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Branch xylem density variations across Amazonia

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Abstract

Measurements of branch xylem density, D_x, were made for 1466 trees representing 503 species, sampled from 80 sites across the Amazon basin. Measured values ranged from 240 kg m^{-3} for a *Brosimum parinarioides* from Tapajos in West Pará, Brazil to 1130 kg m^{-3} for an *Aiouea* sp. from Caxiuana, Central Pará, Brazil. Analysis of variance showed significant differences in average D_x across the sample plots as well as significant differences between families, genera and species. A partitioning of the total variance in the dataset showed that geographic location and plot accounted for 33% of the variation with species identity accounting for an additional 27%; the remaining "residual" 40% of the variance accounted for by tree to tree (within species) variation. Variations in plot means, were, however, hardly accountable at all by differences in species composition. Rather, it would seem that variations of xylem density at plot level must be explained by the effects of soils and/or climate. This conclusion is supported by the observation that the xylem density of the more widely distributed species varied systematically from plot to plot. Thus, as well as having a genetic component branch xylem density is a plastic trait that, for any given species, varies according to where the tree is growing and in a predictable manner. Exceptions to this general rule may be some pioneers belonging to *Pourouma and Miconia* and some species within the genera *Brosimum, Rinorea* and *Trichillia* which seem to be more constrained in terms of this plasticity than most species sampled as part of this study.

1 Introduction

The Amazon Basin remains the home to the most diverse and largest contiguous tropical forest on the planet (Malhi and Grace, 2000; Laurance et al., 2004). Different ecological systems and vegetation formations exist within its boundary creating a mosaic of forests and vegetation types with a floristic complexity the basis of which is still not well understood (Phillips et al., 2003).

How and why species are distributed and where trees can grow in this mosaic of tropical forest types is a central question for tropical ecology (Pitman et al., 2001; Phillips et al., 2003). On the one hand water availability has been considered as an important factor determining tree species distributions at global (Woodward, 1987) and regional scales (Borchert, 1998; Veenendaal and Swaine, 1998; Bongers et al., 1999). Tree physiology data also shows that it may be one key factor determining species distributions in tropical rain forest despite the substantial rainfall they receive (Meinzer et al., 1999; Engelbrecht et al., 2002, 2005, 2006, 2007; Tyree et al., 2003; Baltzer et al., 2008). On the other hand, although water shortage (seasonality and rainfall) is not considered by some as an important selective pressure determining the functional composition of moist and wet tropical forest (Baker et al., 2004b; ter Steege and Hammond, 2004), it clearly does help to determine overall diversity and distribution patterns of canopy tree genera across the Amazon basin (ter Steege et al., 2006). Light as a factor explaining coexistence of trees has also been considered (Poorter and Arets, 2003) and climate more than geographic distance in lowland forest seems also to affect species composition (Pitman et al., 2001) and distributions (Bongers et al., 1999; Baltzer et al., 2008). Additionally, even if there clearly is some “distance-decay” i.e. the similarity between two sites declines as the distance between them increases, see (Soininen et al., 2007) in Amazonian forest communities (Condit et al., 2002; Tuomisto et al., 2003), consistent with the view of plant species distribution as a partly random controlled process (Hubbell, 2001), it is also clear that substrate-mediated processes play a significant deterministic role in controlling species distributions across Amazonian landscapes (Gentry, 1988; Tuomisto et al., 1995, 2003; Phillips et al., 2003), this also being the case for other tropical forests (Harms et al., 2001; Robert et al., 2007). These theories are by no means exclusive, and one of the main purposes of the work described in this special issue (Lloyd et al., 2008a[1]) was to interface dedicated plant physiological trait data with species abundance, climate and soil type information to

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[1] Lloyd, J., Grace, J., and Meir, P.: Introducing the “Biogeochemistry and Function of Amazon Forest” project, Biogeosciences Discuss., in preparation, 2008a.

help understand the underlying factors controlling species distribution, composition and stand dynamics at the Basin-wide scale. In what is the first of a series of papers, we here analyse in detail geographic and taxonomic patterns of tree branch wood density across Amazonia. Although wood density (D_w) is most often measured on tree boles sampled after destructive harvesting, often in association with commercial operations (Baker et al., 2004b; Chave et al., 2006), here we have used an alternative approach – the sampling of the density of the functional xylem or sapwood of small (ca. 1.5 cm diameter) branches. This measurement, referred here as "xylem density", D_x, is a plant trait usually considered in physiological processes studies; for example when looking at wood properties in relation to transpiration, stem water storage capacity, cavitation resistance, mechanical support, photosynthesis and/or growth (Niklas, 1997; Enquist et al., 1999; Stratton et al., 2000; Hacke et al., 2001; Meinzer, 2003; Bucci et al., 2004; Santiago et al., 2004; Jacobsen et al., 2007a, 2007b; Pratt et al., 2007; Scholz et al., 2007). We rationalised that these are all processes that should be expected to influence where a given tree species can survive and thus should ultimately contribute to the shaping of species distributions across landscapes.

For any given species D_x and D_w should be related as both reflect an individual species' water transport strategy and the invariable trade-off against mechanical strength (Taneda and Tateno, 2004; Wagner et al., 1998; Asner and Goldstein, 1997). But D_w may well be affected by factors in addition to those modulating D_x. For example it may also reflect differences in the storage of resins and/or increased of secondary compounds of bole heartwood with time, different biomechanical requirements for maintaining vertical position and support of the whole tree and individual branches, also generally reflecting the longer term growth history of the tree. It means that, D_w may be considered to effectively integrate plant ontogeny, edaphic and climatic effects over a plant's lifetime.

It has long known that D_w is a genetically conserved trait, and this characteristic has been used extensively in tree breeding (Yang et al., 2001) also leading to studies of its phylogenetic inheritance (Enquist et al., 1999; Chave et al., 2006). Nevertheless, it has also long been known that for a given tree species, marked variations may be observed attributable to differences in site quality and/or forest type. There have already been several reports of variations with site/growth conditions of order 10% for plantation tropical tree species (Roque, 2004; Erskine et al., 2005). Similarly, site specific differences have been noted when comparing the same species growing in different forests or site conditions (Gonzalez and Fisher, 1998; Woodcock et al., 2000; Muller-Landau, 2004; Parolin and Ferreira, 2004; Roque, 2004; Nogueira et al., 2005; Nogueira et al., 2007). Lower D_w is often associated with early and secondary succession vegetation (Saldarriaga 1989; Woodcock et al., 2000) and higher growth rates (Wiemann and Williamson, 1989; Erskine et al., 2005; Nogueira et al., 2005; King et al., 2005, 2006).

We thus hypothesised that D_x is a "plastic" trait that reflects both phylogenetic heritage of trees and overall site conditions. Therefore variations in D_x at the stand level across Amazonia should not only reflect differences in species composition, but differences in soil and climate conditions. If a given species can grow in different sites, D_x of that species may converge to an "average" value of that of co-occurring species within each site. If this is true, species with enough phenotypic plasticity can occupy more and larger areas and become more common than species with small plasticity which will occupy restricted areas and become "rare" species at a large-scale but common in just one site.

2 Methods

2.1 Study sites

Eighty forest plots from across the Amazon basin were sampled normally, at the end of the rainy season of the region between January 2001 and December 2005. Additionally, two plots were sampled in Paracou, French Guiana in September 2007 (see details below). These plots form part of the RAINFOR project (www.rainfor.org; Malhi et al., 2002) and span local, regional and Basin-wide environmental gradients. Many of the plots have been described in detail elsewhere (Baker et al., 2004a, b; Malhi et al., 2002; Phillips et al., 2004; Vinceti, 2003) and Appendix A lists all the plots visited, including those not previously described and in some cases with updated information.

2.2 Sampling of plant material

Normally, around 20 trees greater than 10 cm dbh (diameter at breast height i.e. at 1.3 m from the base of the tree) were chosen in each plot. On some occasions, for instance when plots were unusually heterogeneous, as a consequence of topographic variations and/or shape (i.e. 1000×10 m) more trees were sampled (for example Bogi plots in Ecuador). For two of the Caxiuana plots (Central Pará, Brazil) we had sampled in two consecutive years (2002 and 2003) and since there was no statistical difference in D_x for the two years, we merged the data in just one set. When a plot was clearly composed of different defined landscapes, and each landscape was considered as an individual plot with often less than 20 trees sampled within it (e.g. Jacaranda Plots, Km 34 Manaus, Brazil).

Trees were not chosen completely at random but taking into account two factors. First, often there was a selection of three to six contrasting areas (slopes, valleys, gaps, flood, etc) where these were present, a professional tree climber then choose a “climbable tree” within the generally identified areas. Naturally, this “climbable tree” varied from climber to climber according to the technique employed and overall climbing skills. Nevertheless a general rule was that the “climbable tree” was >10 cm dbh with at least some neighbouring trees reachable by a clipper pole. From the climbed tree, the climber sampled one branch from each of the upper, (exposed to the sun), middle (semi light) and lower crown (shade), and one branch from the upper crown of the (usually three to five) surrounding trees.

The only difference for this sampling strategy was for two of the Guyaflux plots at Paracou, French Guiana where only lower branches from subcanopy trees were sampled. An analysis of over 200 trees comparing D_x of branches from the upper, middle and lower crown of the trees using the techniques described in Lloyd et al. (2008b)[2] has, however, shown no statistically significant effect of height on D_x (data not shown). The subcanopy trees sampled at Paracou represented the distribution of the main families present in those plots with D_x showing the same distribution of frequencies found for D_w of 309 trees from Paracou (J. Beauchen, personal communication). In any case, because these measurements were made after the main analysis of this paper we have simply included these values to help illustrate regional patterns (Fig. 1).

