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Do species traits determine patterns of wood production in Amazonian forests?

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Abstract

Understanding the relationships between plant traits and ecosystem properties at large spatial scales is important for predicting how compositional change will affect carbon cycling in tropical forests. Here, we examine the relationships between species wood density, maximum height and wood production for 60 Amazonian forest plots. Firstly, we examine how community-level species traits vary across Amazonia. Average species maximum height and wood density are low in western, compared to eastern, Amazonia and are negatively correlated with aboveground wood productivity and soil fertility. Secondly, we compare biomass growth rates across functional groups defined on the basis of these two traits. In similar size classes, biomass growth rates vary little between trees that differ in wood density and maximum height. However, biomass growth rates are generally higher in western Amazonia across all functional groups. Thirdly, we ask whether the data on the abundance and average biomass growth rates of different functional groups is sufficient to predict the observed, regional-scale pattern of wood productivity. We find that the lower rate of wood production in eastern compared to western Amazonia cannot be estimated on the basis of this information. Overall, these results suggest that the correlations between community-level trait values and wood productivity in Amazonian forests are not causative: direct environmental control of biomass growth rates appears to be the most important driver of wood production at regional scales. This result contrasts with findings for forest biomass where variation in wood density, associated with variation in species composition, is an important driver of regional-scale patterns. Tropical forest wood productivity may therefore be less sensitive than biomass to compositional change that alters community-level averages of these plant traits.

1 Introduction

Understanding the relative roles of species composition and abiotic factors on ecosystem properties at large spatial scales remains a considerable challenge (Hooper et al., 2005). However, understanding these relationships is critical for predicting how compositional and environmental change will influence ecosystem properties such as carbon cycling. These issues are particularly important in tropical forests because of the importance of these ecosystems in the global carbon cycle – tropical forests contain 60% of the carbon stored in living and dead vegetation in forest ecosystems worldwide (Dixon et al., 1994). Experimental studies of the relationships between biodiversity and ecosystem function have shown that plant traits have an important role in determining the relationships between species composition and ecosystem properties (Diaz and Cabido, 2001). Therefore, to predict how feedbacks between environmental and compositional change might operate at large scales in tropical forests, there is a need to test whether current patterns of ecosystem properties are determined by variation in plant traits.

Here, we examine the role of wood density and species maximum height for determining patterns of above-ground wood productivity in Amazonian forests. Wood density and plant maximum height are important plant traits as they quantify species' position along the two major axes of functional variation amongst tropical trees – light demand and maximum size (Turner, 2001; Baker et al., 2003). However, attempting to tease apart the mechanisms linking plant traits and ecosystem functions in field studies is not straightforward. Here, we take a three-stage approach. Firstly, we examine spatial variation between forests in the distribution of trait values, secondly, ask how the traits relate to variation in biomass growth rates and thirdly consider if these patterns are strong enough to generate the observed differences in stand-level productivity.

There is evidence that distributions of both wood density and species maximum size vary between tropical forests. At the stand level, spatial variation in forest functional composition can be examined by comparing community-level averages of species traits

calculated as simple means across species, or weighted by species abundance or basal area (cf. Baker et al., 2004a; Garnier et al., 2004). For Amazonian forests, it is well-established that there is an east-west gradient in average wood density (Baker et al., 2004a; Chave et al., 2006; ter Steege et al., 2006) that matches the three-fold variation in stand-level coarse wood productivity (Malhi et al., 2004). Spatial variation in average maximum height is poorly studied, but may also be significant. For example, understorey communities in tropical forests vary in the relative abundance of understorey species compared to juvenile canopy trees (LaFrankie et al., 2006). In addition, low levels of flowering and fruiting in the understorey in seasonal, neotropical forests on infertile soils (Gentry and Emmons, 1987) suggest that a large proportion of stems in these sites belong to canopy tree species.

The second stage of determining if these traits drive variation in overall productivity is to examine whether species-level variation in wood density and maximum size is related to differences in growth rate. For example, seedling studies of tropical forest tree species have shown that more light-demanding and larger-stature species have higher relative growth rates than more shade-tolerant or smaller-stature species (e.g. Veenendaal et al., 1996) and plot-based studies have shown similar patterns for diameter growth rates of adult trees (e.g. Lieberman and Lieberman, 1987). However, there have been few comparative studies of the biomass growth rates of mature tropical tree species.

