do not appear to be positively correlated at 1-ha scales in African and South American tropical forests, nevertheless forests do exist that are high in both biomass and diversity, and these should be actively targeted for REDD+ projects (Miles and Kapos, 2008). As a whole though, tropical forests still remain some of the most diverse and most carbon dense ecosystems globally.

These findings also highlight the importance of monitoring the wider region in which a REDD+ project is implemented, to avoid leakage of activities that cause deforestation or forest degradation to other forests with potentially greater biodiversity, as well as land-use change in any ecosystem of conservation value (Busch et al., 2011). The active involvement of local communities and indigenous peoples could be a key to success in this regard, since making the livelihood of local populations integral to conservation efforts could help prevent the displacement of damaging activities from one forest region to another. Community managed forests have been found to suffer lower and less variable rates of deforestation than forest protected areas (Porter-Bolland et al., 2012), and when local communities own forest commons they restrict their consumption of forest products (Chhatre and Agrawal, 2009).

The positive diversity–productivity correlations found in South America add further weight to arguments for biodiversity conservation, since diversity may promote productivity through mechanisms such as providing insurance against environmental change. Thus a degree of complementarity between the aims of biodiversity conservation and carbon sink protection could be possible if the carbon sink is driven by productivity increases. However, it is important for specific conservation or sustainable forest management funding or other additional non-REDD funds to be directed towards high-diversity, low-biomass forests that are unlikely to benefit from REDD+ (Harvey et al., 2010; Miles and Kapos, 2008). These funds should also be directed to high diversity, high biomass forests in which REDD+ is not financially viable compared to agriculture or oil palm development, due to the high land value or opportunity costs.

In addition to alpha-diversity, many other aspects of biodiversity are also important for conservation, such as endemism, rarity and threat levels. Rarity appears commonplace for tropical forest tree species. Indeed, 11,000 of the estimated 16,000 Amazonian tree species

account for just 0.12% of individuals according to a recent model (Ter Steege et al., 2013). Due to differing threat levels, some ecoregions may be at heightened risk of fragmentation and habitat loss, although they may not necessarily be the most diverse. For example, West African Forests, the Eastern Arc and Coastal Forests of Tanzania/Kenya, Brazil's Atlantic Forest and the Chocó/Darién/Western Ecuador are recognised as biodiversity hotspots which may be at greater threat from deforestation than the more extensive forests of Amazonia and Central Africa (Myers et al., 2000). It must also be recognised that trees are just one component of forest biodiversity and that many other animal and plant groups require consideration (Sodhi et al., 2004). At a global scale, a strong positive correlation between biomass and the species richness of amphibians, birds and mammals has been found (Strassburg et al., 2010). Insect diversity may in part be a function of plant diversity, since the host specificity of folivorous insects does not differ between tropical and temperate forests (Novotny et al., 2006). However, plant diversity appears to be less important in predicting the diversity of other insect groups such as predatory carabid beetles (Zou et al., 2013).

Diversity–function relations in degraded and secondary forest call for further investigation. The current findings relate solely to intact, old-growth forests. These are all primary forests, of which the importance for biodiversity must be recognised (Gibson et al., 2011). Forest degradation, deforestation and reforestation represent widespread processes. Selectively logged forests can remain valuable habitats (Berry et al., 2010), however, large trees are a key component of forest biomass, accounting for 44.5% and 25.1% of AGB in Africa and South America respectively (for trees ≥ 700 mm; Slik et al., 2013), and are also important in terms of diversity, with populations of some commercially valuable timber species being particularly vulnerable to extinction (Rodan et al., 1992).

Further limitations of the current findings should also be recognised. These findings relate to relationships between alpha-diversity and aboveground biomass with a 1-ha grain size and a continental extent. At national or local scales, different relationships may exist. The forests studied span a broad geographical extent across lowland tropical Africa and South America, but the findings remain dependent on the specific forests sampled, and in other tropical forest regions different diversity–function relations may exist. It must also be remembered that AGB is only one portion of the forest carbon store. Carbon exists in necromass, which is positively related to AGB across Amazonian *terra firme* forests (Chao et al., 2009), within tree roots, and in peat (Page et al., 2011) and other forest soils.

4.6 Conclusion

Forest stand aboveground biomass and tree species diversity appear to be unrelated in tropical forests. This has important implications for forest conservation policies, since explicit measures will need to be taken to protect both diversity and carbon storage in tropical forests. Productivity and diversity are not directly correlated in tropical forests, and appear to be unrelated in Africa. However, in South America I have found positive associations between AGWP and family and genus level diversity measures in linear models that include soil and climate variables. These remain when spatial autocorrelation is accounted for, and using both area- or stem-based diversity metrics. This is the first evidence of significant diversity–productivity relationships spanning extensive tropical forest regions.

5 Does tree diversity predict carbon storage and productivity within tropical forest stands?

5.1 Abstract

Experiments show that reductions in biodiversity are often linked to reductions in key ecosystem functions, such as productivity and carbon storage. However, whether such relationships hold for high-diversity systems such as tropical forests is unknown. Here, I control for most environmental variation that could otherwise be conflated with these diversity–function relationships, by calculating aboveground coarse wood production (AGWP), aboveground biomass (AGB), and a suite of diversity metrics in 20 x 20 m subplots within 169 African and South American tropical forest inventory plots sampled over a mean period of 13.0 years. The diversity metrics are selected to span the richness–evenness spectrum at the species, genus and family levels. I use mixed models with the subplots as the unit of analysis, using random effects to account for variation between plots. Within each plot, there is little heterogeneity in terms of climate and soils, i.e. resource availability does not differ appreciably. The main factors that vary at this scale are diversity and forest structure, and these are both included as fixed effects in the models. To test that diversity effects are not driven by differences in stem density, additional models are developed using richness per ten stems in place of richness per subplot. The selection of model parameters is carried out using an information-theoretic approach. I find that most diversity indices are positively related to AGWP in Africa and South America, separately and when data from both continents are combined. For the combined dataset, a doubling of species richness is associated with an 11% increase in AGWP. Richness per ten stems is even more strongly associated with AGWP than richness per subplot is, showing that stem density does not drive diversity–AGWP relations. When 15 low-diversity monodominant forests are excluded, positive diversity–AGWP relations remain at the species and genus levels but not at the family level, suggesting that functional trait variation associated with productivity may be less important at the family level than at lower taxonomic levels. Richness measures have stronger relations with AGWP than diversity measures more closely related to evenness do, suggesting selection effects or facilitation may be some of the more important mechanisms driving these diversity–AGWP relationships. Hence, in species rich environments like tropical forests, local variation in diversity appears to

have an important effect on ecosystem function. In contrast, diversity appears to be unrelated to AGB in both Africa and South America, and when data from both continents are combined. The exception is when monodominant forests are included in the models, resulting in negative diversity–AGB relations. These appear to be driven by the high biomass and low diversity of the monodominant plots.

5.2 Introduction

5.2.1 Biodiversity and ecosystem functioning

During the past two decades, the role of biodiversity in ecosystem functioning has become a key focus of ecological research (Cardinale et al., 2012; Hooper et al., 2005). A large number of experimental studies (e.g. Tilman et al., 2001) and meta-analyses (Balvanera et al., 2006; Cardinale et al., 2007) have shown that increased levels of biodiversity can enhance productivity and related biomass accumulation. However, while most of the world's biodiversity and most functionally active ecosystems are found in the tropics, very little is known about biodiversity–ecosystem functioning (BEF) relationships within tropical forests.

There are many different mechanisms through which biodiversity has been shown to affect ecosystem functioning. These include effects related to both the identity and the diversity of species (Cardinale et al., 2012). At high levels of diversity, there sometimes comes a point at which redundancy is observed, and further increases in diversity do not produce further increases in productivity (Hector et al., 2001b), but the degree of observed redundancy depends on the number of ecosystem processes and the timescale across which they are measured, as multiple processes over multiple years are maintained by a greater number of species (Hector and Bagchi, 2007; Isbell et al., 2011). Biodiversity may also be important in ensuring ecosystem stability and resilience (Loreau et al., 2001; Tilman et al., 2006).

Many studies of biodiversity and ecosystem functioning involve direct experimental manipulations, ensuring that observed changes in ecosystem functioning cannot be attributed to non-diversity factors, such as changes in environmental conditions (Huston, 1997). The experimental approach is feasible in ecosystems such as temperate grasslands (Tilman et al., 2001), but in tree-dominated systems where the lifespan of individual organisms exceeds the duration of most experiments, an observational approach is necessary, and may be essential when evaluating effects across multiple forest sites. The difficulty in disentangling diversity

effects from the effects of other environmental variables remains a major limitation of observational studies.

In forests, observational BEF studies have previously found mixed effects. While examples of positive correlations between biodiversity and productivity have been found in Midwest American successional forests (Caspersen and Pacala, 2001) and Mediterranean woodlands (Vila et al., 2007), and diversity effects have been observed to be greater in relatively natural conditions than in artificially created ecosystems (Flombaum and Sala, 2008), these studies are limited to assemblages of relatively low diversity.

5.2.2 Biodiversity and ecosystem functioning in tropical forests

In terms of both biodiversity and carbon cycling, tropical forests represent some of the most important ecosystems globally. They currently represent a significant sink of carbon, and are estimated to store 55% of global forest carbon stocks (Pan et al., 2011). Tropical forests also assimilate 34% of global terrestrial gross primary productivity (Beer et al., 2010). The diversity of tropical forests is unparalleled among terrestrial biomes. Containing at least two-thirds of global terrestrial biodiversity (Gardner et al., 2009), tropical forests have been recorded as having up to 329 tree species per ha (Laurance et al., 2010). However, there is considerable variation within the tropics, with African forests typically being less speciose than their Asian and South American counterparts (Parmentier et al., 2007).

This far, little is known about the effects of biodiversity on ecosystem functioning in tropical forests. Total biomass and net primary productivity of tropical forests are very difficult to measure directly, but aboveground biomass (AGB) and aboveground coarse wood productivity of trees (AGWP; Malhi et al., 2004) can be measured readily in permanent plots. Studies from a single mature tropical (Ruiz-Jaen and Potvin, 2010) and a single mature subtropical forest (Vance-Chalcraft et al., 2010) have found local-scale positive correlations between AGB and species richness. In Costa Rican plantations, a majority of the tree species tested showed either comparable or greater growth in mixtures than in monocultures (Redondo-Brenes and Montagnini, 2006), while diversity–AGB relations were not found in managed forest in Panama (Kirby and Potvin, 2007) but were found in a 6-year-old Panama plantation (Ruiz-Jaen and Potvin, 2011). However these are all single-site analyses and comparability is limited by the different sets of protocols and analyses used.

Species richness and productivity have been found to be related in a study of 11 forests, such that a doubling of species richness is associated with a 48% or 5% (depending on whether or

not effects potentially related to stem density are excluded) increase in AGWP (Chisholm et al., 2013). In the same study, a doubling of species richness in 25 forests is associated with a 53% or 7% increase in AGB, depending on whether or not effects potentially related to stem density are excluded. However, this study only included one forest from Africa and two from Amazonia (only one of which had multiple census data). A standardised analysis with a broad tropical forest extent has so far not been attempted, and therefore biodiversity–function relationships within the world's most biodiverse and productive terrestrial biome remain essentially untested.

5.2.3 Potential causal mechanisms for diversity–productivity relationships

At least six hypotheses have been proposed to attempt to explain correlations between diversity and productivity within forest stands. These include both hypotheses in which diversity is expected to be the causal factor and hypotheses in which the correlations between productivity and diversity are driven by productivity. Attributing causality requires careful examination of the assumptions and relationships postulated by the various competing hypotheses.

All of the hypotheses discussed below are shown in Table 5.1. Assuming a given hypothesis is correct, the predicted likelihood of a relationship between productivity and diversity will vary across a suite of diversity measures that includes measures based on different taxonomic levels, from species to family, and measures that are varyingly influenced by richness and evenness. Since the predicted mechanisms of diversity–productivity relationships and their associated effects are different according to each hypothesis, I expect that by using this suite of diversity metrics it may be possible to discover which, if any, of the hypotheses most likely explain observed conditions.

The first potential causal mechanism for diversity–productivity correlations is the hypothesis that the greater the diversity, the greater the chance that particular high- or low-functioning taxa will be present in the plot and will be able to influence plot-level productivity. These selection effects can be positive or negative (Cardinale et al., 2007), with positive selection effects occurring when the more diverse assemblages come to be dominated by relatively high functioning species. If BEF relationships are driven by selection effects, then I can expect species richness should have a stronger relationship with productivity, whether this relationship is positive or negative, than the other diversity indices do, since selection effects are caused by individual species.

In contrast to selection effects, complementarity occurs when increased functioning in the more diverse assemblages is driven by diversity itself, not merely by the presence of particular species in the more diverse assemblages (Loreau and Hector, 2001). In experimental studies, this can be proved by the existence of 'overyielding' (Tilman et al., 2001). There are three potential causes of complementarity effects in tropical forests. The first occurs when diverse assemblages can exploit available resources more fully, through niche partitioning (Ashton, 1969) allowing more complete use of the available niche space (Colwell and Rangel, 2009). Evidence for niche partitioning in relation to soil variation has been found in tropical forests (Paoli et al., 2006). Resource use is dependent on the relative abundance of species, so I expect that measures of diversity that account for abundance (i.e. high evenness) will show the strongest relationship with productivity. The degree of trait conservation will determine at which taxonomic level diversity is most strongly associated with productivity.

A second potential form of complementarity effect, proposed specifically in tropical forests, is caused by the high specificity of density- and distance-dependent pathogens and herbivores (Connell, 1971; Janzen, 1970). This may produce a negative association between the density of a taxon and its productivity (Wills et al., 1997), although competition for resources could also cause similar effects. Depending on the degree of host-specificity, negative interactions can occur among closely related species as well as conspecifics. Evenness represents the density of taxa better than richness does, and is thus expected to show the strongest relationship with productivity if these density-dependent Janzen-Connell effects predominate.

The third cause of complementarity effects is facilitation (Cardinale et al., 2002; Mulder et al., 2001). A classic example of facilitation in tropical forests is the role of leguminous trees in promoting nitrogen fixation, which may benefit other species whose growth would be limited by low soil nitrogen levels. Mycorrhizal networks can also play an important role in the redistribution of carbon, nutrients and water, including transfers of carbon between autotrophic plants (Simard et al., 2012). Facilitative effects are often related to the presence of particular taxa, so the strongest effects on productivity are predicted to be associated with species and genus richness.

According to the number-of-individuals hypothesis, productivity affects diversity indirectly by limiting the maximum stem density (Currie et al., 2004; Šímová et al., 2011). Stem density then controls diversity, in particular limiting maximum richness in highly diverse assemblages which might come close to reaching one species per stem. The number-of-individuals hypothesis makes no statement about direct productivity-diversity relations. Of the various diversity

metrics, I expect species richness to show the strongest correlations with productivity under the number-of-individuals hypothesis, since limits to stem density restrict the maximum potential number of species.