2.3 Species identification

Details of the species identification from the permanent plots are described elsewhere (Baker et al., 2004b) and in this work we have used the new classification given by the Angiosperm Phylogeny Group II (APG 2003, http://www.mobot.org/MOBOT/Research/APweb/), in which *Bombacaceae*, *Sterculiaceae*, and *Tiliaceae* are all included in the *Malvaceae*; *Papillionaceae*, *Caesalpinaceae*, and *Mimosaceae* are included in the *Fabaceae*; *Cecropiaceae* in the *Urticaceae*; and *Flacoutiaceae* in the *Salicaceae*.

2.4 Xylem density determinations

A pair of stem segments of 0.05 to 0.1 m long and 0.01 to 0.02 m diameter were cut from each branch after harvesting and immediately placed in plastic bags to avoid desiccation and returned to the laboratory or field station. Normally within 12 h of sampling (but sometimes as long as 36 h later) the outer bark and phloem were removed from one of the two sample stems and its fresh volume calculated from its stem length and the average diameter of the two equiaxial diameters at each end. When the pith was wider than 2 mm diameter the stem was cut into a small segment (0.02 to 0.05 m long)

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[2] Lloyd, J., Patiño, S., Paiva, R. Q., Nardoto, G., Quesada, C. A., Santos, A. J. B., Baker, T. R., Brand, W. A., Hilke, I., Gielmann, H., Raessler, M., and Mercado, L. M.: Gradients in leaf physiological properties within Amazon forest canopies, Biogeosciences Discuss., in preparation, 2008b.

and the pith removed with a small screw driver or scalpel. When the pith was thinner than 2 mm it was not removed from the stem (as it was thus assumed to be of negligible mass) but its volume subtracted from the volume of the stem without bark. Pith volume was calculated by measuring the average diameter (two measurements of diameter at each end of the stem) and stem length. All stems were then dried at 70–90°C for three to four days (to constant mass) and weighed. Xylem density, D_x, was then determined as the dry mass divided by the green volume of the sample.

2.5 Statistical analysis

Basic statistics shown in Figs. (1), (2), and (3) were performed with Minitab 14 (Minitab Inc.). All Standard Major Axis Regression analysis (Fig. 5) were done using SMATR (Warton et al., 2006). Variance partitioning for Fig. 4 was accomplished by applying Residual Error Maximum Likelihood (REML) analysis (Gilmour et al., 1995) employing GENSTAT Discovery Edition. Mixed-effect modelling (Fig. 6) was carry out with the "lmne" package (Bates et al., 2007) and rank-based linear regression (Fig. 7) accomplished as in Terpstra and McKean (2005), both using the "R" statistical computing package (R Development Core Team, 2007). For the latter analysis, we applied the "high-breakpoint" option (Chang et al., 1999) to account for the possibility of "contaminated" data having been included in any of the D_w values assimilated from a wide range of sources into the RAINFOR "wood density" database.

In order to determine the extent to which D_x changes in a given species within the same plot and between plots, IPP, index of phenotypic plasticity (Valladares et al., 2000), was calculated as the absolute difference between the maximum value and the minimum value divided by the maximum value.

3 Results

We measured D_x of 1466 trees from 80 plots across the Amazon basin (Appendix A) http://www.biogeosciences-discuss.net/5/2003/2008/bgd-5-2003-2008-supplement.pdf. Data for D_x followed a normal distribution with a mean value of 620 kg m^{-3}; normality test (StDev=0.13, N=1466, AD=1.82 P<0.001).

Of all the trees sampled, 92% (1352) had been identified to the family level, 86% (1258) to the genus level, and 69% (1006) to the species level. The trees sampled accounted for 58 families, representing 40% of the total number of families present in the neotropics (Mass and Westra, 1993) with 249 genera, and 503 species being sampled. The most common families sampled were *Fabaceae*, *Sapotaceae*, *Moraceae*, *Lecythidaceae*, *Burseraceae*, *Myristicaceae*, *Lauraceae*, *Euphorbiaceae*, *Chrysobalanaceae*, *Annonaceae*; with the most common genera being *Eschweilera*, *Pouteria*, *Protium*, *Inga*, *Licania*, *Pseudolmedia*, *Virola*, *Pourouma*, *Miconia*. The most common species were *Eschweilera coriacea*, *Pseudolmedia laevis*, *Rinorea guianensis*, *Tetragastris altissima*, *Minquartia guianensis*, *Pourouma guianensis*, and *Pseudolmedia macrophylla*. We had 20 undetermined *Protium* sp., 17 *Pouteria* sp., 14 *Inga* sp., 11 *Ocotea* sp., 10 *Eschweilera* sp.

3.1 Geographic variation

Arithmetic mean D_x for the 80 plots are shown in Fig. 1, which also shows our separation into 13 specified geographical regions and used for subsequent analysis.

From Fig. 1 a gradient of increasing D_x from south and north towards the Amazon River is apparent with high D_x being concentrated along the river itself. Plots located close to the Andes tend to have the lowest D_x. For example, all plots in Ecuador, some in North Perú, South Perú and Bolivia had a relatively low D_x compared to plots in Colombia and North Perú which were all at a lower altitude and closer to the Amazon River (see Appendix A). Similar patterns of low D_w in forests close to the Andes have previously been reported (Chave et al., 2006; Baker et al., 2004b; ter Steege et al., 2006). Taking the basin as a whole (no division into regions), statistically significant differences existed between plot means ($P<0.001$) ranging from $800\pm50\,\mathrm{kg\,m^{-3}}$ (± standard deviation) at the dry experiment plot at Caixuana (Projecto Secaflor), CAX-04, with the nearby control plot CAX-03 being the second highest at $780\pm120\,\mathrm{kg\,m^{-3}}$. These are both terra firme forests located in Central Pará, Brazil (CP-Brazil region). The lowest plot means were for TAM-03 a swamp forests in Tambopata, South Perú (S-Perú & AC-Brazil region) and JAS-05 a forest growing on recently deposited river sediments (fluvisol) in Jatun Sacha in the Ecuador region. Both these plots had a mean D_x of $470\,\mathrm{kg\,m^{-3}}$. Data for all 80 plots are summarised in Appendix B.

Figure 2 gives means (± standard deviations) for all plots, grouped according to region, with regions being presented sequentially from top to bottom according to the overall mean D_x for the trees sampled within them. This shows that, although considerable plot-to-plot variation existed within regions (e.g. N. Perú and Colombia) large statistical differences between regions also existed ($P<0.001$). Of these, the highest overall value was for Central Pará in Brazil ($760\pm130\,\mathrm{kg\,m^{-3}}$, $N=144$) which had significantly higher D_x (Tukey Test) than the rest of the regions while Ecuador had the lowest overall values ($540\pm92\,\mathrm{kg\,m^{-3}}$). Nevertheless, this region did not differ significantly from Acre, Mato Grosso (Brazil), Colombia and Bolivia. Within some regions: PC-Brazil, PE-Brazil, N-Perú, PW-Brazil, Colombia, S-Perú, MT-Brazil, and Ecuador mean D_x of plots varied considerably (Appendix B), while in some regions Bolivia, AC-Brazil, NE-Venezuela, SW-Venezuela, plots were not significantly different from each other.

3.2 Taxonomic variation

In a similar manner to the Region/Plot analysis above, variation in D_x at the family and genera level is summarised in Fig. 3. Overall there were significant differences between the families sampled ($F=8.08$ $DF=57 P<0.001$). Families with D_x higher than the basin mean were *Olacaceae*, *Celastraceae*, *Chrysobalanaceae*, *Humiriaceae*, *Ochnaceae*, *Linaceae*, *Scrophulariaceae*, *Myrtaceae*, and *Lecythidaceae* (Fig. 3). Families with lower D_x were *Boraginaceae*, *Bixaceae*, *Sabiaceae*, *Lepidobotryaceae*, *Lacistemataceae*, *Rhamnaceae*, *Malvaceae*, *Annonaceae*, *Myristicaceae*, *Urticaceae*, *Vochysiaceae*, *Araliaceae*, *Dichapetalaceae*, *Bignoniaceae*, and *Euphorbiaceae*. The remaining families all contained genera characterised by both high and low D_x and include some of the most abundant families across the basin: *Fabaceae*, *Rubiaceae*, *Lauraceae*, *Sapotaceae*, *Apocynaceae* (Fig. 3). There were also significant differences between genera (F=3.78 DF=249 P<0.0001) with the highest density genera being *Aiouea*, *Callichlamys*, *Pithecellobium*, *Vatairea*, *Stachyarrhena*, *Dipteryx*, *Machaerium*. The genera with lower density were *Annona*, *Matisia*, *Tetrorchidium*, *Collophora*, *Onychopetalum*, *Hyeronima*, *Luehea*.