To assess whether plant traits drive variation in productivity where variation in climate, soils or vegetation structure might also be important, a useful approach is to express productivity as:

$$
\text{ANPP} = \frac{\sum_{j=1}^{n_j} \left(N_j \times M_j \times e^{\text{RGR} \times \Delta T} - 1 \right)}{\Delta T}
\tag{1}
$$

(Lavorel and Garnier, 2002). Here, annual net primary productivity, ANPP, over a period, ΔT, is a function of the number of stems, N, of mass M, and relative growth rate

RGR, of all species or lifeforms, j, in the community. Over gradients of productivity, changes in the different components of this equation, related to vegetation structure, growing season length or relative growth rate, can be used to infer which factors are most important in determining variation in ANPP. Lavorel and Garnier (2002) used this method to argue that variation in relative growth rates associated with differences in plant traits such as specific leaf area, rather than variation in the total biomass or growing season length, was the main factor determining variation in ANPP across four herbaceous communities in Central Europe.

In this study, we test the hypothesis that forest functional composition defined in terms of wood density and maximum height determines variation in the aboveground wood production of 60 Amazonian forest plots. Firstly, we present a new dataset of species maximum heights to explore how this trait varies among different Amazonian forests. We then combine this dataset with existing data on wood density to examine patterns of biomass increment between different functional groups. Finally, we develop the approach of Lavorel and Garnier (2002) to test whether variation in functional composition is sufficient to explain the observed variation in rates of wood production.

2 Materials and methods

2.1 Forest plot data

This study used inventory data of all trees ≥10 cm diameter in 60 forest plots across Amazonia, from the RAINFOR database (Peacock et al., 2007; Fig. 1). These plots were categorised into three regions (northwest, southwest and central and eastern Amazonia, Fig. 1) with similar numbers of plots, and in total cover 79.9 ha. Plots have been selected to sample the range of environmental conditions at local and regional scales within Amazonian forests (Malhi et al., 2002). Each plot is typically 1 ha and has data for two or more consecutive censuses, collected using standardised protocols. Diameter growth rates have been checked on a tree-by-tree basis, and outliers treated

following standardised procedures described in Baker et al. (2004b).

The three regions differ broadly in both climate and soils. Forests in northwestern Amazonia have an aseasonal climate, typically with 0–1 month per year with less than 100 mm rainfall. In contrast, forests in both southwestern and central and eastern Amazonia generally experience a 3–4 month dry season (Sombroek, 1999). In terms of edaphic conditions, the forest plots in central and eastern Amazonia are found on predominantly infertile oxisols, whereas more fertile soils are found in lowland forests in western Amazonia (Sombroek, 2000). Most plots are located on tierra firme sites, on clay rich soils. However, a number of the forest plots in northwestern Amazonia (ALP-12, 21 and 30) are located on white sands and one plot (SUC-03) is seasonally flooded.

2.2 Trait data

Maximum height data (m) was sourced from regional floras (Vásquez Martínez, 1997, 732 species; Ribeiro et al., 1999, 21 species; Killeen et al., 1993, 325 species, excluding height estimates for values based on single sterile specimens) and previous compilations from floras and monographs (Chave, 1999, 498 species; Pitman et al., 2001, 452 species). Specimen records including height estimates were also obtained from the Missouri Botanical Garden TROPICOS database via SALVIAS (The SALVIAS Project, 2002 and onward), and the 95th percentile of the distribution of height values used as a measure of maximum height (202 species). Average values were calculated for species where more than one estimate of maximum height was available. Overall, maximum height data were obtained for 1358 species. Wood density data (dry mass/green volume) was derived from a compilation from across the neotropics (Chave et al., 2006) that currently contains data for 2573 species.