Turnover has been suggested as a potential driver of high diversity in tropical forests (Phillips et al., 1994) because high turnover is associated with frequent small disturbances which maintain the heterogeneous conditions that allow the co-existence of species with various niche requirements, as predicted by the intermediate disturbance hypothesis (Connell, 1978). This prevents competitive exclusion and domination such as that which is thought to occur in classical monodominant forests (Ter Steege and Hammond, 2001; Torti et al., 2001). Productivity and turnover are linked since tree deaths can open up the canopy and release new growth; in Amazonia both are highest in the west. Diversity has been found to peak at intermediate disturbance levels in a Guianan forest 10 years after the forest was impacted by a silvicultural experiment (Molino and Sabatier, 2001), and in Ghanaian forests (Bongers et al., 2009), but increased diversity was not found in treefall gaps in Panama (Hubbell et al., 1999). The enhanced opportunities for species co-existence associated with this mechanism should give richness the strongest associations with productivity. If this hypothesis is correct, both richness and AGWP should have correlations with turnover that are at least as strong as or stronger than their correlations with one another.

Table 5.1: Possible causal mechanisms of a relationship between diversity and productivity, with the associated predicted likelihood of diversity–productivity relationships across a set of diversity measures. Diversity measures expected most likely to be related to productivity assuming a given causal mechanism are shown in dark green; diversity measures expected less likely to be related to productivity assuming a given causal mechanism are shown in light green; those expected unlikely to be related to productivity assuming a given causal mechanism are shown in white.

BEF hypothesis	*Process*	*Likelihood of diversity–productivity relations vs. form of diversity*				*Reasoning for assigned likelihood*
			Species	*Genus*	*Family*	
Selection effects	Highly productive species are more likely to be present in diverse plots, and come to dominate production in these plots.	Richness				Selection effects depend on species composition.
		Evenness				
Complementarity: resource partitioning	Niche complementarity means available resources are more fully exploited when more species are present.	Richness				Resource use depends on relative abundance of taxa; traits may vary at any taxonomic level.
		Evenness				
Complementarity: negative density dependence	In tropical forests, low densities of individual taxa reduce impacts of herbivory and disease.	Richness				This process depends on the density of closely related species.
		Evenness				
Complementarity: facilitation	Facilitative interactions, including mutualism and commensalism, increase productivity in diverse plots.	Richness				Facilitative processes may be mediated by individual taxa.
		Evenness				
Number-of-individuals hypothesis	Productivity limits number of individuals, with stem density being correlated with diversity.	Richness				Stem density limits richness, with the greatest effect at the species level.
		Evenness				
Turnover-mediated effects	Frequent disturbances associated with high turnover maintain high diversity. High turnover is associated with high productivity.	Richness				Heterogeneous conditions provide opportunities for species with a variety of niches.
		Evenness				

5.2.4 Potential causal mechanisms for diversity–biomass relationships

There are fewer ways in which diversity and biomass have been predicted to be related. In annual systems and new plantations, biomass at the end of the growing season is essentially equivalent to annual productivity, but in old-growth forests this is not the case. Biomass is proximately driven by productivity and turnover times, therefore any factor that increases productivity or longevity may increase biomass. The positive diversity–AGB relations found by Chisholm et al. (2013) may be mediated by productivity, since AGB and AGWP were also found to be consistently positively related in the same forests. In Chapter 4, positive correlations between AGB and AGWP were found in African and South American forests at 1-ha scales, although others argue that these correlations do not persist in the most productive forests (Keeling and Phillips, 2007).

In addition to effects mediated by productivity, there are other possible mechanisms by which diversity–AGB relationships could exist. Selection effects could impact on biomass, for example if more diverse forests tend to be dominated by species with high wood density or longevity. However, ter Steege and Hammond (2001) find the opposite effect, with lower wood density in more diverse communities, along with other characteristics of superior colonisers, such as small seeds and good dispersal. Complementarity effects of diversity on biomass could be driven by density-dependent pathogens if these cause higher mortality rates in less diverse forests, where the density of conspecific or closely related trees is high. However, there is little evidence that mortality rates of mature, high biomass individuals differ with density, rather than merely mortality rates of seedlings (Comita et al., 2010; Wills et al., 2006).

5.2.5 Aims of the study

This study makes use of an extensive network of tropical forest plots to investigate relationships between the richness and diversity of trees, and their woody productivity and biomass. I aim to answer the questions:

1) Are tree diversity and aboveground wood production related within African and South American tropical forests?
2) Are tree diversity and aboveground biomass related within African and South American tropical forests?

Untangling bivariate diversity–function relations from the effects of co-varying environmental factors is a major difficulty in observational studies. I avoid this by developing a “quasi-experimental” approach, implicitly controlling for climate and soil effects by focusing on the

differences between 20 x 20 m subplots within relatively small homogenous plots. With this approach, the impact of variation in soils and climates is minimised, since these do not vary substantially amongst subplots within a single plot. Therefore any variation in diversity between subplots that is not driven by variation in biomass or productivity is assumed to be mostly due to neutral stochastic processes (Hubbell, 2001).

Using mixed effects models, I assess diversity–function relationships in Africa and South America separately, as well as when plot data from these two continents are combined. I also assess the effect of excluding monodominant forest plots. Variation amongst plots is included in the random effects. I estimate multiple diversity metrics for each subplot, using metrics that span the richness– evenness spectrum at the species, genus and family levels, to investigate which forms of diversity, if any, have the strongest relationships with AGWP, and use this to help differentiate between potential causal factors of any observed relationships.

5.3 Materials and methods

5.3.1 Data sourcing

Permanent sample plot data were obtained for 169 African and Amazonian plots (64 from Africa and 105 from South America), from a single database hosted at www.forestplots.net (Lopez-Gonzalez et al., 2011). Standardised guidelines have been followed for plot establishment and remeasurement (Phillips et al., 2009b). Plots are grouped into 52 clusters, with plots from the same cluster tending to have been sampled at similar times. Selected plots represent mature closed-canopy tropical forests and have been censused at least twice over a period ≥3 years. The mean sampling period is 13.0 years. Plot size ranges from 0.28ha to 10ha, with 78% of plots having a size of 1-ha. Plots achieve key standards of botanical inventory. To qualify for inclusion, the plot must have been visited by a professional botanist and scientific names used to identify species. At least 80% of stems in a plot must have been identified to genus level, and at least some voucher specimens should have been collected from unidentified stems. The selected plots are listed in the attached CD (Table A5.1).

All plots contain at least five 20 x 20 m subplots, with every tree being assigned to a subplot. Having subplots of regular size and shape avoids the pitfalls of comparing diversity across units of different area. Further, long transects or fragmented subplots would violate the experimental design which relies on environmental conditions being constant for all subplots within the same plot, while alpha-diversity varies between subplots.

All subplots in a selected plot are within 500 m of one another. At greater distances, habitat heterogeneity may rise, with plots being more likely to encompass a wider range of conditions in terms of soil type, altitude, aspect, microclimate or other environmental or biotic conditions. The aim of comparing subplots within relatively small plots is to avoid these confounding factors and focus specifically on changes in diversity. If a plot is known to contain more than one distinct soil type, this violates the assumption of minimal within-plot variance in environmental conditions. Therefore, to ensure within-plot variance remains small, in four cases plot portions dominated by different soil types are treated as separate plots.

5.3.2 Estimating biomass, productivity and turnover

Both aboveground biomass and aboveground wood production are estimated at the subplot level. The methodology is described in more detail in Chapter 2. For AGB, I used the diameter (*D*) measurements of all trees ≥100 mm *D*, taken in each plot census. The point of measurement (POM) was at a standard height of 1.3m except in cases of deformation or buttress presence at 1.3m. When it was necessary to change the POM, I used corrections to prevent bias relating to stem taper from affecting the growth estimates. Wood density reference values for the lowest available taxonomic resolution were taken from a pan-tropical database (Chave et al., 2009; Zanne et al., 2009), and height was inferred from diameter using the appropriate regional Weibull height-diameter equation (Feldpausch et al., 2012). I used the diameter, wood density and height estimates to derive AGB according to the Chave et al. (2005) moist forest equation. The AGB values used are the mean of the values from the first and final census of each plot.

I estimated AGWP across a single census interval by summing the gain in AGB of stems present at both the start and end of the interval, and the growth of newly recruited stems that crossed the 100 mm *D* threshold during the interval. I only included the growth of these recruits beyond 100 mm *D* (see Chapter 2), which makes these AGWP estimates comparable with the richness and diversity estimates, which are also limited to stems ≥100 mm *D*. To control for differences in the length of census intervals (Sheil and May, 1996), I applied a correction factor which estimates the unobserved growth of stems that die partway through the interval, on a stem-by-stem basis (see Chapter 2). To estimate mean annual AGWP for each subplot, for the entire period across which it has been sampled, I used the time-weighted mean of the annual AGWP in each interval. Missing diameter values and extreme negative or positive recorded diameter growth was corrected, to prevent and minimise potential errors in the growth estimates (see Chapter 2). For two subplots (out of 5291) the mean AGWP of the entire

subplot was estimated to be slightly negative. These were adjusted to zero, to avoid problems with negative values in statistical analyses.

To estimate turnover of aboveground biomass, I use the sum of the AGB of trees that die and the AGB of newly recruited trees. The 100 mm 'core' is subtracted from the biomass of these trees to ensure equivalency with the procedures used to calculate AGWP. Again following the same procedures as for AGWP, corrections are made to include the recruitment and full biomass at the time of death for trees that die unobserved within census intervals, and known trees that continue to grow and then subsequently die within an interval.

5.3.3 Estimating taxonomic richness and diversity

A range of richness and diversity metrics were estimated at three taxonomic levels: species, genus and family. All of these were based on the stems present at the initial plot census. Most stems were identified by botanists in the field during plot establishment or remeasurement, while the collection of voucher specimens and their inspection in herbaria enabled further taxonomic identification and cross-referencing. Synonyms often present challenges to measuring diversity; however, focusing on the α-diversity of plots at their first census avoided these problems, since within any single plot census identifications were always made by the same botanist.

It was not always possible to identify 100% of stems, so further methods were used in order to provide measures of taxonomic richness that accounted for every single tree within a given plot. These methods included the classification of morphospecies and the identification of stems which, although not fully identified, could be shown to belong to unique taxa within the plot.

Morphospecies were identified from botanists' comments, including where scientific names or affinity to scientific names that were not accepted by the ForestPlots.net database were noted, or where the botanist assigned a numbered morphospecies. After morphospecies classification, I noted all remaining stems that were unidentified at species level but belonged to a genus not otherwise represented in the subplot, or that were unidentified at genus level but belonged to a family not otherwise represented in the subplot. These were assumed to represent additional taxa.

After using these techniques, 96.5% of stems could be placed in species units, 98.6% in genus units, and 99.2% in family units. Stems still remaining unidentified were organised by their available taxonomic information, and the number of additional taxa within the subplot that

each group represented was assumed to be equal to the product of the number of stems in the group and the taxon: stem ratio for fully identified stems in the subplot, rounded to the nearest whole integer (based on Martinez and Phillips, 2000).

The number of stems per subplot may affect the species richness of a subplot. To provide a richness measure independent of stem density differences, I used individual-based rarefaction to compute richness per ten stems at each taxonomic level (Gotelli and Colwell, 2001). Of the 5291 subplots used, 287 (59% of these African) contained less than ten stems and had to be excluded when I used these stem-based measures, leaving 5004 subplots having ≥10 stems.

I chose Shannon diversity (^1D; exponential Shannon entropy) and Simpson diversity (^2D; Simpson's Reciprocal Index) to represent diversity. As measures of 'effective number of species' (Jost, 2006), these are directly comparable with richness values (see Chapter 3 for further explanation). Hill (1973) shows that richness (also denoted ^0D; or diversity of order 0), ^1D and ^2D respectively, belong to a single spectrum. In ^0D, relatively greater weighting is given to stems from rarer species, in ^1D there is equal weighting on a per-stem basis, and in ^2D, greater weighting is given to stems from more abundant species. Thus the use of all three of these measures enables the systematic investigation of differences in effects across this spectrum.

5.3.4 Spatial autocorrelation

Spatial autocorrelation of AGWP, AGB and species richness according to Moran's *I* (Moran, 1950) was calculated amongst the subplots within a given plot. This was done for a subset of 79 plots of 100 x 100 m in which the ordering of subplots followed a standard pattern. Directly adjacent subplots were given a weighting of 2, and diagonally adjacent subplots were given a weighting of 1, to represent their spatial proximity. This was done to investigate whether environmental gradients within plots affected AGWP, AGB or species richness. If any of these variables are affected by environmental gradients, perhaps linked to small-scale variance in soil or topographic position, then they should show positive spatial autocorrelation.

5.3.5 Statistical analysis

The mean values per 0.04-ha subplot and the variance within a plot of diversity, AGWP and AGB were explored. The significance and direction of bivariate diversity–function correlations in each plot were also investigated, using Kendall's τ to test for significance of correlations, as well as the correlations of these variables with the turnover of aboveground biomass.

The relationships of aboveground wood production and aboveground biomass with a set of diversity metrics were then investigated using mixed effects models. These were conducted both separately for Africa and South America and for the two continents combined in a single model. To ensure that observed relationships are not unduly influenced by plots that are unrepresentative of the tropical forest biome, the cross-continental and African models were repeated excluding nine monodominant forest plots, eight of which are from Africa. All analyses were conducted in R version 3.0.2 (R Core Team, 2013), using the nlme library (Pinheiro et al., 2013).

Candidate fixed effects used in the models of AGWP were diversity, AGB, and stem density. Similarly, candidate fixed effects used in the models of AGB were diversity, AGWP, and stem density. Natural logarithms were taken for all variables, improving normality and enabling easy comparison of the effects of doubling each predictor variable. Twelve different diversity metrics were used, with each in a different model. These included richness (^{0}D), ^{1}D and ^{2}D, each calculated at species, genus and family levels. Additionally, rarefied richness per ten stems, which avoids the need to include stem density in the model as a covariate, was also calculated at species, genus and family levels. For each diversity metric, the initial maximal models, including all candidate predictor variables, were the following:

$$Log\ (AGWP) = \beta_0 + \beta_1\ (AGB) + \beta_2\ (stem\ density) + \beta_3\ (diversity\ metric) + \beta_4\ (continent) + \beta_5\ (plot\ cluster) + \beta_6\ (plot) + \varepsilon;$$

$$and\ Log\ (AGB) = \beta_0 + \beta_1\ (AGWP) + \beta_2\ (stem\ density) + \beta_3\ (diversity\ metric) + \beta_4\ (continent) + \beta_5\ (plot\ cluster) + \beta_6\ (plot) + \varepsilon;$$

where β_0, β_1, β_2, β_3, β_4, β_5, and β_6 are subplot-level constants, and ε represents residual error.

Using these maximal models as a base, I first selected the random effects, computing Akaike's Information Criterion (AICc) values corrected for finite sample sizes, for all possible combinations of random effects, up to a maximal structure which included the effects of plot nested within plot cluster, nested within continent (where appropriate). These models were compared using restricted maximum likelihood (REML). Having selected the random effects structure, all possible combinations of fixed effects were then compared to find the model structure with the lowest AICc. Fixed effects were compared using maximum likelihood. The final reporting of coefficient values was done using REML.