3.3 Partialling out geographical and taxonomic differences

In order to apportion the total variance in the dataset observed (Searle et al., 2006) into geographical and taxonomic components, we used Residual Maximum Likelihood (REML) Analysis to fit a model according to

$$D = \mu + r/p + f/g/s + \varepsilon \quad (1)$$

where μ represents the overall mean of the dataset (620 kg m^{-3}); effects of location are incorporated in the term r/p, which denotes that within each region (r) are nested more than one plot (p); genetic effects are represented by the term $f/g/s$, which denotes that within each family (f) are nested various genera (g), within which are nested several species (s); and (ε) represents the residual variance. All effects were taken as random variables, as we had sampled only a limited subset of plots within distinct but not comprehensive regions; also sampling a more or less random (and incomplete) selection of Amazon families, genera and species.

Results of this analysis are shown in Fig. 4. Taken together, the geographical parameters (region and plot) accounted for 33% of the total variation with 26% of this being attributable to between region variations (this effectively representing the average variation between plots in any one region). Taxonomic variability in D_x, was inferred as

27% of the total variability in the dataset, with species and family accounting for about 10% and genus per se accounting only for 6%. Overall, the proportion of the variance in the dataset that remained unexplained was 40%, this also being the "residual variance" reflecting within tree variation (only one branch per tree was sampled), tree-to-tree variation and also may reflect measurement errors. Note that in this analysis we only included species that were observed to occur in more than one site and included families and genera for which more than one species had been sampled. The analysis presented here for D_x differs from others (Chave et al., 2006; Baker et al., 2004b) in that we have not taken overall means for each species; but rather included intra-specific variation and the possibility of systematic plot-to-plot variations in our interpretation.

Figure 4 suggests that geographic location is as important, if not more important than taxonomic identity in determining the value of D_x observed for any given tree but with considerable variation accountable for by neither. This point is demonstrated further in Fig. 5, where we have taken the more widely abundant families, genera and species in our data set and plotted the values observed in all plots were they were sampled as a function of the average tree density of all other trees sampled in the same plot. Detailed results from this analysis (which also included a consideration of likely errors in both mean plot and mean family/genus/species values for that plot) are also given in Appendix C.

Figure 5A shows that nearly all families examined converged to a statistically significant trend for an increase in the average D_x observed with a slope close to 1:1 as the values observed by other families at that site also increased. Likewise the same trend was observed when different genera were examined (Fig. 5B) and, somewhat surprisingly, also for species (Fig. 5C). Notable exceptions did however exist for the families *Urticaceae* (Fig. 4A, panel M) the family containing the genus *Pourouma* which almost entirely consist of pioneer species (Withmore 1989) and *Myrtaceae* (Fig. 4A, panel U) which in our data set includes the genera *Eugenia and Myrcia.* Likewise at the genus level *Pourouma* and *Brosimum* also seemed to vary less than all the genera examined. The relationships for *Miconia* and *Trichilia* were also not highly significant (Appendix

C). Figure 5C shows the same trend for the species examined. Nearly half of the species examined showed significant relationships. Non significant relationships might be related to the "pioneer" character of the examined species i.e. *Pourouma minor*, *Pourouma guianensis* and perhaps to the reduced number of plots where they were collected and use for this analysis (Appendix C).

3.4 Geographical and taxonomic contributions to stand level differences

In order to evaluate the extent to which overall plot-to-plot variations might be accountable in terms of geographical versus taxonomic effects, we utilised estimates of the individual plot and species effects from Eq. (1) and compared them to direct stand level calculations. This was achieved by first estimating the average value for each species within each plot and then obtaining a weighted average value for D_x for that plot according to the observed abundance of each species within it, denoted here as $\langle D_\mathrm{x} \rangle$. A similar calculation was done for the REML "species effects" which are plotted along with REML fixed plot effects (the r/p term from Eq. (1) as a function of $\langle D_\mathrm{x} \rangle$ in Fig. 6. This analysis shows that by far the majority of the variation in $\langle D_\mathrm{x} \rangle$ was accountable in terms of plot-to-plot differences, with the plot effects increasing almost linearly with $\langle D_\mathrm{x} \rangle$ with a slope close to 1.0. By contrast the species (i.e. $f/g/s$) effects were more or less constant (and close to zero) for $\langle D_\mathrm{x} \rangle >$ ca. 550 kg m^{-3}, although declining slightly thereafter. We treated our plot term as a fixed effect for the analysis in Fig. 6 (as opposed to a random effect in Fig. 4), as this permitted us to allow for different plots to have different intrinsic variances which were broadly consistent with difference of plot topographic and soil heterogeneity, also removing a slight bias in residuals which was present when treating the r/p term as random.

3.5 Phenotypic plasticity

In order to determine inter and intra-specific variation we compared the IPP of the same species collected several times within one plot and in many plots. The IPP of one species collected in more than two plots (mean=0.29±0.12, N=86) was significantly higher (mean=0.14±0.10, N=86) than the variation of the same species collected more than twice within one plot (DF=1, F=77.94, P<0001).

4 Discussion

Our results show that there is a large variation of branch xylem density across Amazonia and that considerable plasticity occurs for many species growing in different forests. This suggests that branch xylem density may not be a simple genetically inherited trait that is predictable on the basis of the knowledge of plant taxonomy alone, and that across basin patterns may not be only explained by patterns of species composition and abundance as has been previously suggested for bole wood density (Enquist et al., 1999; Baker et al., 2004b; Chave et al., 2006). But, knowledge of the site conditions is also necessary. For example, irrespective of the genotypic level examined (Fig. 5C), D_x observed varied by as much as 400 kg m^{-3} across sites. Moreover, this variation was systematic with different trees sampled within a given family/genus/species tending to have higher values of D_x along with other trees in the same plot (and vice versa).

Additional evidence for widespread plasticity comes from the REML variance partitioning of Fig. 4 in which the combined effects of Region/Plot are shown to have contributed to about the same proportion of the overall variation in the data set as did Family/Genus/Species. This result differs significantly from those for D_w (Baker et al., 2004b).

Nevertheless, when our species level means for D_x are examined as a function of species mean D_w using an expanded database from that presented in (Baker et al., 2004b) then there is reasonably good relationship (Fig. 7a). And the average D_x for this study, 620 kg m^{-3} is also very similar to previous values reported for D_w for Amazonia. For example (Brown and Lugo, 1984) estimated 620 kg m^{-3} as the average wood density of tropical America, (Chave et al., 2006) reported 650 kg m^{-3} for Central and South America together and (Baker et al., 2004b) estimated 620 kg m^{-3} as the overall species-level mean for Amazonia.

As reflected in Fig. 7b, our results do, however, differ from the above authors in that much of the variation in D_w is attributed to genotype while in our case, variations in D_x does include site and genetic variations. This difference is understandable, as there is a strong tendency of many species, genera and even families to be geographically confined to certain areas of the Basin (ter Steege et al., 2006). Thus, if there is equivalence between D_x and D_w what appears to be a genetic effect for the latter, may in fact be mostly a geographic (site and regional) effect attribute to variations in soils, climate and/or geological origin. In that respect it is only by studying replicated species growing across a wide range of environments that we have been able to show the strong environmental influence on D_x (and by implication D_w). In essence the REML species effect in Fig. 7b represents the inferred value that each species would have were it to be found on some sort of "overall average site".

Also worth noting is that, in contrast to the general trend, pioneer species (Whitmore 1989) -either short and long-lived such as within the genera *Pourouma*, (*Urticaceae*) and *Miconia* (*Melastomataceae*) and some species belonging *Brossimum* (*Moraceae*), *Trichillia* (*Meliaceae*) and *Myrcia* (*Myrtaceae*) among others, often associated to secondary vegetation and/or late stages of forest succession (Banana and Tweheyo, 2001; Peña-Claros, 2003; Vieira et al., 2003; Poorter et al., 2006; Viera and Proctor, 2007; Selaya and Anten, 2008)., showed little tendency to exhibit variation in D_x across the sites where they were found. This brings the question whether species showing little phenotypic plasticity and intermediate D_x values even when present in sites with relative low or high xylem density are more restricted to specific edaphic and microclimatic conditions that sustain colonisation and fast growth i.e. gaps with enough water supply from the soil, light, and nutrients. Also, it is worth noticing that species such as *Pourouma minor* and *P. guianensis*, which are generally considered low density-fast-growing species; were by far the species with the lowest densities in our study; xylem density varied from 410 to 690 kg m^{-3}, being comparable to any slow-growth old forest species in our data set.