Several recent studies have analysed patterns of functional composition in Amazonian forests at the genus level (e.g. ter Steege et al., 2006). In this study, 73.3% of stems identified to species-level were allocated a species-level match for maximum height, and 64.7% for wood density. As both wood density (Baker et al., 2004a; Chave

3599

et al., 2006) and maximum height estimates are phylogenetically constrained (variance components analysis for maximum height dataset: 28.5±4.5% of variation explained by differences among genera, and a further 24.1±7.1% by variation across families), for species where no data was available, or those stems not identified to species-level, generic- or family-level means were used to allocate values, following Baker et al. (2004a). Patiño et al. (2008) find considerable plasticity in the branch wood density of widespread species in Amazonia, suggesting that environmental variation may have an important influence on wood density values of species in any particular location. However, in the absence of evidence for strong interactions between environmental and genetic factors, and the observation that closely related species often have similar ecological roles in different forests (e.g. *Cecropia* sp. are low wood density, pioneer trees across Amazonia; *Rinorea* sp. are important small-stature, understorey species in both western and central Amazonia) it seems reasonable to use the literature trait data as a means of positioning species along these functional axes.

2.3 Data analysis

Firstly, community-level average maximum height was compared between the three regions of Amazonia. Associations between stature class and the 20 most diverse plant families were examined using chi-square tests. Average maximum height was also correlated with long-term, coarse-wood production estimates (Malhi et al., 2004) and soil fertility quantified using plot-level measurements of soil sum of bases, where available (C. Quesada and J. Lloyd, unpublished work). These results were contrasted with those for average wood density. For five, recently established plots comparable coarse-wood production estimates were calculated following the procedures in Malhi et al. (2004), based on the annual rate of basal area gain and a correction for census interval length.

Secondly, the growth rates of different functional groups based on both wood density and maximum height were compared in terms of biomass increment. The high diversity precludes a species-level analysis, so species were classified as subcanopy

3600

(where the maximum height averaged across all sources was up to 20 m), canopy (≥20 and <30 m), or emergent (≥30 m), and as low (<0.5 g cm^{-3}), medium (≥0.5 and <0.7 g cm^{-3}) or high (≥0.7 g cm^{-3}) wood density, resulting in a total of nine functional groups. One census interval was chosen from each plot to calculate the growth rate of each functional group. Census-interval choice was dictated by the need to sample tree growth rates across equivalent time periods and to minimise variation in census-interval length among plots. The data selected therefore incorporate the most recent measurement where data were available and the previous census that fulfilled these conditions. Although there is inevitably some interplot variability, census interval length ($F_{2,57}$=1.88; overall mean 4.8±0.1 years), start ($F_{2,57}$=2.44; overall mean 1997.3±0.3) and end year ($F_{2,57}$=1.92; overall mean 2002.2±0.3) do not differ significantly among regions. In total, the initial census data comprised 48 879 stems, 79.5% identified to species, 93.3% to genus and 94.8% to family, amounting to 2119 identified species in 535 genera and 89 families. Absolute growth rates for all surviving stems during the selected census interval were calculated in terms of biomass, for each functional group, within three diameter classes: 10–19.9 cm, 20–39.9 cm and ≥40 cm. Palms and Strelitziaceae, which have no secondary growth, were excluded from this analysis. Biomass was calculated using two different allometric relationships between diameter and tree biomass developed

1. for forests near Manaus, with a correction factor to account for variation in wood density (Baker et al., 2004a; Chambers et al., 2000, Eq. 2.1) and

2. for all moist tropical forests, incorporating terms for tree diameter and wood density, based on a pantropical compilation of tree biomass data (moist forest equation, excluding tree height, Chave et al., 2005).

As distributions of growth rates are strongly skewed, 95% confidence limits for each subregion/group/size-class combination were determined from the distribution of growth rates obtained by resampling the observed data 1000 times. Significant differences between functional groups were inferred by non-overlapping confidence limits

within each region/size class combination.

Finally, we examined whether variation in the abundance and growth rates of different functional groups was sufficient to predict variation in observed stand-level wood productivity. We calculated estimates of wood production for each plot as the product of the abundance, mean biomass and relative growth rate of trees in different diameter classes, in different functional groups. These estimates were compared with observed data in Malhi et al. (2004).