In each model, I identified the effects as the gradients of the linear regressions between the response variable (AGWP or AGB) and the diversity metric or other predictor variable. When

ordering model terms, I placed diversity metrics after the other variables. This means that in quantifying the observed effects of diversity on productivity, any effects common to both diversity and other model terms (e.g. stem density or AGB) should be included under those other model terms, so that only effects strictly additional to those associated with the other model terms are represented in the observed diversity effects.

5.4 Results

5.4.1 Variability of tropical forest diversity and function

Tropical forests vary substantially, both between and within continents (Table 5.2, Figure 5.1). In terms of mean values per 0.04-ha subplot, aboveground biomass is 26% higher in Africa than in South America, while stem density in Africa is 26% lower than in South America. At these scales, species richness per subplot ranges from 1 to 42 species and is 40% higher in South America than in Africa. Mean diversity metrics do not vary with taxonomic level to as great an extent as they do at larger spatial scales (see Chapter 4). In Africa, mean genus richness is 95% of species richness, and mean family richness is 79% of genus richness.

Table 5.2: Mean diversity, AGB and AGWP of 20 x 20 m subplots within 169 African and South American tropical forest plots.

Variable	*Africa*	*Africa (excluding monodominant forests)*	*South America*
Species richness per subplot	10.3 ± 4.5	11.9 ± 3.8	17.3 ± 5.8
Genus richness per subplot	9.8 ± 4.2	11.2 ± 3.5	14.9 ± 4.7
Family richness per subplot	7.7 ± 3.1	8.8 ± 2.5	11.2 ± 3.2
Species richness per ten stems	7.0 ± 2.0	7.8 ± 1.2	8.6 ± 1.3
Genus richness per ten stems	6.8 ± 1.9	7.5 ± 1.2	8.0 ± 1.3
Family richness per ten stems	5.8 ± 1.7	6.4 ± 1.2	6.8 ± 1.2
Stem density per subplot	16.7 ± 5.1	17.7 ± 5.0	22.7 ± 6.4
Aboveground biomass per subplot (Mg dry mass)	15.6 ± 11.0	13.7 ± 10.1	11.6 ± 7.4
Mean annual AGWP per subplot (Mg dry mass a^{-1})	0.22 ± 0.15	0.22 ± 0.16	0.20 ± 0.10

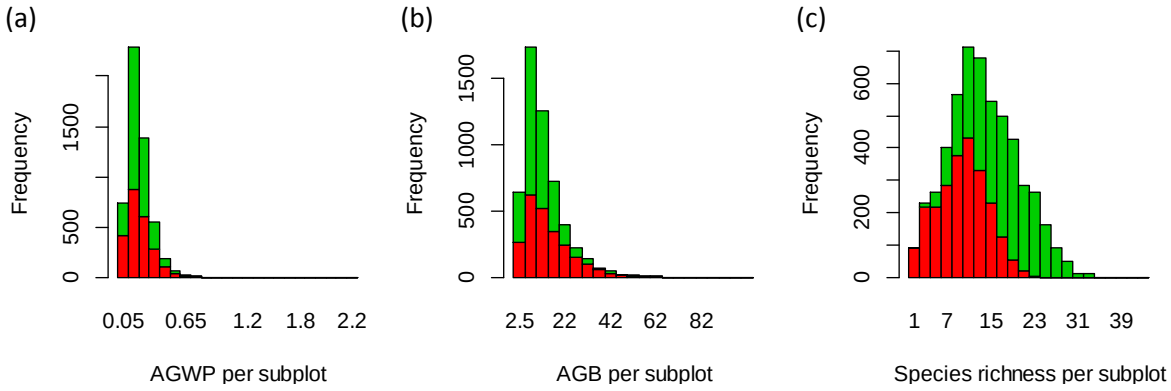


Figure 5.1: The distributions per 0.04-ha subplot of key variables within 169 tropical forest plots. The variables shown are (a) AGWP (Mg dry mass a^{-1}); (b) AGB (Mg dry mass); and (c) species richness. Red bars represent African forests, green bars South American forests.

For subplots within a single plot, the mean range of species richness values per subplot is 13.2 ± 4.2, with a minimum 3 and a maximum 34 (Table 5.3). For genus richness, the mean range for subplots within a plot is 11.8 ± 3.5, minimum 3 and maximum 25. The mean range for family richness is more limited at 8.7 ± 2.1, with a minimum range of 3 and a maximum of 15.

Table 5.3: The absolute and relative variance of richness values per 0.04-ha subplot in 169 tropical forest plots. CV is the coefficient of variation, measured as the standard deviation divided by the mean.

	Species			*Genus*			*Family*		
	Mean	*Range*	*CV*	*Mean*	*Range*	*CV*	*Mean*	*Range*	*CV*
Africa	11.5	11.6	0.28	10.7	10.8	0.28	8.5	8.3	0.27
South America	16.7	14.1	0.22	14.6	12.4	0.22	11.0	8.9	0.21
All plots	14.7	13.2	0.24	13.1	11.8	0.24	10.0	8.7	0.24

5.4.2 Spatial autocorrelation within plots

Spatial autocorrelation between subplots within the same plot is minimal (Figure 5.2). Both for aboveground biomass and for species richness per hectare, mean spatial autocorrelation according to Moran's *I* is not significantly different from zero (using 95% confidence intervals). For aboveground wood production, mean *I* is -0.051, suggesting slight uniformity of distribution, rather than clustering. This shows that environmental gradients do not influence AGWP, AGB or species richness within individual plots.

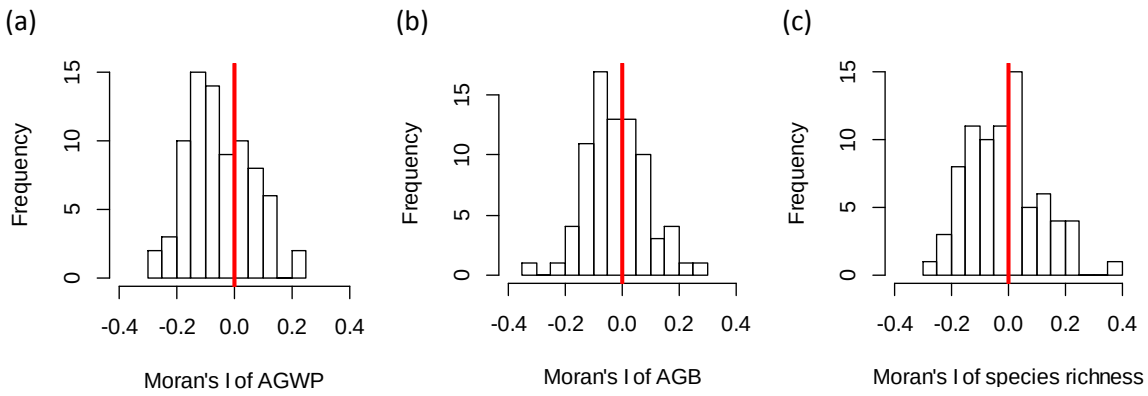
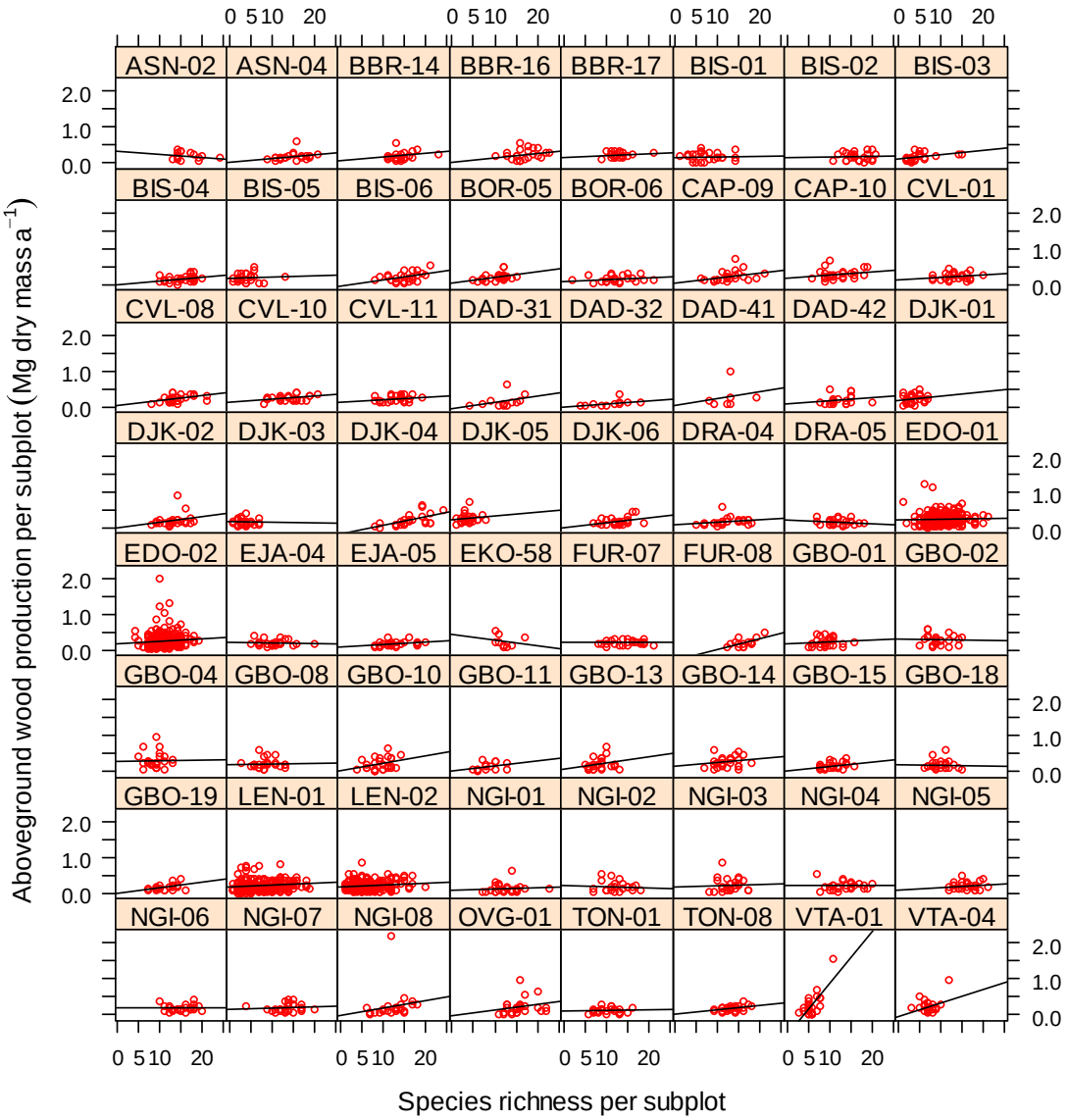


Figure 5.2: Mean spatial autocorrelation among subplots within the same plot. Moran's *I* is calculated for 79 plots of 100 x 100 m in which the subplot ordering follows a standard pattern: (a) spatial autocorrelation of AGWP; (b) spatial autocorrelation of AGB; (c) spatial autocorrelation of species richness per hectare. Red lines denote a Moran's *I* of 0.

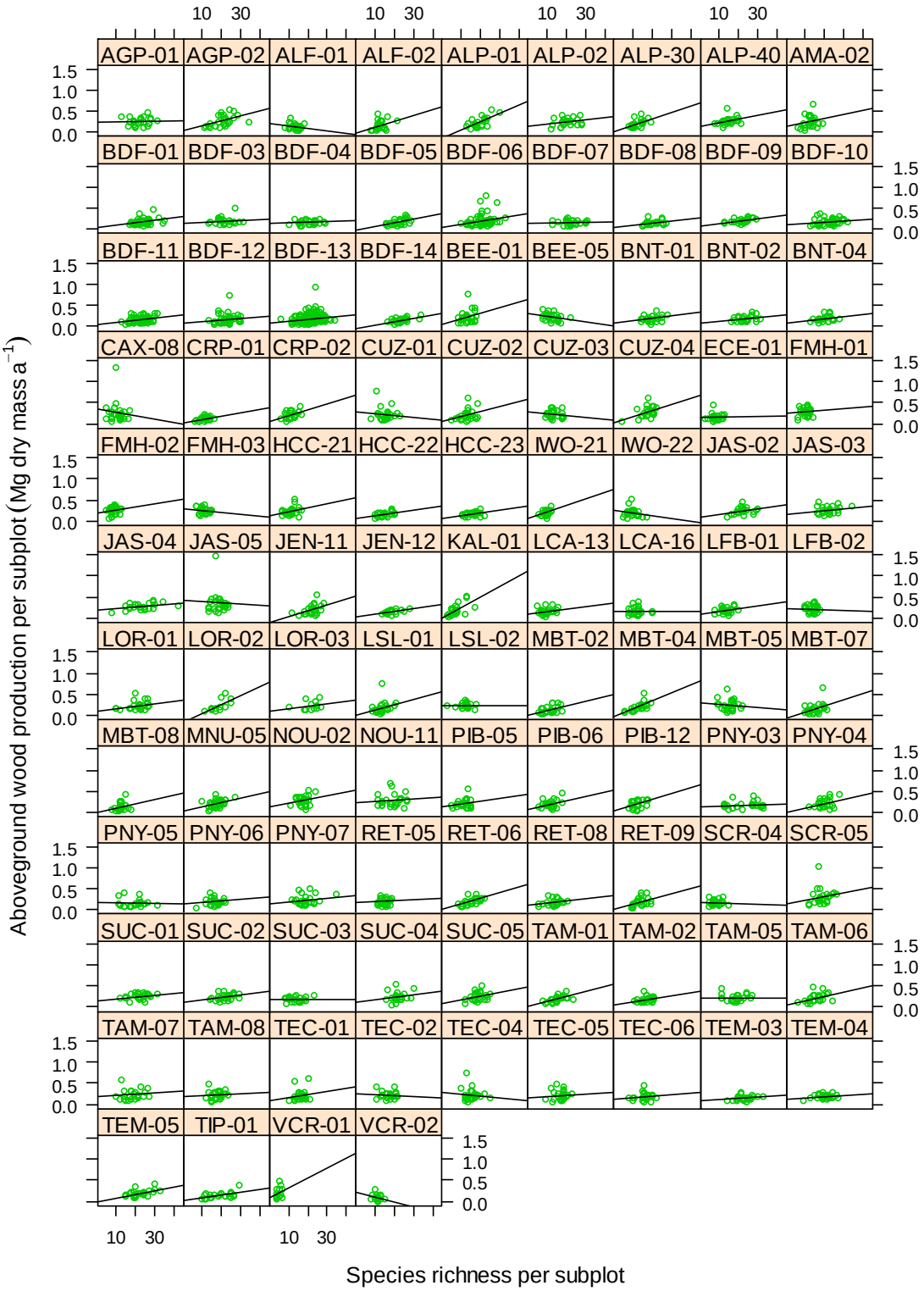
5.4.3 Bivariate diversity–function correlations

Looking at bivariate species richness–AGWP and species richness–AGB correlations among the subplots within individual plots, there is great variation between plots (Figure 5.3). Correlations between species richness and AGWP have positive slopes in 142 plots (84% of plots) and negative slopes in 27 plots. Of the positive correlations, 51 are significant at $p < 0.05$ using Kendall's τ (35 from South America, 16 from Africa), representing 30% of plots, while none of the negative correlations are significant. The species richness–AGB correlations have positive slopes in 130 or 77% of plots. Of these, 43 are significant at $p < 0.05$ (27 from South America and 16 from Africa), representing 25% of plots. Negative correlations between species richness and AGB are found in 39 plots, of which 4 are significantly negative at $p < 0.05$ (2 from each continent). Species and family richness, AGWP and AGB are all positively correlated with AGB turnover in the majority of forest plots, although the number of plots in which these correlations are significant at $p < 0.05$ is relatively small (Table 5.4).