But why should such plasticity in D_x generally occurs? Most likely it is related to variation in resource availability and/or different site dependent soil physical characteristics and hydrological constraints to plant function. There is already abundant evidence of this from across a range of species, environments and controlled experiments (Sabatier et al., 1997; Laurance et al., 1999; Hacke et al., 2000; Vormisto et al., 2000; Pelissier et al., 2002; Baraloto and Goldberg, 2004; Kursar et al., 2005; Baraloto et al., 2007; Madelaine et al., 2007). Further evidence of the influence of site conditions on D_x of trees comes from our own data. For example, in a Mangrove forest in East Pará, Brazil (EP-Brazil, BRA-01, Appendix A). There, only two species were sampled (10 individuals per species) *Avicennia germinans* and *Rhizophora mangle* which mean D_x were 722±87 kg $m^{-3}$and 723±99 kg m^{-3} respectively. The two species are not phylogenetically related since they belong to two different families (*Scrophulariaceae* and *Rhizophoraceae*) and two different orders (*Lamiales* and *Malpighiales*). Nevertheless they converge to an almost identical D_x. An analysis of the most variable species in our data set *Protium paniculatum* (IPP=0.66), collected in two different plots in Caxiuana (Pará, Brazil): CAX-02 (D_x=280 kg m^{-3}) and CAX-04 (D_x=800 kg m^{-3}), and *Perebea tessmannii* (IPP=0.58) two samples collected in the same plot but 900 m apart in BOG-01 with 320 and 760 kg m^{-3}, in both cases low pH, high proportion of sand and low minerals concentrations were be associated with the trees exhibiting high D_x (Quesada et al., 2008[3]; Patiño et al., 2008a[4]). Hacke et al. (2000) have shown remarkable

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[3] Quesada, C. A, Lloyd, J., Schwarz, M., Baker, T. R., Patiño, S., Czimczik, C., Schmerler, J., Hodnett, M., Arneth, A., Lloyd, G., Dezzeo, N., Gasior, R., Herrera, R., Hilke, I., Kuhlmann, I., Phillips, O., Raessler, M., Chaves, E., Cruz, O., Filho, J. M., Luizão, F. J., Pimentel, T., Santos, A. J. B., Almeida, S., Alvarez, E., Arroyo, L., Higuchi, N., Jimenez, E. M., Lezama, A. T., Neill, D. A., Paiva, R., Priante Filho, N., Silva, N., Silveira, M., Prieto, A., Rudas, A., and Vieira, I.: Chemical and physical properties of Amazonian forest soils in relation to their genesis, Biogeosciences Discuss., in preparation, 2008.

[4] Patiño, S., Lloyd, J., Quesada, C. A., Paiva, R. Q., et al.: Factors influencing observed variation of branch xylem density across the Amazon basin, Biogeosciences Discuss., in prepara-

influence of soil texture and porosity on the hydraulic properties of *Pinus taeda*.

In conjunction with concurrent measurements of associated foliar physiological characteristics undertaken on leaves from the branches with which D_x was determined in this study (Lloyd et al., 2008c[5]) as well as associated soil physical and chemical characteristics (Quesada et al., 2008[6]), further papers in this series consider the underlying factors contributing to the strong site effects in Fig. 6 (Patiño et al., 2008a[4]), along with the extent to which these site dependent variations in xylem density reflect a co-ordinated physiological response of different Amazonian tree species to variations in their growth environment (Patiño and Lloyd, 2008b[7]).

Appendix A

More precise coordinates will be available (Anderson and Malhi, 2008[8]). Abbreviations in regions are: AC=Acre, AM=Amazonas, MT=Mato Grosso, CP=Central Pará, EP=East Pará, WP=West Pará, N=North, S=South, NE=North East, SW=South

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tion, 2008a.

[5] Lloyd, J., Patiño, S., Paiva, R. Q., Quesada, C. A., Baker, T. R., and Mercado, L. M.: Basin-wide variations in foliar properties of Amazon forest trees, Biogeosciences Discuss., in preparation, 2008c.

[6] Quesada, C. A., Lloyd, J., Schwarz, M., Baker, T. R., Patiño, S., Czimczik, C., Schmerler, J., Hodnett, M., Arneth, A., Lloyd, G., Dezzeo, N., Gasior, R., Herrera, R., Hilke, I., Kuhlmann, I., Phillips, O., Raessler, M., Chaves, E., Cruz, O., Filho, J. M., Luizão, F. J., Pimentel, T., Santos, A. J. B., Almeida, S., Alvarez, E., Arroyo, L., Higuchi, N., Jimenez, E. M., Lezama, A. T., Neill, D. A., Paiva, R., Priante Filho, N., Silva, N., Silveira, M., Prieto, A., Rudas, A., and Vieira I.: Chemical and physical properties of Amazonian forest soils in relation to their genesis, Biogeosciences Discuss., in preparation, 2008.

[7] Patiño, S. and Lloyd, J.: Integration of branch xylem density variations into the tropical tree physiological spectrum, Biogeosciences Discuss., in preparation, 2008b.

[8] Anderson, L. O. and Malhi, Y.: Landscape patterns of forest biophysical measurements in eastern and western Amazonia, Biogeosciences Discuss., in preparation, 2008.

West,. ** not a permanent plot, samples were taken from trees around the Eddy covariance tower. Additional information of plots may be found in: (Malhi et al., 2002, 2003; Baker et al., 2004; Vinceti, 2003).

Appendix B

Variation of D_x within regions. In the first column the number below the name of the country is the mean followed by the standard deviation in parenthesis. DF=degrees of freedom; F=statistical values, P=probability, N=number of samples, SE=standard error of mean. * means "significantly different".

Appendix C

Regression analysis outputs for family (D1) genera (D2) and species (D3). See Figs. (5A), (5B) and (5C). Notice that for this Appendix units for D_x are given in g cm^{-3}.

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Table A1. More precise coordinates will be available (Anderson and Malhi, 2008[8]). Abbreviations in regions are: AC=Acre, AM=Amazonas, MT=Mato Grosso, CP=Central Pará, EP=East Par, WP=West Par, N=North, S=South, NE=North East, SW=South West,. ** not a permanent plot, samples were taken from trees around the Eddy covariance tower. Additional information of plots may be found in: (Malhi et al., 2002; 2003; Baker et al., 2004; Vinceti, 2003).

Plot Name and Description	Region Code	Region	Plot Code	latitude	longitude	Altitude (m)	Mean T (°C)	Forest Type	Principal Investigator
Sinop	1	MT-Brazil	SIN-01	−11.41	−55.33	325	25.4	Terra firme	M. Silveria
Alta Foresta	1	MT-Brazil	ALF-01	−9.60	−55.94	255	25.6	Terra firme	M. Silveria
Los Fierros Bosque I	2	Bolivia	LFB-01	−14.56	−60.93	230	25.1	Terra firme	T. Killeen
Los Fierros Bosque II	2	Bolivia	LFB-02	−14.58	−60.83	225	25.1	Terra firme	T. Killeen
Huanchaca Dos, plot1	2	Bolivia	HCC-21	−14.56	−60.75	720	25.1	Gallery	L. Arrollo
Huanchaca Dos, plot2	2	Bolivia	HCC-22	−14.57	−60.75	735	25.1	Gallery	L. Arrollo
Las Londras, plot 1	2	Bolivia	LSL-01	−14.41	−61.14	170	25.9	Seasonally flooded	L. Arrollo
Las Londras, plot 2	2	Bolivia	LSL-02	−14.41	−61.14	170	25.9	Seasonally flooded	L. Arrollo
Chore 1	2	Bolivia	CHO-01	−14.39	−61.15	170	25.9	Liana forest	T. Killeen
Tambopata plot zero	3	S-Peru	TAM-01	−12.84	−69.29	205	25.1	Terra firme	O. Phillips and R. Vasquez
Tambopata plot one	3	S-Peru	TAM-02	−12.84	−69.29	210	25.1	Terra firme	O. Phillips and R. Vasquez
Tambopata plot two swamp	3	S-Peru	TAM-03	−12.84	−69.28	205	25.1	Swamp	O. Phillips and R. Vasquez
Tambopata plot two swamp edge clay	3	S-Peru	TAM-04	−12.84	−69.28	205	25.1	Terra firme	O. Phillips and R. Vasquez
Tambopata plot three	3	S-Peru	TAM-05	−12.83	−69.27	220	25.1	Terra firme	O. Phillips and R. Vasquez
Tambopata plot four (cerca rio)	3	S-Peru	TAM-06	−12.84	−69.30	200	25.1	Terra firme	O. Phillips and R. Vasquez
Tambopata plot six	3	S-Peru	TAM-07	−12.83	−69.26	225	25.1	Terra firme	O. Phillips and R. Vasquez
Cuzco Amazonico, CUZAM2E	3	S-Peru	CUZ-03	−12.50	−68.96	195	25.1	Terra firme	O. Phillips and R. Vasquez
Jurua, PAA-05	3	AC-Brazil	PAA-05	−8.88	−72.79	245	26.2	Terra firme	M. Silveira
RESEX Alto Juruá: Seringal Restauração	3	AC-Brazil	RES-02	−9.04	−72.27	275	25.9	Terra firme	M. Silveira
RESEX Chico Mendes: Seringal Porongaba 1	3	AC-Brazil	RES-03	−10.82	−68.78	275	25.8	Terra firme	M. Silveira
RESEX Chico Mendes: Seringal Porongaba 2	3	AC-Brazil	RES-04	−10.80	−68.77	270	25.8	Terra firme	M. Silveira
RESEX Chico Mendes: Seringal Dois Irmãos 1	3	AC-Brazil	RES-05	−10.57	−68.31	200	26.0	Terra firme	M. Silveira
RESEX Chico Mendes: Seringal Dois Irmãos 2	3	AC-Brazil	RES-06	−10.56	−68.30	210	26.0	Bamboo forest	M. Silveira

Table A1. Continued.