More formally, estimates of wood productivity were calculated as:

$$\text{AGWP}_k = \left[\sum_{f=1}^{f=9} \sum_{s=1}^{s=3} \left(N_{s,f(k)} \times \langle M_{s,f} \rangle \times \langle R_{s,f} \rangle \right) \right] A_k^{-1} \tag{2}$$

where AGWP (Mg C ha^{-1}) is the rate of wood production in plot k, $N_{s,f(k)}$ denotes the number of stems in size class s (10–20 cm, 20–40 cm or 40+ cm), in functional group f, in plot k, and A_k is the area (ha) of plot k. $\langle M_{s,f} \rangle$ is the average biomass of a tree in size class s, and functional group f, calculated across the whole dataset. $\langle R_{s,f} \rangle$ is the mean relative growth rate of a tree, r (a^{-1}), in size class s, and functional group f, also calculated across the whole dataset. r was calculated for each tree as the biomass increment divided by the initial biomass, following similar linear formulations for relative diameter increment by Welden et al. (1991). This linear formulation was used to standardise growth rates per size class rather than the classical logarithmic form, as the growth of adult trees is not exponential over time.

Apart from the use of a linear and not exponential form for r, and the exclusion of a term for growing season length for these forests where the majority of species are evergreen, this formulation is identical to Eq. (1) from Lavorel and Garnier (2002).

3   Results

3.1   Variation in maximum height in Amazonian forests

Maximum height averaged across species is 14% lower in the plots in western compared to central and eastern Amazonia ($F_{2,57}=35.6$, $p<0.001$, Fig. 2). This regional difference is also significant if the means are computed on a per-stems basis ($F_{2,57}=10.6$, $p<0.001$) and on a basal-area basis ($F_{2,57}=5.6$, $p<0.01$). These differences occur because of variation in the relative abundance and species richness of understorey trees in different parts of Amazonia (Fig. 2). Stems of species with maximum heights <20 m are over-represented in the western Amazon plots, compared to the plots in central and eastern Amazonia, whilst species with maximum heights between 20–30 m form a greater proportion of the stems in the central and eastern Amazon forests.

As expected, many families are strongly associated with one or more stature classes (Table 1). Four of the 20 most diverse families are understorey specialists, 5 are canopy specialists, and 3 are associated with emergent species. Only 5 of these 20 families are not comprised of species that preferentially occupy a particular stratum of the forest canopy (Table 1). Different families are important in the understorey in the plots in central and eastern, and western Amazonia. Four of the five most diverse families in the understorey are shared by the plots in both northwestern and southwestern Amazonia (Table 2). In contrast, three of the families that are the most diverse in the understorey in central and eastern Amazonia, do not make a major contribution to understorey diversity in the western Amazon plots (Table 2).

Across all plots, both wood density and average maximum height are negatively correlated with wood productivity (Fig. 3; stems basis, wood density, $t=-7.20$, $r^2=0.46$, $p<0.001$; maximum height, $t=-3.65$, $r^2=0.17$, $p<0.001$). For the plots where average values of soil sum of bases (SB) were available, average maximum height is significantly negatively correlated with $\log[SB]$, when calculated on a stems ($t=-3.65$, $r^2=0.23$, $p<0.001$), species ($t=-3.54$, $r^2=0.22$, $p<0.005$) or basal-area basis ($t=-3.56$, $r^2=0.22$, $p<0.001$). Overall, plots in western Amazonia with more fertile

soils and higher rates of wood productivity, typically have a greater relative abundance of stems of taxa with low wood density and low maximum heights (Figs. 2 and 3).

3.2   Rates of biomass increment and implications for stand-level patterns of wood productivity

Estimates of biomass growth rate of all functional groups calculated using the Chambers et al. (2000) or Chave et al. (2005) equations were closely correlated: $r^2=95.5\%$, cf. Peacock et al. (2007). The close correlation means that the choice of biomass equation does not alter the conclusions about the differences in biomass increment between functional groups and we report further values using the equation based on the Manaus allometric relationship (Chambers et al., 2000), consistent with the method used to estimate wood production in Malhi et al. (2004).

Three results emerge from the comparisons of biomass growth rates across functional groups and regions. Firstly, biomass growth rates were generally lower in the plots in central and eastern Amazonia, compared to western Amazonia, across most size classes and functional groups (Fig. 4, southwestern compared to central and eastern Amazonia, biomass growth rates significantly lower in 14/24 comparisons; northwestern compared to central and eastern Amazonia, biomass growth rates significantly lower in 14/24 comparisons). Secondly, there is no trend for higher rates of biomass increment in species of low wood density. In fact, higher rates of biomass increment tend to be found in taxa with high, compared to low, wood density (Fig. 4, 5/24 comparisons significant). Thirdly, biomass growth rates were also generally significantly higher in emergent compared to subcanopy trees, within any particular size class (Fig. 4, 14/24 comparisons significant).