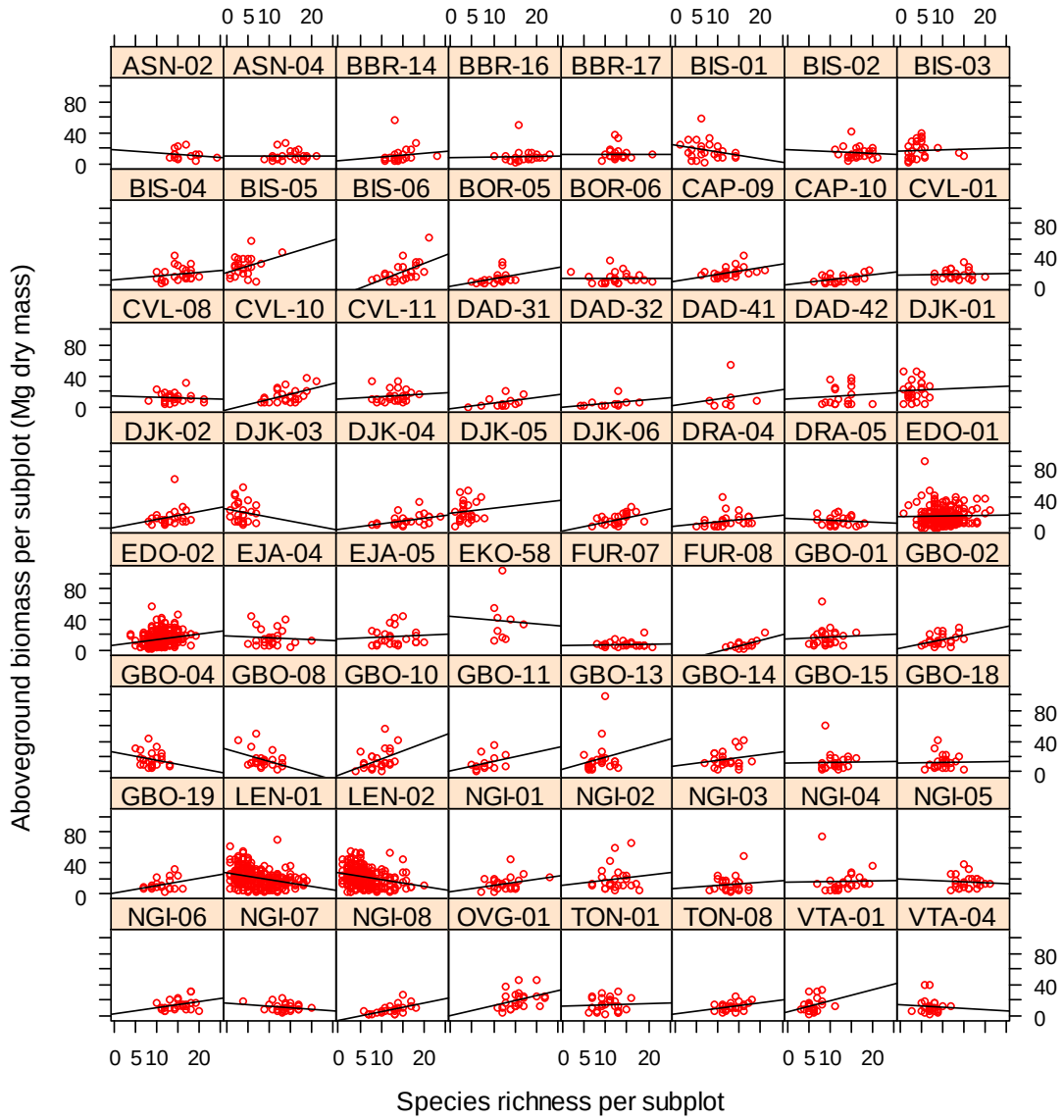
(a)


ASN-02
ASN-04
BBR-14
BBR-16
BBR-17
BIS-01
BIS-02
BIS-03
BIS-04
BIS-05
BIS-06
BOR-05
BOR-06
CAP-09
CAP-10
CVL-01
CVL-08
CVL-10
CVL-11
DAD-31
DAD-32
DAD-41
DAD-42
DJK-01
DJK-02
DJK-03
DJK-04
DJK-05
DJK-06
DRA-04
DRA-05
EDO-01
EDO-02
EJA-04
EJA-05
EKO-58
FUR-07
FUR-08
GBO-01
GBO-02
GBO-04
GBO-08
GBO-10
GBO-11
GBO-13
GBO-14
GBO-15
GBO-18
GBO-19
LEN-01
LEN-02
NGI-01
NGI-02
NGI-03
NGI-04
NGI-05
NGI-06
NGI-07
NGI-08
OVG-01
TON-01
TON-08
VTA-01
VTA-04
0 5 10 20
0.0
1.0
2.0
Aboveground wood production per subplot (Mg dry mass a^{-1})
Species richness per subplot

(b)


AGP-01 AGP-02 ALF-01 ALF-02 ALP-01 ALP-02 ALP-30 ALP-40 AMA-02
BDF-01 BDF-03 BDF-04 BDF-05 BDF-06 BDF-07 BDF-08 BDF-09 BDF-10
BDF-11 BDF-12 BDF-13 BDF-14 BEE-01 BEE-05 BNT-01 BNT-02 BNT-04
CAX-08 CRP-01 CRP-02 CUZ-01 CUZ-02 CUZ-03 CUZ-04 ECE-01 FMH-01
FMH-02 FMH-03 HCC-21 HCC-22 HCC-23 IWO-21 IWO-22 JAS-02 JAS-03
JAS-04 JAS-05 JEN-11 JEN-12 KAL-01 LCA-13 LCA-16 LFB-01 LFB-02
LOR-01 LOR-02 LOR-03 LSL-01 LSL-02 MBT-02 MBT-04 MBT-05 MBT-07
MBT-08 MNU-05 NOU-02 NOU-11 PIB-05 PIB-06 PIB-12 PNY-03 PNY-04
PNY-05 PNY-06 PNY-07 RET-05 RET-06 RET-08 RET-09 SCR-04 SCR-05
SUC-01 SUC-02 SUC-03 SUC-04 SUC-05 TAM-01 TAM-02 TAM-05 TAM-06
TAM-07 TAM-08 TEC-01 TEC-02 TEC-04 TEC-05 TEC-06 TEM-03 TEM-04
TEM-05 TIP-01 VCR-01 VCR-02
10 30
0.0 0.5 1.0 1.5
Aboveground wood production per subplot (Mg dry mass a^{-1})
Species richness per subplot

(c)


ASN-02
ASN-04
BBR-14
BBR-16
BBR-17
BIS-01
BIS-02
BIS-03
BIS-04
BIS-05
BIS-06
BOR-05
BOR-06
CAP-09
CAP-10
CVL-01
CVL-08
CVL-10
CVL-11
DAD-31
DAD-32
DAD-41
DAD-42
DJK-01
DJK-02
DJK-03
DJK-04
DJK-05
DJK-06
DRA-04
DRA-05
EDO-01
EDO-02
EJA-04
EJA-05
EKO-58
FUR-07
FUR-08
GBO-01
GBO-02
GBO-04
GBO-08
GBO-10
GBO-11
GBO-13
GBO-14
GBO-15
GBO-18
GBO-19
LEN-01
LEN-02
NGI-01
NGI-02
NGI-03
NGI-04
NGI-05
NGI-06
NGI-07
NGI-08
OVG-01
TON-01
TON-08
VTA-01
VTA-04
0 5 10 20
0 40 80
Aboveground biomass per subplot (Mg dry mass)
Species richness per subplot

(d)

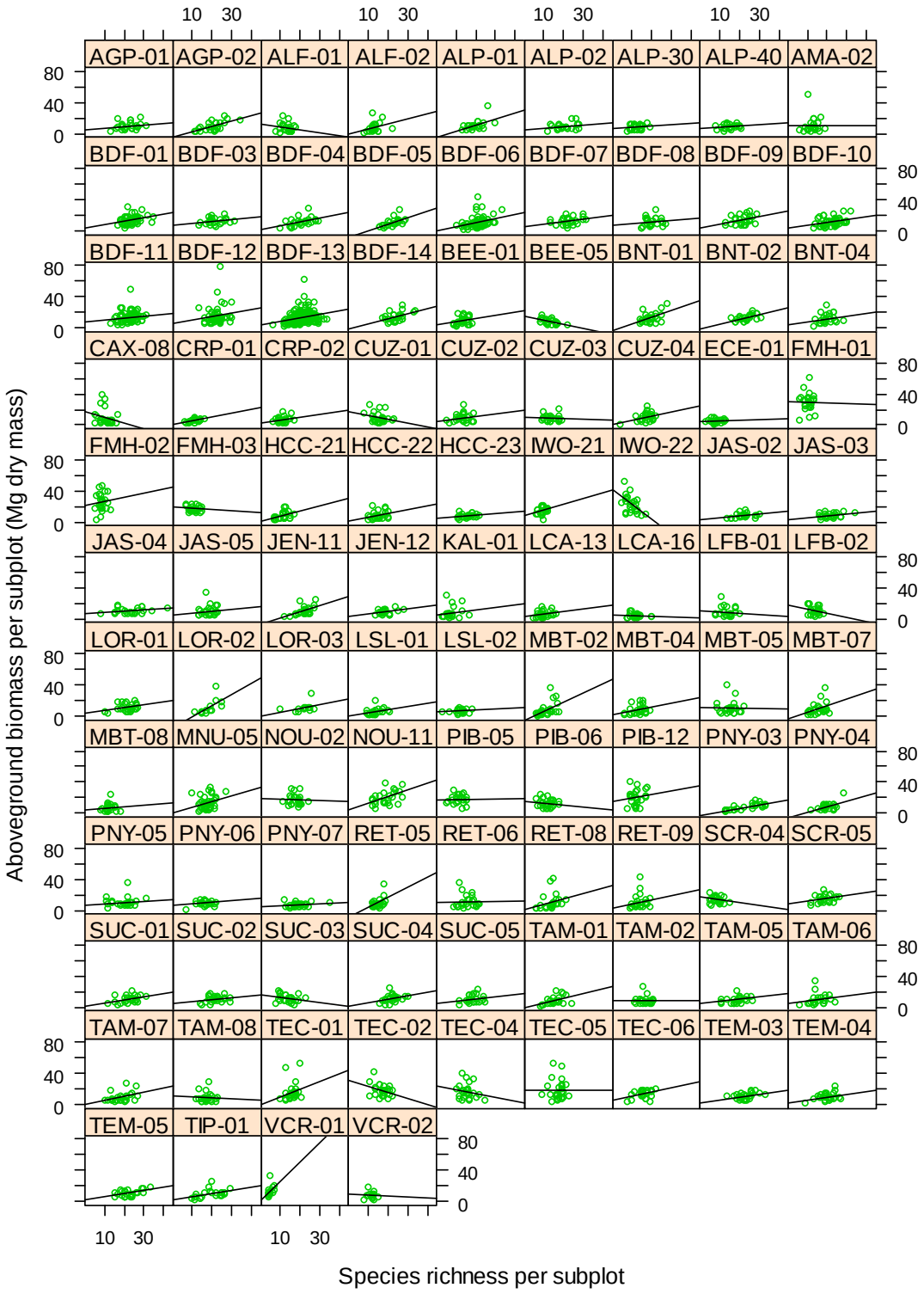


Figure 5.3: Plot-by-plot diversity–function correlations in 0.04-ha subplots. Linear regression lines are fitted for observational purposes, regardless of the significance of correlations. (a) Correlations between species richness and AGWP in African forests; (b) Correlations between species richness and AGWP in South American forests; (c) Correlations between species richness and AGB in African forests; (d) Correlations between species richness and AGB in South American forests.

Table 5.4: Correlations of forest function and taxonomic richness variables with aboveground biomass turnover within 169 tropical forest plots. The number of plots in which these correlations are positive or negative is listed, along with the number of correlations that are significant ($p < 0.05$) using Kendall's τ.

	Number of plots in which variable is positively correlated with AGB turnover	*Number of plots in which variable is negatively correlated with AGB turnover*
AGWP	118 (17 significantly)	51 (3 significantly)
AGB	106 (11 significantly)	63 (5 significantly)
Species richness	122 (16 significantly)	47 (2 significantly)
Family richness	113 (11 significantly)	56 (2 significantly)

5.4.4 Mixed models of productivity

Considering diversity–productivity relations across both Africa and South America, the lowest AICc models show strong associations between tree diversity and AGWP (Table 5.5; no other models exist within 2 AICc units). All of the diversity metrics are positively related to AGWP. For example, a doubling of species richness is associated with an 11% increase in AGWP. The effects of a doubling of diversity tend to be strongest with stem-based richness values, although this is slightly misleading, since the standard deviation of species richness per ten stems is only 0.29 of the mean, while the standard deviation of species richness per 0.04-ha is 0.45 of the mean (see Table 5.2). The effects are weaker with Simpson diversity (^{2}D). Aboveground biomass and stem density also have consistently positive relations with AGWP. As expected, there is variation in AGWP (as more stems and higher AGB can produce more AGWP) between plots and between clusters, as well as considerable remaining variation unattributed to any of these factors. Random effects of continent were not present in the lowest AICc models, presumably because continental effects are already sufficiently encapsulated within the random effects of plot and plot cluster.

When monodominant forests are excluded, the association between diversity and AGWP is slightly reduced in magnitude and remains for species and genus level metrics, but not for family level metrics (Table 5.6), although family level metrics do appear in models within 2 AICc units (Table 5.10a). The same findings apply to South American forests treated separately (Table 5.9 and Table 5.10c), and to African forests when monodominant plots are excluded (Table 5.8 and Table 5.10b). For African forests including monodominant plots, all diversity metrics have positive relations with AGWP (Table 5.7), and no other models exist within 2 AICc units.