Plot Name and Description	Region Code	Region	Plot Code	latitude	longitude	Altitude (m)	Mean T (˚C)	Forest Type	Principal Investigator
Allpahuayo A, poorly drained	4	N-Peru	ALP-11	−3.95	−73.43	125	26.5	Terra firme	O. Phillips and R. Vasquez
Allpahuayo A, well drained	4	N-Peru	ALP-12	−3.95	−73.43	125	26.5	Terra firme	O. Phillips and R. Vasquez
Allpahuayo B, sandy	4	N-Peru	ALP-21	−3.95	−73.43	125	26.5	Terra firme	O. Phillips and R. Vasquez
Allpahuayo B, clayed	4	N-Peru	ALP-22	−3.95	−73.43	115	26.4	Terra firme	O. Phillips and R. Vasquez
Alpahuayo C	4	N-Peru	ALP-30	−3.95	−73.43	125	26.4	Tall caatinga	O. Phillips and R. Vasquez
Sucusari A	4	N-Peru	SUC-01	−3.23	−72.90	110	26.4	Terra firme	O. Phillips and R. Vasquez
Sucusari B	4	N-Peru	SUC-02	−3.23	−72.90	110	26.4	Terra firme	O. Phillips and R. Vasquez
Sucursari C	4	N-Peru	SUC-03	−3.25	−72.93	110	26.4	Seasonally flooded	O. Phillips, A. Monteagudo
Sucursari D	4	N-Peru	SUC-04	−3.25	−72.89	160	26.4	Terra firme	O. Phillips, A. Monteagudo, T. Baker
Yanamono A	4	N-Peru	YAN-01	−3.43	−72.85	105	26.4	Terra firme	O. Phillips and R. Vasquez
Yanamono B	4	N-Peru	YAN-02	−3.43	−72.84	105	26.4	Terra firme	O. Phillips and R. Vasquez
Jenaro Herrera A- Clay rich high terrace	4	N-Peru	JEN-11	−4.88	73.63	130	26.8	Terra firme	T.R. Baker and O. Phillips
Jenaro Herrera B- sandy	4	N-Peru	JEN-12	−4.90	−73.63	130	26.8	Terra firme	T.R. Baker and O. Phillips
Sumaco	5	Ecuador	SUM-01	−1.75	−77.63	1200	–	Premontane forest	D. Neill
Jatun Sacha 2	5	Ecuador	JAS-02	−1.07	−77.60	435	23.3	Terra firme	D. Neill
Jatun Sacha 3	5	Ecuador	JAS-03	−1.07	−77.67	410	23.3	Terra firme	D. Neill
Jatun Sacha 4	5	Ecuador	JAS-04	−1.07	−77.67	430	23.3	Terra firme	D. Neill
Jatun Sacha 5	5	Ecuador	JAS-05	−1.07	−77.67	395	23.3	Terra firme	D. Neill
Bogi 1	5	Ecuador	BOG-01	−0.70	−76.48	270	26.0	Terra firme	N. Pitman, and T. DiFiore
Bogi 2	5	Ecuador	BOG-02	−0.70	−76.47	270	26.0	Terra firme	N. Pitman, and T. DiFiore
Tiputini 3	5	Ecuador	TIP-03	−0.64	−76.16	250	26.0	Seasonally flooded	N. Pitman
Tiputini 5	5	Ecuador	TIP-05	−0.64	−76.14	245	26.0	Terra firme	N. Pitman
Amacayacu: Lorena E	6	Colombia	LOR-01	−3.06	−69.99	95	25.9	Terra firme	A. Rudas and A. Prieto
Amacayacu: Lorena U	6	Colombia	LOR-02	−3.06	−69.99	95	25.9	Terra firme	A. Rudas and A. Prieto
Amacayacu: Agua Pudre E	6	Colombia	AGP-01	−3.72	−70.31	105	25.8	Terra firme	A. Rudas and A. Prieto
Amacayacu: Agua Pudre U	6	Colombia	AGP-02	−3.72	−70.30	110	25.8	Terra firme	A. Rudas and A. Prieto
EL Zafire: Varillal	6	Colombia	ZAR-01	−4.01	−69.91	130	25.6	Caatinga	M.C.Penuela and E. Alvarez
EL Zafire: Rebalse	6	Colombia	ZAR-02	−4.00	−69.90	120	25.6	Seasonally flooded	M.C.Penuela and E. Alvarez
EL Zafire: Terra Firme	6	Colombia	ZAR-03	−3.99	−69.90	135	25.6	Terra firme	M.C.Penuela and E. Alvarez
EL Zafire: Altura	6	Colombia	ZAR-04	−4.01	−69.90	120	25.6	Terra firme	M.C.Penuela and E. Alvarez
San Carlos Oxisol	7	SW-Venezuela	SCR-01	1.93	−67.02	120	26.0	Terra firme	R. Herrera

Table A1. Continued.

Plot Name and Description	Region Code	Region	Plot Code	latitude	longitude	Altitude (m)	Mean T (˚C)	Forest Type	Principal Investigator
San Carlos Tall Caatinga	7	SW-Venezuela	SCR-04	1.93	−67.04	120	26.0	Tall caatinga	R. Herrera
San Carlos Yevaro	7	SW-Venezuela	SCR-05	1.93	−67.04	120	26.0	Terra firme	R. Herrera
Rio Grande, plots DA1 (RIO-01) and DA2 (RIO-02)	8	NE-Venezuela	RIO-12	8.11	−61.69	270	24.9	Terra firme	A. Torres-Lezama
El Dorado, km 91, plots G1 (ELD-01) and G2 (ELD-02)	8	NE-Venezuela	ELD-12	6.10	−61.40	200	24.9	Terra firme	A. Torres-Lezama
El Dorado, km 98, plots G3 (ELD-03) and G4 (ELD-04)	8	NE-Venezuela	ELD-34	6.08	−61.41	360	24.9	Terra firme	A. Torres-Lezama
Manaus K34, plato	9	AM-Brazil	MAN-01	−2.61	−60.21	65	27.3	Terra firme	N. Higuchi
Manaus K34, vertiente	9	AM-Brazil	MAN-02	−2.61	−60.21	50	27.3	Terra firme	N. Higuchi
Manaus K34, campinarana	9	AM-Brazil	MAN-03	−2.60	−60.22	65	27.3	Tall caatinga	N. Higuchi
Manaus K34, baxio	9	AM-Brazil	MAN-04	−2.61	−60.22	45	27.3	Caatinga/swampy valley	N. Higuchi
Bionte 4: Manaus K 23	9	AM-Brazil	BNT-04	−2.63	−60.15	105	27.3	Terra firme	N. Higuchi
Manaus K14. Tower**	9	AM-Brazil	MAN-05	−2.59	−60.,12	108	27.3		??
Tapajos, RP014, 1-4	10	WP-Brazil	TAP-01	−3.31	−54.94	187	26.5	Terra firme	N. Silva
Tapajos, RP014, 5-8	10	WP-Brazil	TAP-02	−3.31	−54.95	187	26.5	Terra firme	N. Silva
Tapajos, RP014, 9-12	10	WP-Brazil	TAP-03	−3.31	−54.94	187	26.5	Terra firme	N. Silva
Tapajos, LBA Tower, Transects 1, 2, 3 and 4	10	WP-Brazil	TAP-04	−2.85	−54.96	73	26.5	Terra firme	S. Saleska, Hammond-Pyle, Hutyra, Wofsy,de Camargo, Vieira
Caxiuaná 1	11	CP-Brazil	CAX-01	−1.74	−51.46	40	25.6	Terra firme	S. Almeida
Caxiuaná 2	11	CP-Brazil	CAX-02	−1.74	−51.46	40	25.6	Terra firme	S. Almeida
Caxiuana 3: A (Control drought experiment). Esecaflor	11	CP-Brazil	CAX-03	−1.73	−51.46	15	25.6	Terra firme	S. Almeida, A. L. da Costa, L de Sa, J. Grace, P. Meir and Y. Malhi
Caxiuana 4: B (Drought experiment). Esecaflor	11	CP-Brazil	CAX-04	−1.73	−51.46	15	25.6	Terra firme	S. Almeida, A. L. da Costa, L de Sa, J. Grace, P. Meir and Y. Malhi
Caxiuana 5: Eddy tower	11	CP-Brazil	CAX-05	−1.72	−51.46	15	25.6	Terra firme	S. Almeida, L de Sa, J. Grace, P. Meir and Y. Malhi
Jari 1	11	CP-Brazil	JRI-01	−0.89	−52.19	127	26.5	Terra firme	N. Silva
Braganca	12	EP-Brazil	BRA-01	−0.83	−46.64	10	25.8		A. L. da Costa and Y. Malhi
Mocambo 1	12	EP-Brazil	MBO-01	−1.45	−48.45	24	26.8	Terra firme	R. Salomao
Capitao Poço	12	EP-Brazil	CPP-01	−2.19	−47.33	66	25.9	Terra firme	I. Viera and E. Leal
Guyaflux 7	13	Guiana	GFX-07			10	25.7	flooded	D. Bonal
Guyaflux 9	13	Guiana	GFX-09			40	25.7	Terra firme	D. Bonal

Table B1. D_x distribution across the Amazon basin. Plots and Regions are indicated in the right and left axes respectively. Horizontal lines represent the standard deviation. Vertical straight lines represent the Tukey test in which regions joined by the line are not significantly different while regions not included within a line are significant different.