Estimates of wood productivity based on the size structure and abundance of different functional groups calculated using Eq. (2), are significantly correlated with the observed values (Fig. 5a, $F_{1,56}=15.1$, $p<0.001$). This correlation is driven by variation in size structure among the plots. However, the estimated values do not account for the regional differences in productivity: observed values of wood productivity are

significantly different between regions for any given estimated value (Fig. 5a, ancova, $F_{2,56}$=41.3, p<0.001). More simply, the estimated values do not predict the higher observed average biomass growth rates in the western Amazonian plots (Fig. 5b, regional differences in observed values: $F_{2,57}$=35, p<0.001; estimated values: $F_{2,57}$=2.1, ns). In this network of forest plots, it is not possible to predict the regional patterns of wood production solely on the basis of the abundance, mean biomass and relative growth rate of trees in different diameter classes and functional groups. The consistently higher biomass growth rates across all functional groups in the western Amazonian plots (Fig. 4), appears to be the key factor determining the regional scale pattern.

4 Discussion

4.1   Variation in species maximum heights in Amazonian forests

The lower community-level maximum height in plots in western compared to central and eastern Amazonia (Fig. 2), is consistent with studies of forest phenology and variation in shrub and sapling composition. For example, flowering and fruiting in the understorey is less frequent in forests near Manaus, compared to a range of other neotropical sites (Gentry and Emmons, 1987) suggesting that these forests contain few specialist understorey species. In addition, a smaller proportion of species are classified as shrubs in the species list for the Reserva Ducke near Manaus compared to western Amazon floras (Phillips et al., 2003). Furthermore, in a pan-tropical comparison of six forests, the highest abundance of small-statured species, amongst saplings 1–2 cm diameter, was found in western Amazonia – at Yasuní, Ecuador (LaFrankie et al., 2006). Overall, these studies and the results here suggest that a suite of plant families contribute to a distinctive, diverse and abundant understorey flora in western Amazonian forests.

Climatic factors appear unlikely to drive this pattern, as dry season length varies strongly within western Amazonia – from greater than five, to less than one month with

less than 100 mm rainfall (Sombroek, 1999) – without similar variation in community-level average maximum height. Variation in soil fertility may be more important, following the suggestion of Gentry and Emmons (1987) that seasonal drought in combination with low soil fertility may be a strong limitation to growth and reproduction in the shade in central Amazonia. This hypothesis is supported by the significant correlation between log[SB] and average maximum height in this study and experimental work on seedling growth: root competition is a greater limitation to growth of seedlings in the understorey on nutrient-poor compared to nutrient-rich soils in tropical forests (Lewis and Tanner, 2000; Barberis and Tanner, 2005). Soil fertility may also indirectly affect the understorey light environment through its relationship with tree mortality rates (Phillips et al., 2004). For example, the higher tree mortality rates in western Amazonian forests may allow greater light to the forest floor in these sites, promoting the growth of understorey plants in these forests.

The correlations between soil fertility and community-level maximum height may not however hold for all tropical forests. Firstly, other factors, such as disturbance, may be more important for individual sites: one structurally similar western Amazon forest, for example, has a depauperate understorey flora thought to result from a failure of these taxa to recolonise following a catastrophic disturbance (Pitman et al., 2006). Secondly, these relationships may not hold for tropical forests on other continents. For example, in Ghanaian tropical forests, Swaine and Becker (1999) found no overall relationship between soil fertility and the proportion of treelet and shrub species in 155, 0.0625 ha plots and Poorter et al. (2008) found no change in the proportion of small stature species in a one hectare plot network along an annual rainfall gradient from 1200–2100 mm associated with a marked decline in soil fertility. The strong drought stress, and also greater disturbance impacts (Poorter et al., 2008), in the most fertile sites in these forests may override any effect of soil fertility on this aspect of functional composition. Biogeographical differences between continents might also be important, as the families of the understorey specialists that determine the high abundance of small-statured species in the 1–2 cm diameter size classes in wet neotropical sites, are

not found in paleotropical forests (LaFrankie et al., 2006).