Table 5.5: The effects of diversity and forest structure on AGWP within forest plots, using plots from both Africa and South America. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGB per subplot on AGWP*[a]	*Effect of stem density per subplot on AGWP*[b]	*Effect of diversity on AGWP*	*Random effect of plot on AGWP*[f]	*Random effect of plot cluster on AGWP*[f]	*Random effect of continent on AGWP*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+43%	+14%	+11%[c]	16%	19%	NA	61%
	Exp(*H'*) (^{1}D)	+43%	+18%	+8%[d]	16%	19%	NA	61%
	1/λ (^{2}D)	+43%	+20%	+7%[d]	16%	19%	NA	61%
	Richness per ten stems	+47%	NA	+17%[e]	16%	20%	NA	58%
Genus	Richness (^{0}D)	+43%	+15%	+11%[c]	16%	19%	NA	61%
	Exp(*H'*) (^{1}D)	+43%	+18%	+8%[d]	16%	19%	NA	61%
	1/λ (^{2}D)	+43%	+20%	+7%[d]	16%	19%	NA	61%
	Richness per ten stems	+46%	NA	+16%[e]	16%	20%	NA	59%
Family	Richness (^{0}D)	+43%	+20%	+6%[c]	16%	19%	NA	61%
	Exp(*H'*) (^{1}D)	+43%	+23%	+4%[d]	16%	19%	NA	61%
	1/λ (^{2}D)	+43%	+24%	+3%[d]	16%	19%	NA	61%
	Richness per ten stems	+46%	NA	+10%[e]	16%	20%	NA	59%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters/continents); [g] standard deviation of the remaining error.

Table 5.6: The effects of diversity and forest structure on AGWP within forest plots, using plots from both Africa and South America and excluding monodominant forests. Each row contains the terms present in the lowest AICc model selected when the diversity metric listed in that row is used as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGB per subplot on AGWP*[a]	*Effect of stem density per subplot on AGWP*[b]	*Effect of diversity on AGWP*	*Random effect of plot on AGWP*[f]	*Random effect of plot cluster on AGWP*[f]	*Random effect of continent on AGWP*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+45%	+10%	+9%[c]	15%	22%	NA	54%
	Exp(*H'*) (^{1}D)	+45%	+13%	+6%[d]	15%	22%	NA	54%
	1/λ (^{2}D)	+45%	+14%	+4%[d]	15%	22%	NA	54%
	Richness per ten stems	+47%	NA	+13%[e]	15%	23%	NA	54%
Genus	Richness (^{0}D)	+45%	+11%	+8%[c]	15%	22%	NA	54%
	Exp(*H'*) (^{1}D)	+45%	+13%	+6%[d]	15%	22%	NA	54%
	1/λ (^{2}D)	+45%	+15%	+4%[d]	15%	22%	NA	54%
	Richness per ten stems	+47%	NA	+11%[e]	15%	23%	NA	54%
Family	Richness (^{0}D)	+45%	+17%	NA	16%	22%	NA	54%
	Exp(*H'*) (^{1}D)	+45%	+17%	NA	16%	22%	NA	54%
	1/λ (^{2}D)	+45%	+17%	NA	16%	22%	NA	54%
	Richness per ten stems	+47%	NA	NA	16%	23%	NA	54%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters/continents); [g] standard deviation of the remaining error.

Table 5.7: The effects of diversity and forest structure on AGWP within African forest plots. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGB per subplot on AGWP*[a]	*Effect of stem density per subplot on AGWP*[b]	*Effect of diversity on AGWP*	*Random effect of plot on AGWP*[f]	*Random effect of plot cluster on AGWP*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+45%	+22%	+11%[c]	18%	17%	75%
	Exp(*H'*) (^{1}D)	+46%	+25%	+9%[d]	18%	17%	75%
	1/λ (^{2}D)	+46%	+27%	+8%[d]	18%	17%	75%
	Richness per ten stems	+49%	NA	+18%[e]	18%	15%	71%
Genus	Richness (^{0}D)	+46%	+21%	+12%[c]	18%	17%	75%
	Exp(*H'*) (^{1}D)	+46%	+25%	+10%[d]	18%	17%	75%
	1/λ (^{2}D)	+46%	+27%	+9%[d]	18%	18%	75%
	Richness per ten stems	+49%	NA	+19%[e]	18%	15%	71%
Family	Richness (^{0}D)	+45%	+28%	+7%[c]	18%	18%	75%
	Exp(*H'*) (^{1}D)	+45%	+30%	+6%[d]	17%	18%	75%
	1/λ (^{2}D)	+45%	+32%	+5%[d]	17%	18%	75%
	Richness per ten stems	+48%	NA	+13%[e]	18%	16%	72%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters); [g] standard deviation of the remaining error.

Table 5.8: The effects of diversity and forest structure on AGWP within African forest plots, excluding monodominant forests. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGB per subplot on AGWP*[a]	*Effect of stem density per subplot on AGWP*[b]	*Effect of diversity on AGWP*	*Random effect of plot on AGWP*[f]	*Random effect of plot cluster on AGWP*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+49%	+15%	+6%[c]	19%	17%	64%
	Exp(*H'*) (^{1}D)	+49%	+18%	+4%[d]	19%	17%	64%
	1/λ (^{2}D)	+49%	+20%	NA	20%	17%	64%
	Richness per ten stems	+50%	NA	+8%[e]	19%	17%	65%
Genus	Richness (^{0}D)	+49%	+14%	+9%[c]	19%	17%	64%
	Exp(*H'*) (^{1}D)	+49%	+17%	+6%[d]	19%	18%	64%
	1/λ (^{2}D)	+49%	+18%	+5%[d]	19%	18%	64%
	Richness per ten stems	+50%	NA	+10%[e]	19%	17%	65%
Family	Richness (^{0}D)	+49%	+20%	NA	20%	17%	64%
	Exp(*H'*) (^{1}D)	+49%	+20%	NA	20%	17%	64%
	1/λ (^{2}D)	+49%	+20%	NA	20%	17%	64%
	Richness per ten stems	+50%	NA	NA	19%	17%	65%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters); [g] standard deviation of the remaining error.

Table 5.9: The effects of diversity and forest structure on AGWP within South American forest plots. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGB per subplot on AGWP*[a]	*Effect of stem density per subplot on AGWP*[b]	*Effect of diversity on AGWP*	*Random effect of plot on AGWP*[f]	*Random effect of plot cluster on AGWP*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+41%	+6%	+10%[c]	15%	20%	47%
	Exp(*H'*) (^{1}D)	+41%	+10%	+7%[d]	15%	20%	47%
	1/λ (^{2}D)	+41%	+11%	+5%[d]	15%	20%	47%
	Richness per ten stems	+44%	NA	+15%[e]	15%	20%	47%
Genus	Richness (^{0}D)	+41%	+9%	+7%[c]	15%	20%	47%
	Exp(*H'*) (^{1}D)	+41%	+12%	+4%[d]	15%	20%	47%
	1/λ (^{2}D)	+41%	+13%	+3%[d]	15%	20%	47%
	Richness per ten stems	+44%	NA	+9%[e]	15%	20%	47%
Family	Richness (^{0}D)	+41%	+15%	NA	15%	21%	47%
	Exp(*H'*) (^{1}D)	+41%	+15%	NA	15%	21%	47%
	1/λ (^{2}D)	+41%	+15%	NA	15%	21%	47%
	Richness per ten stems	+44%	NA	NA	15%	21%	47%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters); [g] standard deviation of the remaining error.

Table 5.10: Mean change in AGWP with a doubling of diversity. Among a total of 7 models for area-based diversity metrics and 3 models for stem-based diversity metrics, the number of these with Δ AICc < 2 is shown, as well as the number of low AICc models in which each diversity metric is present. The mean change in AGWP with a doubling of diversity is averaged across those low AICc models in which the metric is present. Plots are selected from: (a) Both Africa and South America, excluding monodominant forests; (b) Africa, excluding monodominant forests; and (c) South America. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

Diversity metric		*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean effect on diversity (where present)*
Species	^{0}D	1	1	+9%
	^{1}D	1	1	+6%
	^{2}D	1	1	+4%
	Richness per ten stems	1	1	+13%
Genus	^{0}D	1	1	+8%
	^{1}D	1	1	+6%
	^{2}D	1	1	+4%
	Richness per ten stems	1	1	+11%
Family	^{0}D	2	1	+1%
	^{1}D	2	1	+1%
	^{2}D	2	1	+0.3%
	Richness per ten stems	2	1	+2%

(b)

Diversity metric		*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean effect on diversity (where present)*
Species	^{0}D	2	1	+6%
	^{1}D	2	1	+4%
	^{2}D	2	1	+3%
	Richness per ten stems	2	1	+8%
Genus	^{0}D	1	1	+9%
	^{1}D	1	1	+6%
	^{2}D	2	1	+5%
	Richness per ten stems	2	1	+10%
Family	^{0}D	2	1	-0.5%
	^{1}D	2	1	-0.5%
	^{2}D	2	1	-0.5%
	Richness per ten stems	2	1	+1%

Table 5.10 (continued)

(c)

Diversity metric		*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean effect on diversity (where present)*
Species	^{0}D	2	2	+12%
	^{1}D	1	1	+7%
	^{2}D	1	1	+5%
	Richness per ten stems	1	1	+15%
Genus	^{0}D	1	1	+7%
	^{1}D	1	1	+4%
	^{2}D	1	1	+3%
	Richness per ten stems	1	1	+9%
Family	^{0}D	2	1	+2%
	^{1}D	2	1	+0.3%
	^{2}D	2	1	-0.1%
	Richness per ten stems	2	1	+2%

5.4.5 Mixed models of biomass

Using data from Africa and South America combined, aboveground biomass is negatively related to all of the area- and stem-based tree diversity metrics, such that a doubling of species richness per hectare is associated with an 18% decrease in aboveground biomass (Table 5.11). In all cases, no further models exist within 2 AICc units of the lowest AICc model. The strongest negative relationships with biomass are found when stem-based measures are used (although again the smaller standard deviation of the stem-based measures must be recognised), followed by area-based richness (^{0}D). However, when monodominant forests are excluded, there is less evidence for negative diversity–AGB relationships. In the lowest AICc models, most diversity metrics show no relationship with AGB (Table 5.12), although negative relationships are retained for all diversity metrics in models within 2 AICc units of the lowest AICc model (Table 5.16a). In all models, stem density and AGWP are consistently positively related with AGB. Random effects at the plot, plot cluster and continental levels also suggest that AGB shows considerable spatial variation.

When African plots are treated separately, negative diversity–AGB relations are present when monodominant forests are included (Table 5.13; no other low AICc models exist). When monodominant forests are excluded, negative diversity–AGB relationships are found in models with Δ AICc < 2 (Table 5.16b), but rarely in the lowest AICc models (Table 5.14). In South

American forests, diversity and AGB appear unrelated (Table 5.15), while both positive and negative diversity–AGB relationships are found in models with Δ AICc < 2 (Table 5.16c).

Table 5.11: The effects of diversity and forest structure on AGB within forest plots, using plots from both Africa and South America. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGWP per subplot on AGB*[a]	*Effect of stem density per subplot on AGB*[b]	*Effect of diversity on AGB*	*Random effect of plot on AGB*[f]	*Random effect of plot cluster on AGB*[f]	*Random effect of continent on AGB*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+44%	+45%	-18%[c]	17%	36%	16%	60%
	Exp(*H'*) (^{1}D)	+44%	+38%	-15%[d]	17%	36%	16%	60%
	1/λ (^{2}D)	+44%	+33%	-12%[d]	17%	36%	16%	60%
	Richness per ten stems	+48%	NA	-22%[e]	15%	37%	NA	59%
Genus	Richness (^{0}D)	+44%	+42%	-17%[c]	17%	35%	17%	60%
	Exp(*H'*) (^{1}D)	+44%	+36%	-14%[d]	17%	35%	17%	60%
	1/λ (^{2}D)	+44%	+31%	-12%[d]	17%	36%	17%	60%
	Richness per ten stems	+48%	NA	-21%[e]	15%	36%	NA	59%
Family	Richness (^{0}D)	+44%	+37%	-15%[c]	16%	35%	17%	61%
	Exp(*H'*) (^{1}D)	+43%	+32%	-13%[d]	16%	35%	17%	61%
	1/λ (^{2}D)	+43%	+29%	-11%[d]	16%	35%	17%	61%
	Richness per ten stems	+48%	NA	-18%[e]	14%	36%	NA	60%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters/continents); [g] standard deviation of the remaining error.

Table 5.12: The effects of diversity and forest structure on AGB within forest plots, using plots from both Africa and South America and excluding monodominant forests. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGWP per subplot on AGB*[a]	*Effect of stem density per subplot on AGB*[b]	*Effect of diversity on AGB*	*Random effect of plot on AGB*[f]	*Random effect of plot cluster on AGB*[f]	*Random effect of continent on AGB*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+49%	+29%	NA	16%	36%	16%	56%
	Exp(*H'*) (^{1}D)	+49%	+29%	NA	16%	36%	16%	56%
	1/λ (^{2}D)	+49%	+29%	NA	16%	36%	16%	56%
	Richness per ten stems	+52%	NA	-8%[e]	15%	36%	NA	57%
Genus	Richness (^{0}D)	+49%	+29%	NA	16%	36%	16%	56%
	Exp(*H'*) (^{1}D)	+49%	+29%	NA	16%	36%	16%	56%
	1/λ (^{2}D)	+49%	+29%	NA	16%	36%	16%	56%
	Richness per ten stems	+52%	NA	-5%[e]	15%	36%	NA	57%
Family	Richness (^{0}D)	+49%	+29%	NA	16%	36%	16%	56%
	Exp(*H'*) (^{1}D)	+49%	+29%	NA	16%	36%	16%	56%
	1/λ (^{2}D)	+49%	+29%	NA	16%	36%	16%	56%
	Richness per ten stems	+52%	NA	NA	15%	36%	NA	57%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters/continents); [g] standard deviation of the remaining error.

Table 5.13: The effects of diversity and forest structure on AGB within African forest plots. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGWP per subplot on AGB*[a]	*Effect of stem density per subplot on AGB*[b]	*Effect of diversity on AGB*	*Random effect of plot on AGB*[f]	*Random effect of plot cluster on AGB*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+42%	+43%	-22%[c]	20%	33%	71%
	Exp(*H'*) (^{1}D)	+42%	+35%	-19%[d]	20%	33%	71%
	1/λ (^{2}D)	+42%	+30%	-17%[d]	20%	33%	71%
	Richness per ten stems	+47%	NA	-24%[e]	19%	32%	69%
Genus	Richness (^{0}D)	+43%	+42%	-22%[c]	20%	33%	71%
	Exp(*H'*) (^{1}D)	+42%	+34%	-19%[d]	20%	33%	71%
	1/λ (^{2}D)	+42%	+29%	-18%[d]	19%	34%	71%
	Richness per ten stems	+47%	NA	-24%[e]	19%	32%	69%
Family	Richness (^{0}D)	+42%	+35%	-20%[c]	20%	33%	72%
	Exp(*H'*) (^{1}D)	+42%	+29%	-19%[d]	19%	32%	72%
	1/λ (^{2}D)	+42%	+26%	-18%[d]	19%	32%	72%
	Richness per ten stems	+47%	NA	-23%[e]	18%	32%	70%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters); [g] standard deviation of the remaining error.