Region/Country	DF	F	P	Plot Code	N	Mean	SE Mean	StDev
CP-Brazil 0.757 (0.132)	5	4.32	0.001	CAX-02 *	15	0.669	0.052	0.203
				CAX-05	19	0.733	0.019	0.084
				CAX-01	20	0.740	0.037	0.166
				JRI-01	20	0.757	0.026	0.116
				CAX-03 *	38	0.788	0.018	0.112
				CAX-04 *	32	0.797	0.019	0.105
AM-Brazil 0.702 (0.082)	5	2.11	0.74	MAN-02 *	6	0.639	0.043	0.106
				MAN-04	10	0.675	0.023	0.072
				MAN-01	13	0.688	0.019	0.067
				MAN-05	20	0.694	0.021	0.095
				MAN-03	9	0.729	0.032	0.097
				BNT-04 *	21	0.736	0.011	0.051
EP-Brazil 0.668 (0.109)	3	4.58	0.014	MBO-01	18	0.627	0.030	0.126
				CPP-01	20	0.649	0.021	0.092
				BRA-01 *	20	0.723	0.020	0.091
N-Peru 0.664 (0.117)	12	4.89	<0.001	YAN-02 *	8	0.521	0.023	0.065
				YAN-01 *	17	0.570	0.024	0.101
				SUC-01 *	19	0.629	0.028	0.120
				ALP-12	9	0.644	0.021	0.064
				SUC-04	20	0.657	0.017	0.077
				JEN-11	19	0.659	0.032	0.138
				SUC-02	16	0.659	0.022	0.090
				ALP-11	10	0.672	0.036	0.114
				ALP-22	12	0.678	0.022	0.075
				SUC-03	18	0.694	0.030	0.125
				ALP-21	6	0.720	0.055	0.135
				JEN-12 *	20	0.746	0.026	0.115
				ALP-30 *	12	0.765	0.017	0.058
WP-Brazil 0.663 (0.114)	3	3.07	0.032	TAP-04 *	33	0.627	0.024	0.136
				TAP-01	16	0.659	0.028	0.113
				TAP-03	20	0.673	0.014	0.060
				TAP-02 *	19	0.722	0.022	0.096
SW-Venezuela 0.610 (0.106)	2	2.35	0.102	SCR-04	26	0.594	0.019	0.098
				SCR-05	34	0.596	0.017	0.101
				SCR-01	21	0.653	0.026	0.117

Table B1. Continued.

Region/Country	DF	F	P	Plot Code	N	Mean	SE Mean	StDev
S-Peru & AC-Brazil 0.589 (0.100)	13	2.90	0.001	TAM-03 *	6	0.468	0.040	0.098
				CUZ-03	23	0.573	0.015	0.070
				TAM-01	22	0.578	0.021	0.099
				TAM-04	15	0.588	0.025	0.095
				TAM-06	21	0.588	0.018	0.081
				TAM-02	19	0.625	0.026	0.114
				TAM-07	20	0.637	0.022	0.100
				TAM-05	20	0.642	0.020	0.090
				POR-01	19	0.545	0.023	0.100
				DOI-02	18	0.551	0.022	0.093
				POR-02	20	0.557	0.024	0.105
				RST-01	20	0.583	0.024	0.107
				DOI-01	18	0.613	0.018	0.075
				JUR-01	13	0.634	0.030	0.109
MT-Brazil 0.575 (0.093)	1	9.55	0.004	ALF-01 *	26	0.543	0.013	0.068
				SIN-01 *	17	0.625	0.026	0.105
NE-Venezuela 0.568 (0.125)	2	1.29	0.284	ELD-34	16	0.528	0.030	0.121
				RIO-12	19	0.582	0.024	0.102
				ELD-12	16	0.593	0.037	0.149
Bolivia 0.561 (0.106)	6	0.74	0.62	LSL-02	16	0.530	0.021	0.085
				CHO-01	18	0.549	0.025	0.107
				HCC-22	21	0.550	0.025	0.114
				LFB-01	18	0.560	0.023	0.098
				LSL-01	14	0.569	0.037	0.140
				HCC-21	20	0.574	0.027	0.121
				LFB-02	16	0.601	0.017	0.068
Colombia 0.593 (0.103)	7	8.00	< 0.001	ZAR-02	20	0.572	0.019	0.084
				ZAR-03	18	0.612	0.018	0.078
				ZAR-04	20	0.616	0.018	0.082
				ZAR-01 *	20	0.712	0.020	0.088
				LOR-02	16	0.513	0.033	0.130
				AGP-02	20	0.545	0.019	0.087
				AGP-01	20	0.574	0.022	0.097
				LOR-01	17	0.582	0.020	0.081
Ecuador 0.535 (0.089)	8	2.32	0.021	JAS-05*	20	0.472	0.016	0.074
				SUM-01	18	0.510	0.016	0.069
				JAS-03	19	0.526	0.017	0.073
				JAS-02	21	0.531	0.019	0.086
				BOG-02	33	0.536	0.017	0.100
				TIP-03	20	0.550	0.012	0.054
				BOG-01	44	0.554	0.015	0.098
				JAS-04	22	0.559	0.018	0.084
				TIP-05	11	0.568	0.035	0.115

Table C1. Regression analysis outputs for family (D1) genera (D2) and species (D3). See Figs. (5A), (5B) and (5C). Notice that for this Appendix units for D_x are given in $\mathrm{g\,cm^{-3}}$.

Family	n	R^2	*p*	Slope	LowCI	UppCI	**Interc**	LowCI	UppCI	Ymean	Xmean
Fabaceae	64	0.679	<0.001	1.1629	1.0076	1.3421	−0.08505	−0.1903	0.02019	0.641	0.625
Sapotaceae	53	0.371	<0.001	1.1979	0.9602	1.4945	−0.10343	−0.27174	0.064871	0.645	0.625
Moraceae	48	0.263	<0.001	1.5312	1.19	1.9702	−0.34804	−0.58443	−0.11165	0.573	0.601
Myristicaceae	44	0.235	0.001	1.6258	1.2423	2.1279	−0.44166	−0.71386	−0.16946	0.548	0.609
Lecythidaceae	41	0.414	<0.001	1.2409	0.9709	1.5861	−0.10415	−0.29929	0.09099	0.677	0.629
Burseraceae	37	0.281	0.001	1.1498	0.8629	1.532	−0.1152	−0.32422	0.093814	0.597	0.619
Lauraceae	37	0.345	<0.001	1.7984	1.3671	2.3659	−0.52294	−0.83807	−0.20781	0.603	0.626
Annonaceae	33	0.539	<0.001	1.9531	1.5269	2.4984	−0.64874	−0.94373	−0.35376	0.528	0.603
Euphorbiaceae	30	0.411	<0.001	1.2956	0.9666	1.7365	−0.20745	−0.44246	0.027548	0.578	0.606
Malvaceae	27	0.457	<0.001	1.8604	1.3796	2.5087	−0.55923	−0.89383	−0.22463	0.536	0.589
Meliaceae	27	0.299	0.003	1.5244	1.0869	2.138	−0.28627	−0.596	0.02345	0.607	0.586
Chrysobalanaceae	26	0.477	<0.001	1.4788	1.0952	1.9967	−0.21232	−0.50491	0.080268	0.74	0.644
Urticaceae	20	0.019	0.557	0.9531	0.5942	1.5289	−0.01937	−0.29461	0.255877	0.538	0.585
Olacaceae	17	0.575	<0.001	1.3773	0.969	1.9575	−0.15213	−0.46956	0.165301	0.725	0.637
Rubiaceae	17	0.238	0.047	1.4992	0.9431	2.3832	−0.24574	−0.668	0.176529	0.626	0.581
Violaceae	16	0.255	0.046	1.4414	0.895	2.3215	−0.31222	−0.76893	0.144483	0.603	0.635
Apocynaceae	14	0.271	0.056	1.9349	1.1571	3.2355	−0.58654	−1.26576	0.092692	0.668	0.648
Clusiaceae	12	0.443	0.018	1.4535	0.8779	2.4063	−0.27101	−0.74962	0.207597	0.634	0.623
Melastomataceae	12	0.546	0.006	1.3648	0.8629	2.1588	−0.17818	−0.56802	0.211669	0.637	0.597
Salicaceae	12	0.324	0.054	1.2708	0.7324	2.205	−0.11586	−0.54314	0.311417	0.618	0.577
Myrtaceae	11	0.004	0.849	1.1165	0.5572	2.2374	−0.02775	−0.56646	0.510964	0.68	0.634
Bignoniaceae	10	0.568	0.012	1.2924	0.7736	2.1591	−0.21989	−0.64258	0.202799	0.563	0.606
Sapindaceae	10	0.199	0.196	1.0605	0.539	2.0867	−0.00513	−0.48015	0.469884	0.641	0.609
Elaeocarpaceae	9	0.471	0.041	1.254	0.6805	2.3108	−0.12868	−0.6266	0.369239	0.633	0.607