4.2 Variation in biomass growth rates between functional groups and implications for stand-level productivity

The lack of consistent differences in biomass increment across wood density classes contrasts with results from seedling experiments, which typically show higher rates of carbon gain in more light-demanding species at high light levels (e.g. Veenendaal et al., 1996). Studies of biomass increment in mature tropical trees are rare, but two other studies have reported similar results. Chambers et al. (2004) found no difference in rates of biomass increment across 72 tree species when the biomass estimates incorporated interspecific variation in wood density, and in dry forest in Mexico, Enquist et al. (1999) found that variation in diameter growth rates was smaller when they were adjusted for interspecific variation in wood density. On fertile soils in northwestern Amazon forests, trees of high wood density species may even tend to have higher rates of biomass increment than species with low wood density (H. Keeling, T. R. Baker, O. L. Phillips, unpublished work). Overall, the lack of a consistent relationship between biomass increment and wood density class in this study suggests that the well-known variation in diameter increment between species that differ in wood density, reflects differences in carbon allocation strategies as adult trees, rather than differences in rates of net carbon gain. There is stronger evidence that species maximum size is positively related to rates of biomass increment (Fig. 4). Higher rates of biomass increment in species with greater maximum size is consistent, for example, with higher leaf-level photosynthetic rates of saplings of species that have greater adult maximum heights (Thomas and Bazzaz, 1999).

In contrast to patterns across functional groups, consistent differences are found in biomass growth rates across regions, with lower growth rates in central and eastern Amazon forests (Fig. 4). Overall, the relatively small differences in biomass growth rates between functional groups compared to the large differences between regions, suggests that environmental effects are more important than these plant traits for deter-

3607

mining regional differences in aboveground productivity. This conclusion is supported by the values of stand-level productivity based only on the composition of the stands: these estimates fail to predict the regional differences in wood productivity (Fig. 5). These results support the suggestion that the direct effect of edaphic conditions is the main driver of the regional patterns of wood productivity (Malhi et al., 2004).

In contrast to these conclusions, experimental studies of grassland ecosystems have demonstrated that functional composition, such as the presence of nitrogen fixing, non-nitrogen fixing, annual or perennial species, can influence net primary productivity (e.g. Wardle et al., 2000). One explanation for our opposite conclusions may concern the traits that we studied. There may be important variation amongst traits (e.g. specific leaf area, SLA) or functional groups (e.g. nitrogen/non-nitrogen fixers) of tropical trees that were not studied here, that may influence spatial patterns of productivity. A second explanation is that the differences in functional composition in Amazonian forests are simply too small to have a detectable impact on wood productivity. For example, in tropical agroforestry systems, in comparisons of very different lifeforms, such as between maize and tree crops, productivity can vary greatly at the same site (Ewel and Bigelow, 1996). However, productivity may not differ between more similar species combinations, such as enriched versus natural successional forest vegetation (Ewel and Bigelow, 1996).

A third, related explanation is that the large influence of environmental factors in broad-scale field comparisons of productivity, makes it difficult to detect small compositional effects. In general, relationships between biodiversity and ecosystem functioning may differ depending on the scale of study (e.g. for invasion resistance, Levine, 2000). Field studies of the relationship between productivity and plant traits are often carried out within single areas (e.g. Garnier et al., 2004), at spatial scales where effects of species characteristics will be more easily detected (Lavorel and Garnier, 2002). At larger scales, it may be more difficult to detect these relationships. For example, in terms of the effect of species richness on productivity in forests at large spatial scales, Vilà et al. (2003) found no effect when variation due to climate and bedrock was also

3608

considered, in a study of pine forests in Spain, and Vilà et al. (2007) report a small, but significant, effect in Mediterranean forests. However, even in the second case, the significant effects of environmental variables were far larger than the effect of species richness.