Table 5.14: The effects of diversity and forest structure on AGB within African forest plots, excluding monodominant forests. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGWP per subplot on AGB*[a]	*Effect of stem density per subplot on AGB*[b]	*Effect of diversity on AGB*	*Random effect of plot on AGB*[f]	*Random effect of plot cluster on AGB*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+52%	+23%	NA	22%	31%	66%
	Exp(*H'*) (^{1}D)	+52%	+23%	NA	22%	31%	66%
	1/λ (^{2}D)	+52%	+25%	-3%[d]	22%	32%	66%
	Richness per ten stems	+54%	NA	NA	21%	30%	67%
Genus	Richness (^{0}D)	+52%	+23%	NA	22%	31%	66%
	Exp(*H'*) (^{1}D)	+52%	+23%	NA	22%	31%	66%
	1/λ (^{2}D)	+52%	+25%	-4%[d]	22%	32%	66%
	Richness per ten stems	+54%	NA	NA	21%	30%	67%
Family	Richness (^{0}D)	+52%	+23%	NA	22%	31%	66%
	Exp(*H'*) (^{1}D)	+52%	+23%	NA	22%	31%	66%
	1/λ (^{2}D)	+52%	+25%	-4%[d]	21%	31%	66%
	Richness per ten stems	+54%	NA	NA	21%	30%	67%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters); [g] standard deviation of the remaining error.

Table 5.15: The effects of diversity and forest structure on AGB within South American forest plots. Each row contains the terms present in the lowest AICc model selected using the diversity metric listed in that row as a candidate predictor variable.

Diversity metric and taxonomic level		*Effect of AGWP per subplot on AGB*[a]	*Effect of stem density per subplot on AGB*[b]	*Effect of diversity on AGB*	*Random effect of plot on AGB*[f]	*Random effect of plot cluster on AGB*[f]	*Remaining error*[g]
Species	Richness (^{0}D)	+46%	+34%	NA	13%	36%	50%
	Exp(*H'*) (^{1}D)	+46%	+34%	NA	13%	36%	50%
	1/λ (^{2}D)	+46%	+34%	NA	13%	36%	50%
	Richness per ten stems	+50%	NA	-7%[e]	11%	37%	51%
Genus	Richness (^{0}D)	+46%	+34%	NA	13%	36%	50%
	Exp(*H'*) (^{1}D)	+46%	+34%	NA	13%	36%	50%
	1/λ (^{2}D)	+46%	+34%	NA	13%	36%	50%
	Richness per ten stems	+50%	NA	NA	11%	37%	51%
Family	Richness (^{0}D)	+46%	+34%	NA	13%	36%	50%
	Exp(*H'*) (^{1}D)	+46%	+34%	NA	13%	36%	50%
	1/λ (^{2}D)	+46%	+34%	NA	13%	36%	50%
	Richness per ten stems	+50%	NA	NA	11%	37%	51%

[a] Effect on AGWP of a doubling of AGB (per 0.04-ha subplot); [b] Effect on AGWP of a doubling of stem density per subplot; [c] Effect on AGWP of a doubling of taxonomic richness per subplot; [d] Effect on AGWP of a doubling of effective taxonomic richness per subplot; [e] Effect on AGWP of a doubling of taxonomic richness per ten stems; [f] Standard deviation of the difference in AGWP with random effects, (i.e. difference in AGWP between plots/plot clusters); [g] standard deviation of the remaining error.

Table 5.16: Mean change in AGB with a doubling of diversity. Among a total of 7 models for area-based diversity metrics and 3 models for stem-based diversity metrics, the number of these with Δ AICc < 2 is shown, as well as the number of low AICc models in which each diversity metric is present. The mean change in AGB with a doubling of diversity is averaged across those low AICc models in which the metric is present. Plots are selected from: (a) Both Africa and South America, excluding monodominant forests; (b) Africa, excluding monodominant forests; and (c) South America. ^{0}D is taxonomic richness; ^{1}D is Shannon diversity; ^{2}D is Simpson diversity.

(a)

Diversity metric		*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean effect on diversity (where present)*
Species	^{0}D	2	1	-2%
	^{1}D	2	1	-1%
	^{2}D	2	1	-2%
	Richness per ten stems	1	1	-8%
Genus	^{0}D	2	1	-1%
	^{1}D	2	1	-1%
	^{2}D	2	1	-2%
	Richness per ten stems	2	1	-5%
Family	^{0}D	2	1	-1%
	^{1}D	2	1	-1%
	^{2}D	2	1	-1%
	Richness per ten stems	2	1	-4%

(b)

Diversity metric		*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean effect on diversity (where present)*
Species	^{0}D	2	1	-3%
	^{1}D	2	1	-3%
	^{2}D	2	1	-3%
	Richness per ten stems	2	1	-7%
Genus	^{0}D	2	1	-4%
	^{1}D	2	1	-4%
	^{2}D	2	1	-4%
	Richness per ten stems	2	1	-7%
Family	^{0}D	2	1	-4%
	^{1}D	2	1	-4%
	^{2}D	2	1	-4%
	Richness per ten stems	2	1	-5%

(c)

Diversity metric		*Number of models with ΔAICc <2*	*Number of low AICc models containing diversity metric*	*Mean effect on diversity (where present)*
Species	^{0}D	2	1	+0.5%
	^{1}D	2	1	+3%
	^{2}D	2	1	-0.3%
	Richness per ten stems	2	1	-7%
Genus	^{0}D	2	1	+1%
	^{1}D	2	1	+3%
	^{2}D	2	1	+1%
	Richness per ten stems	2	1	-1%
Family	^{0}D	2	1	+1%
	^{1}D	2	1	+2%
	^{2}D	2	1	+1%
	Richness per ten stems	2	1	-1%

5.5 Discussion

5.5.1 Variance of tropical forests at small scales and bivariate diversity–function correlations

Diversity, AGB and AGWP vary consistently across tropical forests in Africa and South America. At a 0.04-ha scale, species richness is a mean 40% higher in South America than in Africa, while mean AGB is 26% higher in Africa and mean AGWP varies little between the two continents. This is similar to the variation of these factors in the same forests at larger scales, although differences between African and South American forests are even more pronounced at the 1-hectare scale, where species richness in South American forests is double that in African forests (Chapter 4).

Bivariate correlations between subplot species richness and AGWP are positive in 84% of plots, and significantly positive in 30% of plots, while these bivariate correlations are not significantly negative in any plots. Bivariate correlations between subplot species richness and AGB are positive in 77% of plots, significantly positive in 25% of plots, and significantly negative in just four plots (Figure 5.3). The fact that these bivariate correlations are consistently positive, while at a 1-ha scale (see Chapter 4) no richness measures were significantly correlated with AGB or AGWP, may show that richness, AGB, and AGWP are more closely related in small 20 x 20 m subplots containing an average of around 20 stems than at large spatial scales. Furthermore, a higher proportion of these correlations are significantly positive than are the correlations of

AGWP, AGB, species richness and family richness with the turnover of aboveground biomass (Table 5.4).

5.5.2 Generality of the observed diversity–function relations

The plots used cover a wide environmental range of undisturbed tropical moist forests. The large number of plots and good geographical coverage across Amazonia and Africa would suggest that these results are widely applicable. Major variables affecting forest function at a local scale include those related to forest structure. For this reason, both stem density and AGB are included as variables in the AGWP models, and stem density and AGWP are included as variables in the AGB models. In addition, further models are developed using measures of richness per ten stems. Stem density, AGB and AGWP are present in all of the relevant lowest AICc models, confirming that these are indeed positively correlated at the subplot scale. However, when diversity metrics are present in the lowest AICc models that include these forest structure variables, these diversity effects appear unlikely to be due solely to correlations with forest structure, especially as variables representing diversity were always placed last when ordering model terms.

Hidden treatments are a potential source of error in observational studies (Huston, 1997), since effects attributed to a particular variable may in fact be caused by an unobserved covariate. The fact that plot and plot cluster were represented as random effects in the models means that any differences among plots in large-scale environmental factors that affect productivity, diversity or both, such as temperature (Lewis et al., 2013; Raich et al., 2006), rainfall (Kreft and Jetz, 2007; Lewis et al., 2013) or dry season length (Malhi et al., 2006; Quesada et al., 2012; Ter Steege et al., 2003), will be represented within the random effects, and are unlikely to have caused the observed diversity–function correlations. This approach also avoids potential bias from drivers of diversity that vary at large scales, such as the historical happenstance of speciation, extinction and other biogeographic processes (Dexter et al., 2012; Parmentier et al., 2007).

Intra-plot environmental heterogeneity or gradients are not the cause of the observed diversity–function functions. All plots containing two identifiably different soil types or geological substrates were excluded or treated as two separate units if each unit still conformed to my inclusion criteria, and within each unit the median distance between subplots was <50m. If intra-plot environmental variability had affected diversity, AGB, or AGWP, perhaps in relation to topographical position or aspect, or differences in soil fertility or soil physical properties that went unnoticed (Svenning, 1999), then they would produce

patterns of spatial autocorrelation characterised by clustering (Ruiz-Jaen and Potvin, 2010). I detected no significant spatial autocorrelation of species richness or AGB amongst subplots within the 79 1-ha plots in which spatial autocorrelation was calculated. Aboveground wood production showed weak negative spatial autocorrelation within these plots, indicating some uniformity of distribution. However, mean *I* is just -0.051, so the degree of spatial autocorrelation of AGWP is small. Given also that species richness and AGB are not spatially autocorrelated, this suggests that the observed diversity–function relations are not caused by spatial autocorrelation, and certainly not by intra-plot environmental gradients.

5.5.3 Diversity–productivity relations in mixed models

Linear mixed models showed positive relationships between aboveground woody productivity and a suite of diversity metrics within 169 tropical forest plots. Positive relationships with AGWP were found for diversity metrics representing a broad spectrum from richness to evenness, as well as for richness per ten stems. These positive relations were consistently found at the species and genus levels, but were only found at the family level in the lowest AICc models when monodominant forests were included. The constancy of the species and genus level findings show that the associations are not driven by unusual plots, but rather are characteristic of BEF relations within more typical tropical forest ecosystems.

5.5.3.1 Differences between diversity metrics: implications for potential causal mechanisms

The use of multiple measures of diversity enables differentiation of the likelihood of potential causal mechanisms of the observed diversity–AGWP relationships. It is thus important to compare diversity–function relations across a broad set of diversity metrics (Vance-Chalcraft et al., 2010; Zhang et al., 2012) rather than solely using species richness. When I considered diversity metrics as comprising a spectrum from richness (^{0}D) to Simpson diversity (^{2}D), which is more closely related to evenness, richness measures had the strongest associations with AGWP. Richness thus appears to be more important than evenness in its association with productivity.

In terms of taxonomic resolution, there is less evidence of positive diversity–AGWP relationships at the family level than at lower taxonomic levels. One potential reason for family diversity to lack a positive association with AGWP within forest stands could be due to the limited number of stems at this scale. This could mean the range of values of family richness per 0.04-ha subplot is too small for any correlations of family richness with AGWP to become apparent. However, this does not appear to be the case, since the coefficient of variation (CV)

of family richness amongst subplots within the same plot is almost identical to the CV of genus richness and of species richness amongst subplots within the same plot (Table 5.3).

Alternatively, the lack of family level diversity–AGWP relations may suggest that inter-family differences are functionally less important for productivity than lower-level taxonomic differences are. The importance of differences at a given taxonomic level depends on the degree of phylogenetic clustering of the relevant functional traits (Kraft and Ackerly, 2010; Swenson et al., 2007). At higher taxonomic levels, such as families, inconsistencies can also arise because these have been classified according to a multitude of opinions over a long historical timeframe, and as such two groups of the same Linnaean rank are not necessarily more comparable than groups of different ranks (Bertrand et al., 2006).

Under the number-of-individuals hypothesis (Currie et al., 2004), productivity–diversity relations are driven indirectly, through the influence of productivity on the number of individuals. Therefore, there should be no correlation between stem-based richness and AGWP. In both Africa and South America, stem-based richness showed strong positive correlations with AGWP. Therefore this hypothesis can be rejected as a potential driver of the observed BEF relationships.

Relationships mediated by turnover also appear unlikely to be driving the observed diversity–AGWP relations within forest stands. If turnover mediates diversity–AGWP relations, then richness should be more closely linked to AGWP than evenness is. This is the case. However, when exploring bivariate correlations within each plot, more plots have positive, or significantly positive, bivariate correlations between AGWP and species richness than have positive, or significantly positive, correlations between AGWP and turnover of AGB, or between species richness and turnover of AGB. This suggests that the effects of turnover are not the most important cause of positive relations between AGWP and diversity within forest stands.

Hypothesised diversity-driven mechanisms include selection effects and complementarity effects (Reiss et al., 2009). Selection effects appear likely to be at least partly responsible for the observed diversity–productivity associations. This is consistent given the observed results, since species richness (^{0}D) showed the strongest relations with AGWP, and selection effects are determined by species composition. If selection effects are present, it means that species with high productivity are more likely to occur in high diversity subplots. If the traits that make species highly productive are poorly conserved at family level, then this could explain the lack of association between family diversity and AGWP.

Various mechanisms could produce complementarity effects. Density-dependent processes are unlikely given the present results in which richness measures were the most closely related to AGWP. Density-dependent processes may be more important for seedlings than for mature trees (Webb et al., 2006). Niche partitioning remains a possible driver of diversity–AGWP relations, but again measures that account for abundance would be expected to show the strongest relationships with AGWP under this hypothesis. However, rather than processes such as growth-mortality trade-offs (Wright et al., 2010) that allow greater resource use at a given point in time, richer subplots could perhaps be more likely to contain enough species that will continue to grow throughout the total range of environmental conditions experienced in the plot, over long time periods (Isbell et al., 2011). Since the mean sampling period of the plots is 13.0 years, at times during this period many plots are likely to have experienced adverse environmental conditions, such as the recent Amazonian droughts in 2005 and 2010 (Phillips et al., 2009a). In addition, traits controlling productivity may vary less systematically at the family level than they do at the species and genus levels.

Facilitative interactions represent another potential mechanism for diversity–productivity relations which is well-supported, since the propensity of facilitative interactions was predicted to be influenced most strongly by species richness, rather than any other diversity metric. Facilitation could promote non-linear increases in productivity, either at all times (Cardinale et al., 2002) or in times of environmental stress (Mulder et al., 2001). There are various means by this could take place. Facilitation could be enabled through mycorrhizal networks (MN) (Selosse et al., 2006; Simard et al., 2012). These can allow the transfer of C and nutrients including P and N between trees of different species, with patterns of uptake and release affected by tree growth rates, and able to change or reverse at different points within phenological cycles. Transfers through MN have been found to benefit multiple species, such as the transfer of carbon from paper birch to Douglas fir seedlings in summer and from Douglas fir to paper birch in spring and autumn (Philip et al., 2010), but could also be a factor in the development of monodominant stands in tropical forests (Bever et al., 2010). Alternatively, if more diverse stands are more likely to contain tree species, such as those in the Fabaceae, that have symbiotic relations with nitrogen fixing bacteria, then this could act to raise the accessibility of fixed nitrogen in the soil, potentially improving growth rates for other species as well as themselves.