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Table C1. Continued

Genera	n	R^2	p	Slope	LowCI	UppCI	Interc	LowCI	UppCI	Ymean	Xmean
Eschweilera	38	0.338	<0.001	1.208	0.9206	1.585	−0.08035	−0.2913	0.130594	0.68	0.629
Pouteria	33	0.296	0.001	1.0817	0.7992	1.4641	0.001807	−0.20788	0.211497	0.678	0.625
Virola	30	0.186	0.017	1.7252	1.2248	2.4299	−0.51423	−0.88692	−0.14154	0.542	0.612
Inga	29	0.457	<0.001	1.3303	0.9983	1.7727	−0.18135	−0.41348	0.050783	0.611	0.595
Protium	26	0.207	0.02	1.2025	0.8332	1.7355	−0.15964	−0.44904	0.129751	0.604	0.635
Licania	22	0.435	0.001	1.2808	0.9083	1.8062	−0.07048	−0.36435	0.223384	0.761	0.649
Pourouma	19	0.022	0.544	0.9597	0.5899	1.5612	−0.02545	−0.31228	0.261382	0.537	0.586
Pseudolmedia	18	0.241	0.039	1.2907	0.8257	2.0178	−0.17457	−0.52217	0.173022	0.575	0.581
Brosimum	16	0.002	0.858	1.8749	1.087	3.234	−0.59057	−1.25315	0.072006	0.559	0.613
Ocotea	15	0.201	0.094	1.0427	0.6243	1.7415	−0.07265	−0.42995	0.284653	0.589	0.634
Tachigali	15	0.653	<0.001	1.4829	1.0492	2.0957	−0.27776	−0.60405	0.048518	0.64	0.619
Micropholis	14	0.453	0.008	1.1959	0.7625	1.8757	−0.14913	−0.50019	0.201939	0.601	0.627
Iryanthera	13	0.362	0.03	1.0244	0.6165	1.7023	−0.06124	−0.39904	0.276568	0.572	0.618
Guarea	11	0.705	0.001	1.2925	0.8671	1.9267	−0.14834	−0.45503	0.158345	0.596	0.576
Rinorea	11	0.219	0.147	1.5798	0.8456	2.9515	−0.42908	−1.13096	0.272803	0.617	0.662
Swartzia	11	0.627	0.004	0.9748	0.6244	1.522	0.046443	−0.25213	0.345019	0.69	0.661
Miconia	10	0.207	0.187	2.068	1.054	4.0574	−0.58253	−1.46005	0.294994	0.623	0.583
Minquartia	10	0.721	0.002	1.5284	1.006	2.322	−0.27196	−0.71201	0.168102	0.743	0.664
Tetragastris	10	0.689	0.003	1.2043	0.7754	1.8703	−0.15214	−0.49909	0.194811	0.606	0.63
Trichilia	10	0.146	0.275	1.8155	0.9054	3.6406	−0.42628	−1.22306	0.370506	0.627	0.58
Lecythis	9	0.488	0.036	1.4459	0.7917	2.6408	−0.30197	−0.92802	0.324076	0.672	0.673
Manilkara	9	0.469	0.042	1.9199	1.0411	3.5408	−0.61887	−1.46185	0.22411	0.666	0.669
Aspidosperma	8	0.455	0.066	1.4701	0.7426	2.9102	−0.19256	−0.89258	0.507471	0.75	0.641

Table C1. Continued.

Group	n	R^2	p	Slope	LowCI	UppCI	Interc	LowCI	UppCI	Ymean	Xmean
Eschweilera coriacea	14	0.461	0.008	0.9686	0.6197	1.514	0.09245	−0.18433	0.3692	0.687	0.614
Pseudolmedia laevis	12	0.334	0.049	1.8039	1.0434	3.1185	−0.47096	−1.0828	0.1409	0.589	0.588
Minquartia guianensis	9	0.678	0.006	1.5032	0.9229	2.4485	−0.25345	−0.77122	0.2643	0.76	0.674
Virola-calophylla	8	0.84	0.001	1.727	1.1702	2.5488	−0.5144	−0.9361	−0.093	0.537	0.609
Licania-heteromorpha	7	0.445	0.101	0.9109	0.4193	1.9789	0.21779	−0.30486	0.7404	0.825	0.667
Rinorea-guianensis	7	0.213	0.297	2.5887	1.0575	6.337	−1.18212	−3.03119	0.667	0.627	0.699
Virola-pavonis	7	0.441	0.104	1.363	0.6259	2.9681	−0.32976	−1.10846	0.4489	0.573	0.662
Iryanthera-juruensis	6	0.485	0.124	0.729	0.3027	1.7556	0.10677	−0.35901	0.5726	0.571	0.636
Micropholis-guyanensis	6	0.711	0.035	1.6374	0.821	3.2654	−0.44742	−1.24398	0.3491	0.617	0.65
Pourouma-guianensis	6	0.45	0.144	0.7968	0.3234	1.9634	0.05047	−0.42126	0.5222	0.507	0.573
Pourouma-minor	6	0.112	0.517	0.7733	0.2617	2.2851	0.10734	−0.46931	0.684	0.546	0.567
Pseudolmedia-macrophylla	6	0.69	0.041	1.8901	0.9279	3.85	−0.5422	−1.39521	0.3108	0.56	0.583
Tetragastris-altissima	6	0.169	0.418	1.7954	0.6238	5.1678	−0.49947	−1.8346	0.8357	0.554	0.587

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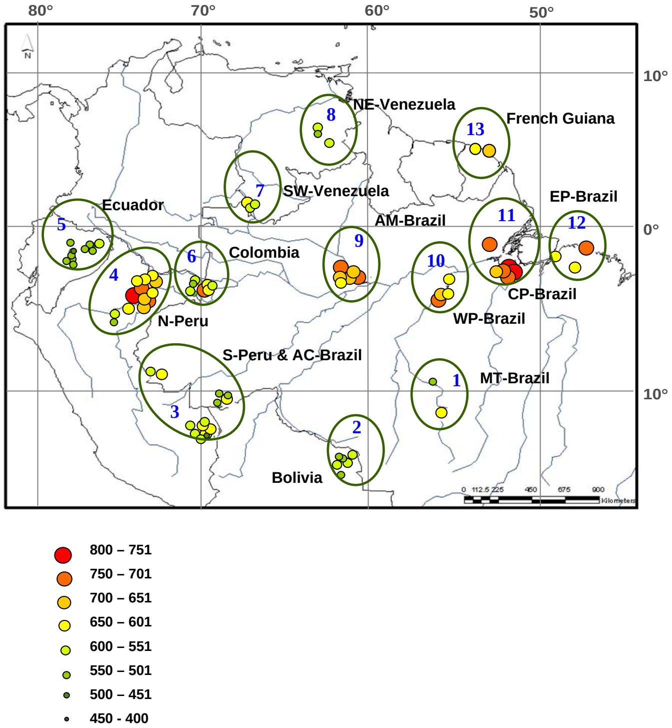

Fig. 1. Schematic representation of regions across the Amazon Basin. Each symbol represent one plot and the size of the symbol shows the arithmetic mean D_x (kg m^{-3}). Coordinates were changed to avoid overlapping of points in the map, correct coordinates are in Appendix A. Numbers in blue indicate the number of each Region in which we have grouped the sampled plots. Abbreviations in regions follow those in legend for Appendix A. Regions are: 1. MT-Brazil; 2. Bolivia; 3. S-Peru and AC-Brazil; 4. N-Peru; 5. Ecuador; 6. Colombia; 7. SE-Venezuela; 8. NE-Venezuela; 9. AM-Brazil; 10. WP-Brazil; 11. CP Brazil 12. Brazil-EP, 13. F-Guiana.

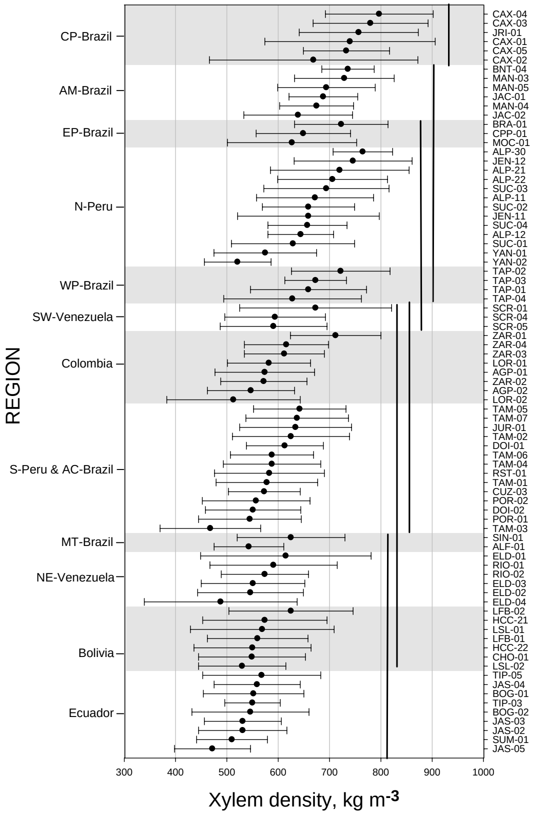

Fig. 2. D_x distribution across the Amazon basin. Plots and Regions are indicated in the right and left axes respectively. Horizontal lines represent the standard deviation. Vertical straight lines represent the Tukey test in which regions joined by the line are not significantly different while regions not included within a line are significant different.