In conclusion, it is noteworthy that the relationship between plant traits and ecosystem properties differs for wood productivity and biomass in Amazonian forests. As wood density is an important trait in biomass estimation (Chave et al., 2005), spatial variation in this trait directly influences variation in biomass estimates (Baker et al., 2004a). As a result, compositional changes that alter community-aggregated values of wood density may therefore alter forest biomass (cf. Bunker et al., 2005). One mechanism that might lead to such a change in forest functional composition is the observed increase in the rate of tree turnover in Amazonian forests (Phillips et al., 2004) that may favour species with lower wood density. Our study shows that at large spatial scales, in contrast to forest biomass, wood productivity is not influenced by variation in these plant traits and therefore may be less sensitive to such trajectories of compositional change.

3609

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3610

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Table 1. Associations between stature class and species richness for the 20 most diverse families of trees ≥10 cm diameter in 60 Amazonian forest plots. For each family, associations tested using chi-square tests, using records where species-level data on maximum height was available. For families where a significant association was found, instances where family species richness exceeded expected values listed.

| | | Over-represented in | |
No association	Understorey (0–19.9 m)	Canopy (20–29.9 m)	Emergent (≥30 m)
Fabaceae	*Euphorbiaceae*	*Annonaceae*	*Moraceae*
Lauraceae	*Rubiaceae*	*Moraceae*	*Sapotaceae*
Myristicaceae	*Salicaceae*	*Chrysobalanaceae*	*Lecythidaceae*
Apocynaceae	*Melastomataceae*	*Euphorbiaceae*	*Elaeocarpaceae*
Clusiaceae	*Sapindaceae*	*Burseraceae*	
		Meliaceae	
		Urticaceae	

3615

Table 2. Five most diverse families of understorey trees ≥10 cm diameter, in three regions of Amazonia, in descending order of species richness.

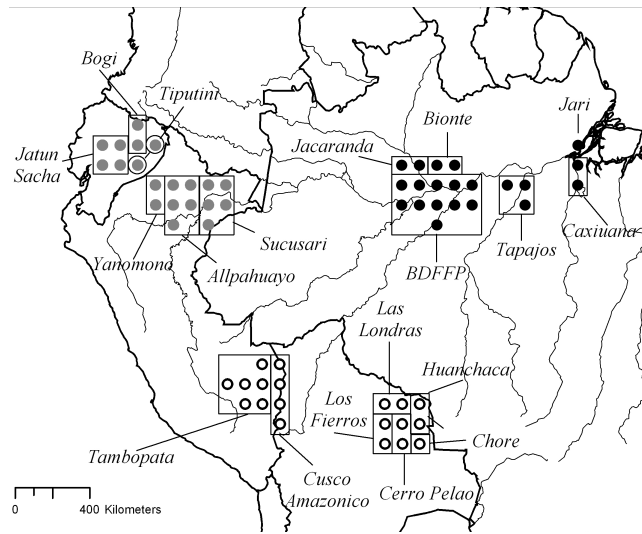| Northwestern Amazonia	Central and eastern Amazonia	Southwestern Amazonia
Fabaceae	*Annonaceae*	*Fabaceae*
Rubiaceae	*Myrtaceae*	*Salicaceae*
Salicaceae	*Fabaceae*	*Euphorbiaceae*
Euphorbiaceae	*Burseraceae*	*Melastomataceae*
Annonaceae	*Sapindaceae*	*Rubiaceae*