5.5.4 Diversity–biomass relations in mixed models

Diversity and AGB were found to be negatively related when models included data from monodominant forests, but appear unrelated when these monodominant plots were excluded. Monodominant forests such as those of *Gibertiodendron dewevrei* in Central Africa tend to have higher than average biomass and many large trees (Peh et al., 2011; Torti et al., 2001). These findings may be driven in particular by two monodominant plots from the Democratic Republic of the Congo of 10ha size (LEN-01 and LEN-02), in which strong negative diversity–AGB relations exist. Elsewhere, differing biomass amongst subplots may be strongly influenced by Individual large trees. Slik et al. (2013) find that large trees (≥700 mm) explain around 70% of variation in tropical forest AGB. The presence of random effects of continent in the lowest AICc models of AGB but not the equivalent models of AGWP confirms that African and South American forests differ in their AGB more consistently than in their AGWP, as found in Table 5.2.

5.5.5 Synthesis of the observed diversity–function relations within and among forest stands

There are some similarities between the observed diversity–function relations within forest stands presented in this chapter, and the diversity–function relations among forest stands presented in Chapter 4, but there are also several important ways in which these findings differ. A key similarity is that no positive relations between AGB and tree diversity are found within or among non-monodominant forest stands. This is the case in both Africa and South America, and when data from the two continents are combined. Direct effects of diversity on tree mortality or loss of biomass, through mechanisms such as high diversity moderating the impact of distance- or density-dependent herbivores or pathogens, would provide a means for diversity to be positively associated with biomass. These processes do not appear to occur in African or South American forests.

When data from the two continents are combined, negative among-plot AGB–diversity relations are observed, but only in the OLS models – when spatial autocorrelation is taken into account (African forests tend to have higher AGB (Slik et al., 2013) and lower tree diversity (Parmentier et al., 2007) than their South American counterparts) there are no consistent AGB–diversity relationships. Negative within-plot AGB–diversity relations are also observed when monodominant forests are included, but stands within monodominant forests tend to have a high density of large trees and very low tree diversity (Peh et al., 2011), which influences the overall AGB–diversity relations. It thus appears that after accounting for spatial

autocorrelation, neither negative nor positive AGB–diversity relationships exist in non-monodominant tropical forests.

Both within and among forest stands, positive tree diversity–AGWP relations have been found in South America for certain forms of diversity. However, in African forests these relationships are only present within stands. Furthermore, even in South American forests, there are some key differences, suggesting that different mechanisms may be responsible for the diversity–AGWP relationships observed within and among forest stands.

In Chapter 4, family- and genus-level tree diversity were found to be positively associated with AGWP among South American forest plots after accounting for environmental variables, but species-level diversity was not, and positive diversity–AGWP relations were not found in African forests or when data from the two continents were combined. It was suggested in Chapter 4 that the impacts of high temperatures in moisture-limited conditions could limit AGWP in African forests, while the lack of observed diversity–AGWP relationships across larger spatial extents here may also be due to the influence of other covarying factors, particularly soil variables, which are not sufficiently accounted for in Africa. When comparing African and South American forests, there is a great range of potential covarying factors that can affect forest diversity and/or function, such as the differing floristic composition and biogeographical histories of the forests in these two continents (van der Hammen and Hooghiemstra, 2000; Maley, 2002).

The positive family- and genus-level diversity–AGWP relations found among forest stands in South America in Chapter 4 are suggested to be related to the impacts of turnover on the forest. High turnover could promote a patchy environment conducive to a wide range of species (Sheil and Burslem, 2003), with multiple patches likely to occur within a 1-ha plot. In support of this suggestion, there are significant positive bivariate correlations between AGB turnover and species richness, family richness, and AGWP among South American forests, but not between species or family richness and AGWP. A possible explanation for the lack of relationship between species-level diversity and AGWP among South American forests could be connected to the fact that species richness is more variable at plot level than genus and family richness. This may be because species richness is more greatly affected by other factors such as neutral processes (Hubbell, 2001) than richness at higher taxonomic levels is, and these other factors may mask the effects of turnover on species diversity.

Conversely, in the current chapter consistent positive tree diversity–AGWP relations are found within forest stands in Africa, South America, and when data from both continents are

combined. Associations between these variables are found to exist for species- and genus-level diversity measures on both a per-stem and per-area basis, but not for family-level diversity measures. In contrast to the among-plots analysis, bivariate correlations of species richness and AGWP with AGB turnover are significantly positive within much fewer plots than those in which direct species richness–AGWP correlations are significantly positive. Therefore turnover appears unlikely to be driving diversity–AGWP relations within plots. Instead, diversity effects may be present, with selection effects and facilitation both being probable mechanisms, since the associations with AGWP are stronger for ^{0}D (richness) than for ^{2}D (Simpson diversity). The lack of positive family-level diversity–AGWP relations within plots could thus show that the relevant functional traits vary mostly at the species and genus levels.

5.6 Conclusion

Tree diversity and aboveground wood production are found to be positively related amongst subplots within 169 tropical forest plots in Africa and South America. These positive associations are consistent at the species and genus levels but not at the family level. Mixed models showed a positive relationship between species richness and AGWP, such that the addition of one extra species per subplot is associated with an 11% increase in AGWP. By contrast, biomass and tree diversity are not directly related when considering the same tropical forest plots, except in a small number of naturally-occurring monodominant forests, where a negative relationship between biomass and diversity exists.

The design of the study means that the observed correlations appear to represent a direct relationship, not confounded by other co-varying environmental factors. Richness measures show the strongest association with AGWP suggesting that the most likely causal mechanisms of this association are selection effects and facilitation. Spatial autocorrelation cannot explain the observed positive relationships, and they are not driven by monodominant plots. This is an important step forward in our understanding of the ecological functioning of tropical forests.

6 Conclusion

6.1 Main findings

Positive relationships between biodiversity and ecosystem functioning have been observed in many ecosystems, but in the two largest tropical forest continents it has so far remained unknown whether such relationships exist. Investigating biodiversity–function relations in these forests can greatly improve our understanding of the role of biodiversity in highly diverse systems, and aid in the establishment of priorities for the conservation of tropical forest biodiversity and carbon stocks.

The aims of this thesis were to assess whether tree diversity is related to carbon dynamics and storage in the tropical forests of Africa and South America. The main objectives were 1) to improve methodologies for the estimation of aboveground wood production (AGWP; see Chapter 2) and tree diversity (see Chapter 3), 2) to investigate whether tree diversity covaries with aboveground biomass (AGB) or AGWP across tropical forests, both directly and after environmental variables and spatial autocorrelation have been accounted for (see Chapter 4), and 3) to investigate whether tree diversity and AGB or tree diversity and AGWP are directly related within tropical forest stands (see Chapter 5).

The estimation of AGWP from forest inventory plot data is affected in particular by three sources of error which are magnified when plots are compared that have been sampled over long and variables time-spans. I develop a suggested scenario to deal with these problems, and use this scenario in the following chapters. Firstly, the height of the point of measurement (POM) of stem diameter is normally set at 1.3 m, but when encroachment of buttresses or other stem deformities appears likely, the POM is raised. Changes in POM height affect diameter estimates due to stem taper (Niklas, 1995). I find that if corrections are not made to adjust for POM changes, AGWP is underestimated by 9%. Between the five correction procedures assessed, results do not differ greatly, and I recommend a technique that makes maximum use of the actual diameter measurements taken in the field.

The second widespread source of error in AGWP estimation relates to the unobserved growth of trees that takes place within a census interval (Sheil and May, 1996). This increases in importance with the length of the intervals, and when comparing plots in which different intervals lengths have been used. I assess two methods for census interval correction, of which a method that makes full use of census data from individual trees shows the most promise. In the plots used, failure to control for the length of census intervals results in a 3%

underestimation of AGWP. Thirdly, when forest plots are sampled a minimum diameter threshold must be chosen, and growth of stems below this diameter threshold will not be observed (Malhi et al., 2004). Three methods are proposed for dealing with this, the choice of method depending on the effects being studied. Estimates of AGWP using these methods differ by up to 8%.

It is important to produce estimates of richness and diversity that represent all of the trees within a plot. It is common for some trees to remain unidentified in the field and at herbaria, and I develop an approach to account for these trees when estimating diversity. Some stems can be assigned to morphospecies, if the correct scientific name is not known but the stems are nevertheless believed by a botanist to belong to a distinct species. Other partially identified stems can be shown to belong to distinct taxa within a plot. After following these methods, some uncertainty in richness will remain. I detail a preferred richness estimate and quantify the remaining uncertainty. If 95% of the stems in a 1-ha plot have been identified to species level, this uncertainty band in species richness is constrained to 20 species on average.

Using all of these techniques for dealing with unidentified stems, I have found that the differences in diversity between African and South American tropical forests are even greater than previously observed (Parmentier et al., 2007). In 152 plots of 1-ha size, mean species richness according to the preferred estimates in South American forests is 158 species per hectare, double the mean richness in African forests of 78 species per hectare. Diversity according to Fisher's α is three times higher in the South American forests than in the African forests. Across the spectrum of community-level (alpha) diversity from richness to measures increasingly influenced by abundance, diversity metrics are linearly related to one another, showing that the most highly diverse forests according to one measure tend to also be the most diverse forests in terms of other aspects of alpha-diversity. Exponential functions relate species richness to genus and family richness.

Investigating diversity–function relations across African and South American forests at large spatial extents, I have found that diversity and aboveground biomass do not covary in these forests. There is no bivariate correlation between AGB and diversity, and relations do not emerge when taking account of the influence of soil and climate and spatial autocorrelation. Similarly, within forest stands AGB and diversity are unrelated. A negative relationship between AGB and diversity within forest stands is observed only when monodominant forest plots are included in the models, and thus appears to be driven by the influence of these forests. This suggests that in mixed forests, there are no direct causal relationships between

tree diversity and AGB. Although this appears to contradict other findings in which AGB and species richness were related in forests at 1-ha scales (Chisholm et al., 2013; Ruiz-Jaen and Potvin, 2010; Vance-Chalcraft et al., 2010), all of these studies included only a very small number of tropical forests. The current study is the first to assess these relations across large numbers of forest plots using standardised methodologies in the two largest tropical forest continents.

I find positive relationships between biodiversity and aboveground coarse wood production in tropical forests. Comparing the diversity and AGWP of 1-ha plots at large spatial extents, positive correlations are found in South America when using diversity at the family and genus levels, but not with species level diversity, while no relations are found in Africa or when data for the two continents are combined. In contrast, within forest stands, positive diversity–AGWP relations are found in Africa, South America, and for both continents combined, using both species and genus level diversity, but results are mixed for family diversity. All of the positive diversity–AGWP relationships observed are independent of stem density, since they remain when richness per ten stems is used instead of an area-based measure of richness.

The observed diversity–AGWP relations at large spatial extents in South American forests may be due to effects related to turnover, as predicted by Phillips et al. (1994). Aboveground biomass turnover is significantly positively correlated with family richness, species richness, and AGWP (Figure 4.8), while family richness and AGWP are not themselves significantly positively correlated (Figure 4.3), which suggests that turnover may be mediating relationships between diversity and AGWP. In forests with high turnover, diversity may be maintained through non-equilibrium processes, following the intermediate disturbance hypothesis (IDH) (Connell, 1978), by which the cycle of gap dynamics maintains the simultaneous existence of conditions suitable for species with a wide range of niches. Intermediate disturbance has been shown to influence diversity in forests in French Guiana (Molino and Sabatier, 2001), and Ghana (Bongers et al., 2009), although in Ghana these effects were very weak except in dry forests. The lack of intermediate disturbance effects observed in Barro Colorado Island, Panama (Hubbell et al., 1999), could in part be related to the 20 x 20 m grain size used, since it is the patchiness of the environment created by disturbance that enables species co-existence (Sheil and Burslem, 2003). This could explain the finding in chapter 5 that, in the 20 x 20 m subplots within a plot, while AGWP and species richness were positively correlated with AGB turnover in the majority of plots, the number of plots in which these relationships were positive (or significantly positive) was smaller than the number in which direct AGWP–species richness correlations were positive (or significantly positive). It thus appears that the influence

of turnover on diversity may be more important at larger grain sizes where between-patch effects become apparent.

The lack of observed covariance of diversity and AGWP across large spatial extents in African forests may have several possible causes. The African forest plots I used all have relatively low rainfall, which could explain the negative association between temperature and AGWP in these plots, since in moisture-limited dry season conditions, higher temperatures could limit photosynthesis and increase respiration costs. When comparing forests across large spatial extents, there are a very large number of potential factors that can influence diversity and carbon dynamics. I account for changes in key soil and climate variables, but there may remain many further aspects of soil and climate variability, as well as other environmental variables, that were not fully controlled in the analysis. In particular, the soil data for 95% the African plots comprised Harmonised World Soil Database estimates for the closest location having the same reference soil group as the plot, while in 30% of South American plots I was able to use soil data collected from the plots themselves. This means it is likely that variation in soil parameters is less accurately characterised in Africa than in South America. There are also major floristic differences between African and South American forests. All of these factors could explain the lack of observed diversity–AGWP relations in African forests and when data from both continents were combined, and the low R^2 values obtained in these models.

In 1-ha plots, diversity is more variable at the species level than at the genus and family levels (Table 4.5). Dispersal limitation and neutral processes (Hubbell, 2001) may have greater impacts at the species level than at higher taxonomic levels, and this could reduce the apparent strength of the impacts of AGWP on species diversity. Species diversity may also be more greatly affected than genus and family level diversity are by drivers, such as mid-domain effects (Colwell and Lees, 2000), that cause variance at regional scales and were not fully accounted for in the models. Per hectare, there also remains more uncertainty in species diversity (Figure 3.5) than in genus or family diversity, due to the greater number of unidentified stems at the species level, while this is not a problem at the 0.04-ha scale due to the very small number of unidentified stems.

The rationale for investigating diversity–function relations within individual forest stands was that at this scale, very few factors vary apart from diversity and forest structure. Essentially, most environmental variation is controlled for in the experimental set-up. The fact that I was able to find positive diversity–AGWP relations in Africa, South America and when data from both continents were combined reveals the power of this analysis. The causal mechanisms of

relationships at this scale appear different to the causal mechanisms of the previously discussed relationships at large spatial extents.

Variations in the strength of diversity–AGWP relations within forest stands across a suite of diversity indices enable inferences to be made about the possible mechanisms that may be driving these processes. Across the suite of diversity metrics from richness to measures increasingly influenced by species abundances, richness has the strongest association with AGWP. Concurrently, species and genus level diversity metrics are positively related to AGWP but family level diversity is not. This pattern, in which species richness shows the strongest association with AGWP within forest stands, suggests that selection effects and facilitation are the most likely processes that may be driving these relationships. Selection effects relate to the impacts that individual species have in more diverse stands, and facilitation relates to interactions between particular species, therefore both of these processes are consistent with the current findings.

The lack of positive relations between family level diversity and AGWP within forest stands cannot be an artefact of the limited range of family richness at these small scales, since the coefficients of variation of family level diversity are almost identical to those for genus and species level diversity. Instead, it suggests that the relevant traits of the species involved in selection effects or facilitation are not conserved at a family level. Foliar properties and other traits of Amazonian trees differ greatly in their plasticity, and in the proportions of the genetic component that can be attributed to family, genus and species levels (Fyllas et al., 2009; Patiño et al., 2012), and this may be useful in helping to reveal which of these traits are most important in influencing wood production.