Fig. 1. Location of 60 permanent forest plots in Amazonia. Grey circles, northwestern Amazonia; open circles, southwestern Amazonia; black circles, central and eastern Amazonia. For clarity, plot location is approximate.
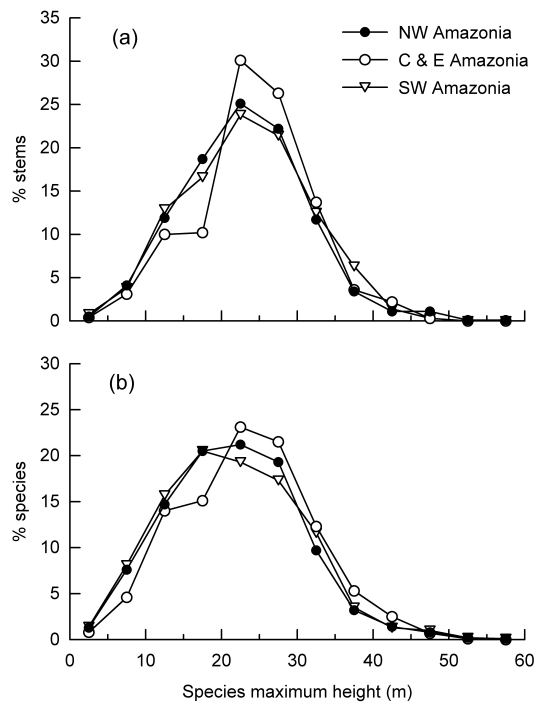
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Fig. 2. Relative abundance of **(a)** stems, and **(b)** species of different maximum heights, in three regions of Amazonia.
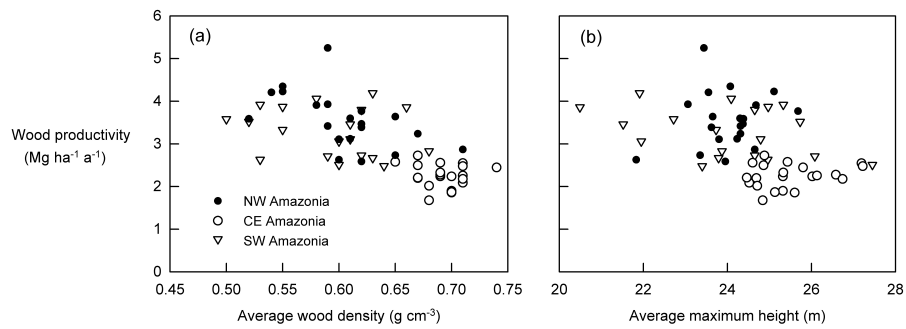
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Fig. 3. Relationship between average wood density and average maximum height per plot calculated on a stems basis and wood productivity for 60 Amazonian forest plots.
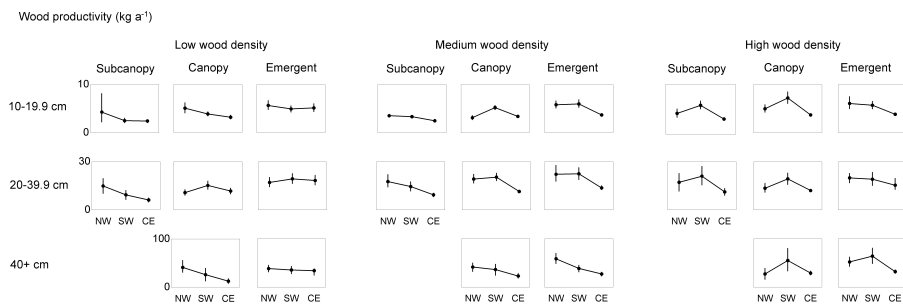
3619

Fig. 4. Mean biomass growth rates for nine functional groups in three size classes in three regions of Amazonia. Error bars are 95% confidence limits based on resampling the original data 1000 times.
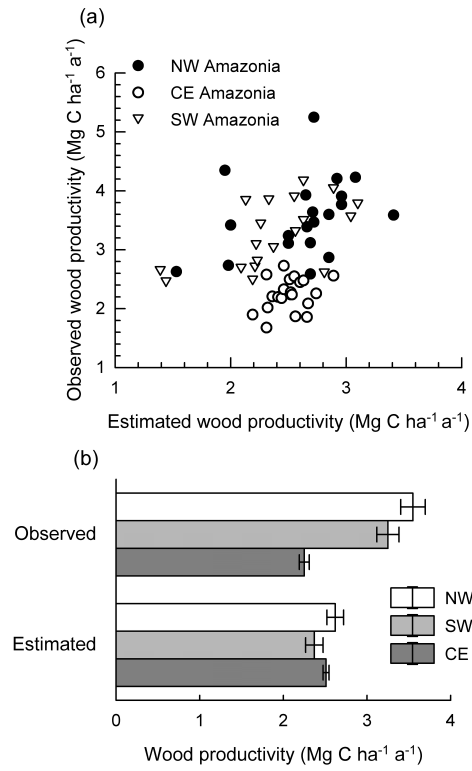
Fig. 5. (a) Relationship between observed wood productivity and estimated values calculated in this study based on the functional composition of the stand. **(b)** Regional comparison of mean (±S.E.) observed and estimated values of wood productivity.