6.2 Impact on current state of knowledge

Across the two largest tropical forest continents, there is no relationship between aboveground biomass carbon storage and tree diversity. Therefore, maximising protection of carbon storage does not necessarily maximise protection of biodiversity. If REDD+ projects focus solely on protecting the forest carbon sink, they may cause negative implications for tropical forest diversity. In published maps of global carbon storage and biodiversity (Strassburg et al., 2010; UNEP-WCMC, 2008), it has already been recognised that the most important regions for these functions do not always coincide at national and international scales. However, these maps both make use of IPCC Tier-1 default values for biomass carbon (Ruesch and Gibbs, 2008), based on Global Land Cover 2000 classes (Global Land Cover 2000 Database, 2003) rather than ground data. The current findings make use of tree diameter

measurements within an extensive forest plot network, and can thus reveal carbon gradients within lowland tropical forests, rather than merely classifying evergreen broadleaf forests as having higher biomass carbon than other land cover classes such as grasslands.

For the biodiversity co-benefits of REDD+ projects to be realised, biodiversity conservation should be explicitly included in the aims of national initiatives and individual projects. Particular effort should be taken to avoid leakage, recognising the major national and local drivers of land-use change, since the displacement of damaging activities to other forest regions could potentially cause increased harm for biodiversity. However, there remain many opportunities for trade-offs between carbon and diversity to be avoided. Forests that are high in both biodiversity and carbon storage do exist, for example in Gabon (out of the currently used African plots), and these should be the highest funding priority for REDD+ schemes. Non-REDD+ conservation funds can be preferentially directed towards forests that are low in carbon but high in biodiversity, or high-carbon, high-biodiversity forests where the high land value or opportunity costs mean REDD+ is not economically viable (Miles and Kapos, 2008). It must also be recognised that biodiversity is multifaceted and that forests with high tree diversity may not have the highest concentrations of rare, threatened, and range-restricted species, or be the most diverse forests in terms of other taxonomic groups.

There has been extensive study of biodiversity and ecosystem relations in recent years, but much of this has been concentrated in ecosystems such as grasslands, in which experimental manipulations can be more easily conducted. To date, the knowledge of BEF relations in high diversity systems such as tropical forests is limited. My findings show that even at very high levels of diversity, positive relations between biodiversity and AGWP can still exist. A doubling of species richness is associated with an 11% increase in AGWP. This suggests that redundancy does not prevent diversity effects from occurring in these forests. The findings may be relevant to other high diversity systems such as coral reefs or Coleoptera assemblages. Indeed, some of the ecological processes that take place in coral reefs may be similar to those found in tropical forests, since diversity of corals also appears to be greatest at intermediate disturbance levels (Connell, 1978).

6.3 Future research directions

Biodiversity and ecosystem functioning is a rapidly growing research field. The current findings have shown that the form of diversity matters. Diversity–AGWP relations within forest stands are stronger using richness than using abundance-based measures of diversity. Relationships also differ depending on whether diversity is measured at the species, genus or family level.

The positive relations between AGWP and diversity that I have found within tropical forest stands appear most likely to be caused by selection effects or facilitation. Further research is required to investigate and differentiate these mechanisms, acknowledging the likelihood that both coexist (Hector et al., 2011). If selection effects occur, this shows that highly productive species are more likely to be present in more diverse stands. So what are the identities of these high functioning species? What are the traits of these species that cause their high productivity, and do the most productive species tend to share similar trait values? Alternatively, if facilitation occurs, what are the mechanisms by which tree growth is facilitated? Are these similar to mechanisms found elsewhere, such as transfer of carbon and nutrients through mycorrhizal networks (Philip et al., 2010)?

One method that may aid in distinguishing between selection effects and facilitation could be to use the Price equation (Fox, 2006) to partition the effects of diversity on AGWP into effects related to the identities of individual species found in the more diverse subplots, effects related to the number of species present, and context-dependent effects related to changes in the functioning of the species that remain present. If effects related to species composition are found to predominate, this suggests a major role for selection effects, while if effects related to species richness are found to predominate, this suggests facilitation may be more important. However, the applicability of this approach is limited, since all of the species found in lower diversity plots must be present in the more diverse plots.

Indices of phylogenetic diversity (Cadotte et al., 2009; Webb, 2000) provide a means to account for the relatedness of species that does not rely on the vagaries of the classification of higher taxonomic groups (Harper and Hawksworth, 1995). Such indices could be used to further explore the ways in which evolutionary relationships among species determine their effects on ecosystem functioning. However, functional traits of individual trees, rather than their species identity *per se*, actually directly affect their ecological interactions, so investigation of the functional traits of any key taxa, as well as more widespread analysis of functional diversity (Petchey and Gaston, 2002), could provide further illumination of the processes involved in these ecological interactions.

The potential relationships between AGWP and diversity across larger spatial extents mediated by turnover also call for further study. While AGWP and residence times appear to be linked by a power function (Galbraith et al., 2013; Malhi et al., 2004), the causality of this relationship remains unclear. Growth-defence trade-offs could be important, or attacks by enemies such as herbivores and pathogens could be more severe in the climatic zones that also favour high

productivity (Stephenson et al., 2011). Determinants of mortality will also vary with tree size, and between canopy and subcanopy species (Stephenson et al., 2011). The strength of the relationship of diversity with turnover and disturbance remains uncertain (Bongers et al., 2009; Hubbell et al., 1999; Molino and Sabatier, 2001).

My findings relate to forests plots that have been sampled over relatively long time periods, averaging 11.5 years for the plots used in Chapter 4 and 13.0 years for those used in Chapter 5. For many plots, these intervals have spanned drought periods, such as the Amazon droughts of 2005 and 2010 (Phillips et al., 2009a). High diversity may increase the mean AGWP of a forest during normal years with average climatic conditions, or high diversity may allow the forests to maintain functioning throughout periods of difficult climatic conditions. Further research could investigate which of these processes occurs, by assessing the interval-by-interval temporal stability of wood production in plots of varying diversity which have been regularly sampled at short intervals (e.g. every one or two years) over long periods of time, including time periods which have spanned events such as the 2005 and 2010 Amazon droughts.

All of the forests sampled are in the African and South American tropics, and different processes may occur in other tropical forest regions such as Southeast Asia, Australia and New Guinea. Asian forests are dominated by Dipterocarpaceae, which are rarely found elsewhere. In Borneo, soil fertility is an important environmental correlate of AGB, while wood density is not (Paoli et al., 2008; Slik et al., 2010); this differs from Amazonian forests (Baker et al., 2004).

Deforestation rates are high throughout many tropical regions, with widespread regrowth of secondary forests. The carbon source and sink related to these processes is globally significant (Pan et al., 2011). Selective logging is also a major economic activity which has important implications for tropical forests, especially in terms of carbon storage, since much of the biomass carbon is concentrated in large trees (Slik et al., 2013). More research is required to assess biodiversity–function relations in these anthropogenically impacted forests.

6.4 Summary

In the first large-scale study of diversity–function relations across multiple tropical forest sites, tree diversity and aboveground wood production are found to be positively related within African and South American forests. The most likely causal mechanisms of these positive relationships within forest stands are selection effects and facilitation. At larger spatial extents, positive relationships between some aspects of tree diversity and AGWP are present in South American forests but not in African forests, and may be caused by effects mediated by turnover. Tree diversity and aboveground biomass are not related in tropical forests. This

means policies for forest conservation and carbon mitigation will require careful consideration if biodiversity and carbon storage are both to receive the best possible protection.

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8 List of Abbreviations

^0D	Diversity of order 0
^1D	Diversity of order 1
^2D	Diversity of order 2
AGB	Aboveground biomass
AGWP	Aboveground coarse wood production
AICc	Second order Akaike Information Criterion
ANPP	Aboveground net primary production
BEF	Biodiversity and ecosystem functioning
$Best_f$	Preferred family richness estimate
$Best_g$	Preferred genus richness estimate
$Best_s$	Preferred species richness estimate
C	Carbon
CIC	Census interval correction
CO_2	Carbon dioxide
CV	Coefficient of variation
D	Diameter at 1.3 m or above buttresses
D_{mean}	Mean of diameter at the old and new POMs
D_{new}	Diameter at the new POM
D_{old}	Diameter at the old POM
FA	Fisher's alpha
GPP	Gross primary production
H'	Shannon entropy
HWSD	Harmonised World Soil Database
IPCC	Intergovernmental Panel on Climate Change

MAP	Mean annual precipitation
MAT	Mean annual temperature
Max_f	Maximum family richness estimate
Max_g	Maximum genus richness estimate
Max_s	Maximum species richness estimate
Min_f	Minimum family richness estimate
Min_g	Minimum genus richness estimate
Min_s	Minimum species richness estimate
ML	Maximum likelihood
MN	Mycorrhizal networks
NPP	Net primary production
OLS	Ordinary least squares
PCA	Principal components analysis
P_{DM}	Precipitation in the driest month
P_{DQ}	Precipitation in the driest quarter
POM	Point of measurement of stem diameter
P_S	Seasonality of precipitation
REDD+	Reducing Emissions from Deforestation and Forest Degradation
REML	Restricted maximum likelihood
SEVM	Spatial eigenvector mapping
TEB	Total extractable bases
UNFCCC	United Nations Framework Convention on Climate Change
λ	Simpson's concentration

9 Appendix A: Classification of morphospecies

Table 9.1: List of morphospecies codes and the corresponding assignment of morphospecies identities according to the core and extended morphospecies definitions. Y = stem assumed to belong to unique morphospecies in the plot/subplot; N = stem not assumed to belong to morphospecies; Ex = stem assumed to belong to species already existing within the plot/subplot.

Code	*Morphospecies core definition*		*Morphospecies extended definition*		*Details of stem comment*
	Plot	Subplot	Plot	Subplot	
0	N	N	N	N	Stem either fully identified or not fully identified but not thought to be a morphospecies.
1	Y	Y	Y	Y	Numbered morphospecies, scientific name, or affinity to scientific name, which is not already present in the plot. This can include stems which have also been given voucher numbers.
2	N	N	Y	Y	Compare with (cf.) a named species which is not already present in the plot
3	N	N	Y	Y	Stem belongs to one of two or three possible species /morphospecies (none of which are present in the plot)
4	N	N	Y	Y	Specimen collected or voucher number provided (but stem does not qualify for code 1).
5	N	N	Y	Y	Vernacular name or botanist's field code given
6	N	N	N	N	General vernacular name given, of which more specific versions are known to exist, or which has been applied to more than one species
7	N	N	N	Y	Stem belongs to one of two or three possible species /morphospecies; at least one of these is already present in the plot but not in the same subplot
8	N	N	N	N	Stem belongs to one of two or three possible species /morphospecies, but at least one of these is already present in the subplot. Or if subplots are not assigned, at least one of the possible species/morphospecies is already present in the plot.
9	N	N	Ex	Y	Compare with (cf.) a named species which is already present in the plot but not in the subplot
10	N	N	Ex	Ex	Compare with (cf.) a named species which is already present in the subplot. Or if subplots are not assigned, the named species is already present in the plot.
11	Ex	Y	Ex	Y	Scientific name or affinity to scientific name, of species which is already present in the plot but not in the subplot
12	Ex	Ex	Ex	Ex	Scientific name or affinity to scientific name, of species which is already present in the subplot. Or if subplots are not assigned, the named species is already present in the plot.

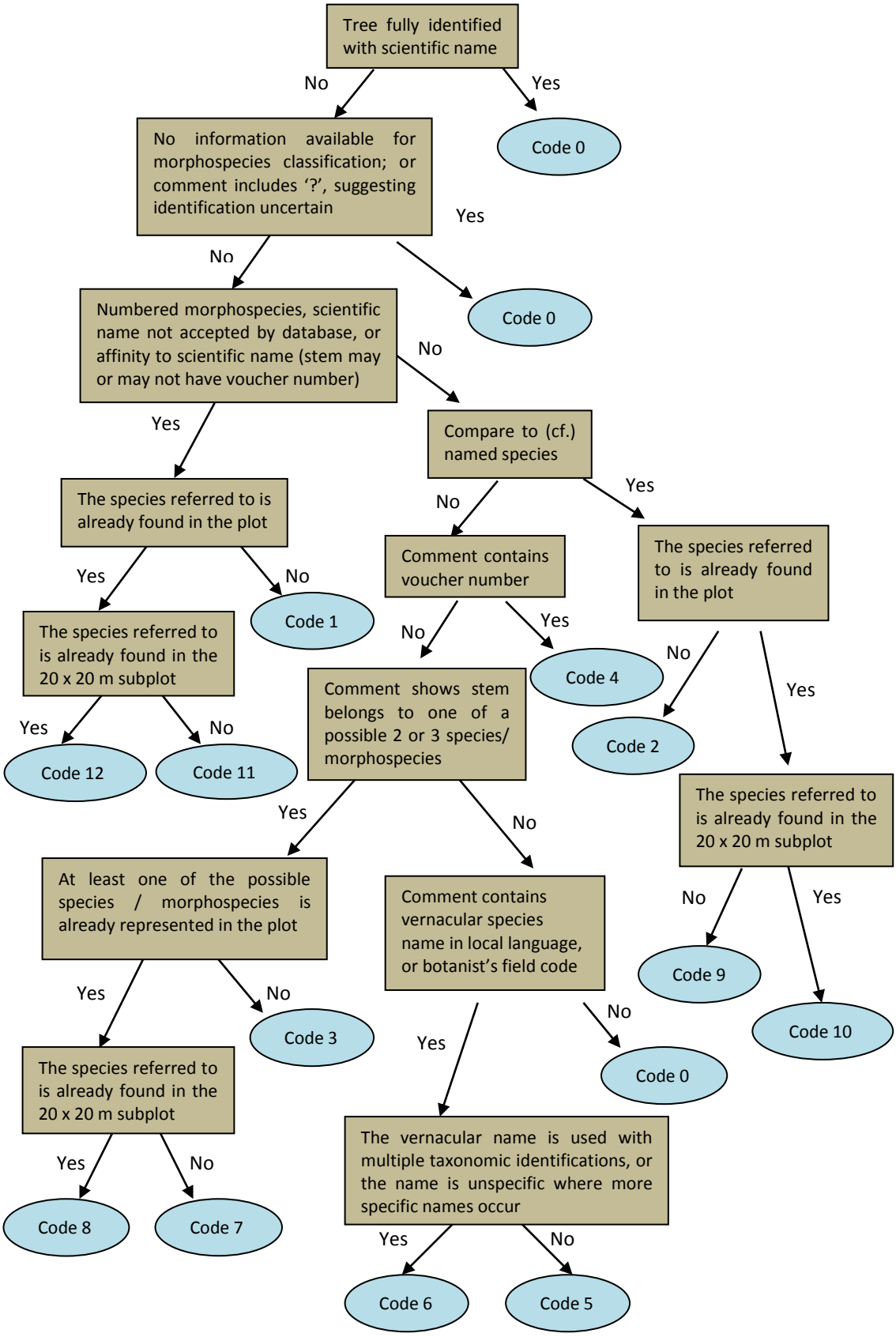

Figure 9.1: Decision tree for the assignment of morphospecies codes based on botanists' comments