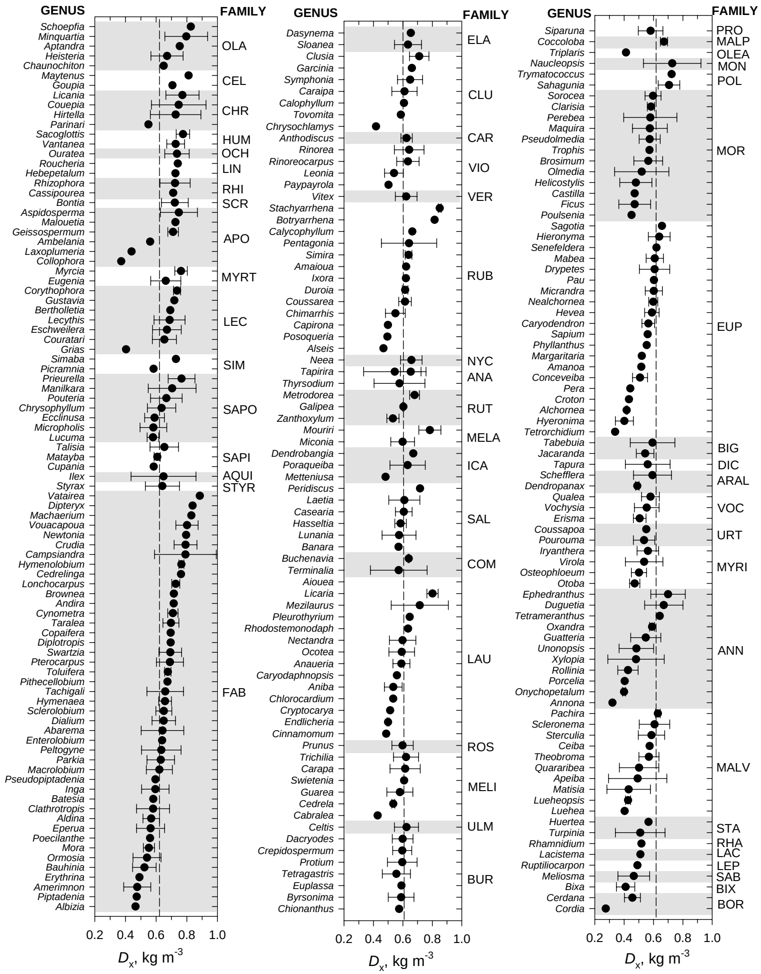
GENUS
FAMILY
Schoepfia
Minquartia
Aptandra
Heisteria
Chaunochiton
Maytenus
Goupia
Licania
Couepia
Hirtella
Parinari
Sacoglottis
Vantanea
Ouratea
Roucheria
Hebepetalum
Rhizophora
Cassipourea
Bontia
Aspidosperma
Malouetia
Geissospermum
Ambelania
Laxoplumeria
Collophora
Myrcia
Eugenia
Corythophora
Gustavia
Bertholletia
Lecythis
Eschweilera
Couratari
Grias
Simaba
Picramnia
Prieurella
Manilkara
Pouteria
Chrysophyllum
Ecclinusa
Micropholis
Lucuma
Talisia
Matayba
Cupania
Ilex
Styrax
Vatairea
Dipteryx
Machaerium
Vouacapoua
Newtonia
Crudia
Campsiandra
Hymenolobium
Cedrelinga
Lonchocarpus
Brownea
Andira
Cynometra
Taralea
Copaifera
Diplotropis
Swartzia
Pterocarpus
Toluifera
Pithecellobium
Tachigali
Hymenaea
Sclerolobium
Dialium
Abarema
Enterolobium
Peltogyne
Parkia
Macrolobium
Pseudopiptadenia
Inga
Batesia
Clathrotropis
Aldina
Eperua
Poecilanthe
Mora
Ormosia
Bauhinia
Erythrina
Amerimnon
Piptadenia
Albizia
OLA
CEL
CHR
HUM
OCH
LIN
RHI
SCR
APO
MYRT
LEC
SIM
SAPO
SAPI
AQUI
STYR
FAB
0.2
0.4
0.6
0.8
1.0
D_x, kg m^{-3}
GENUS
FAMILY
Dasynema
Sloanea
Clusia
Garcinia
Symphonia
Caraipa
Calophyllum
Tovomita
Chrysochlamys
Anthodiscus
Rinorea
Rinoreocarpus
Leonia
Paypayrola
Vitex
Stachyarrhena
Botryarrhena
Calycophyllum
Pentagonia
Simira
Amaioua
Ixora
Duroia
Coussarea
Chimarrhis
Capirona
Posoqueria
Alseis
Neea
Tapirira
Thyrsodium
Metrodorea
Galipea
Zanthoxylum
Mouriri
Miconia
Dendrobangia
Poraqueiba
Metteniusa
Peridiscus
Laetia
Casearia
Hasseltia
Lunania
Banara
Buchenavia
Terminalia
Aioue
Licaria
Mezilaurus
Pleurothyrium
Rhodostemonodaph
Nectandra
Ocotea
Anaueria
Caryodaphnopsis
Aniba
Chlorocardium
Cryptocarya
Endlicheria
Cinnamomum
Prunus
Trichilia
Carapa
Swietenia
Guarea
Cedrela
Cabralea
Celtis
Dacryodes
Crepidospermum
Protium
Tetragastris
Euplassa
Byrsonima
Chionanthus
ELA
CLU
CAR
VIO
VER
RUB
NYC
ANA
RUT
MELA
ICA
SAL
COM
LAU
ROS
MELI
ULM
BUR
0.2
0.4
0.6
0.8
1.0
D_x, kg m^{-3}
GENUS
FAMILY
Siparuna
Coccoloba
Triplaris
Naucleopsis
Trymatococcus
Sahagunia
Sorocea
Clarisia
Perebea
Maquira
Pseudolmedia
Trophis
Brosimum
Olmedia
Helicostylis
Castilla
Ficus
Poulsenia
Sagotia
Hieronyma
Senefeldera
Mabea
Drypetes
Pau
Micrandra
Nealchornea
Hevea
Caryodendron
Sapium
Phyllanthus
Margaritaria
Amanoa
Conceveiba
Pera
Croton
Alchornea
Hyeronima
Tetrorchidium
Tabebuia
Jacaranda
Tapura
Schefflera
Dendropanax
Qualea
Vochysia
Erisma
Coussapoa
Pourouma
Iryanthera
Virola
Osteophloeum
Otoba
Ephedranthus
Duguetia
Tetrameranthus
Oxandra
Guatteria
Unonopsis
Xylopia
Rollinia
Porcelia
Onychopetalum
Annona
Pachira
Scleronema
Sterculia
Ceiba
Theobroma
Quararibea
Apeiba
Matisia
Lueheopsis
Luehea
Huertea
Turpinia
Rhamnidium
Lacistema
Ruptiliocarpon
Meliosma
Bixa
Cerdana
Cordia
PRO
MALP
OLEA
MON
POL
MOR
EUP
BIG
DIC
ARAL
VOC
URT
MYRI
ANN
MALV
STA
RHA
LAC
LEP
SAB
BIX
BOR
0.2
0.4
0.6
0.8
1.0
D_x, kg m^{-3}

Fig. 3.

Fig. 3. Variation of D_x (kg m^{-3}) within and between families (genera within families). Each dot represents the average D_x of genera. Left vertical axes represent genera, right vertical axes represent families and X-axis is the D_x. Grey and white shadows separate the families. Vertical dashed line represents the mean D_x of the basin. Horizontal lines represent the Standard Deviation. Families in the Fig. are sorted from high to low D_x from top-right (panel A) to left-bottom (Panel C). The three panels (A, B, and C) represent one continuous Fig., divided only for purpose of presentation. Abbreviation of the families are listed below D_x: OLA= *Olacaceae*, CEL=*Celastraceae*, CHR=*Chrysobalanaceae*, HUM=*Humiriaceae*, OCH=*Ochnaceae*, LIN=*Linaceae*, RHI=*Rhizophoraceae*, SCR=*Scrophulariaceae*, APO= *Apocynaceae*, MYRT=*Myrtaceae*, LEC=*Lecythidaceae*, SIM=*Simaroubaceae*, SAPO=*Sapotaceae*, SAPI=*Sapindaceae*, AQUI=*Aquifoliaceae*, STYR=*Styracaceae*, FAB= *Fabaceae*, ELA=*Elaeocarpaceae*, CLU=*Clusiaceae*, CAR=*Caryocaraceae*, VIO=*Violaceae*, VER=*Verbenaceae*, RUB=*Rubiaceae*, NYC=*Nyctaginaceae*, ANA= *Anacardiaceae*, RUT=*Rutaceae*, MELA=*Melastomataceae*, ICA=*Icacinaceae*, SAL=*Salicaceae*, COM=*Combretaceae*, LAU=*Lauraceae*, ROS=*Rosaceae*, MELI= *Meliaceae*, ULM=*Ulmaceae*, BUR=*Burseraceae*, PRO=*Proteaceae*, MALP=*Malpighiaceae*, OLEA=*Oleaceae*, MON=*Monimiaceae*, POL=*Polygonaceae*, MOR= *Moraceae*, EUP=*Euphorbiaceae*, BIG=*Bignoniaceae*, DIC=*Dichapetalaceae*, ARAL=*Araliaceae*, VOC=*Vochysiaceae,* URT=*Urticaceae*, MYRI=*Myristicaceae*, ANN= *Annonaceae*, MAL=*Malvaceae*, STA=*Staphyleaceae,* RHA=*Rhamnaceae*, LAC=*Lacistemataceae*, LEP=*Lepidobotryaceae*, SAB= *Sabiaceae*, BIX=*Bixaceae*, and BOR= *Boraginaceae*

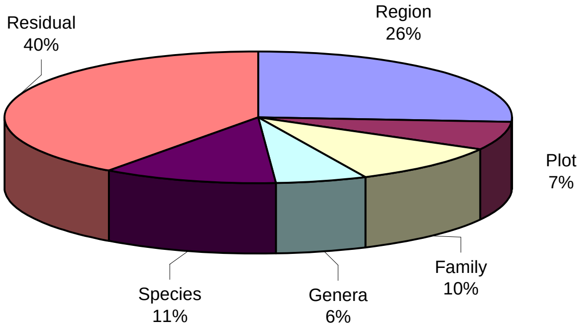

Fig. 4. Apportion of the total variance of D_x in the data set.

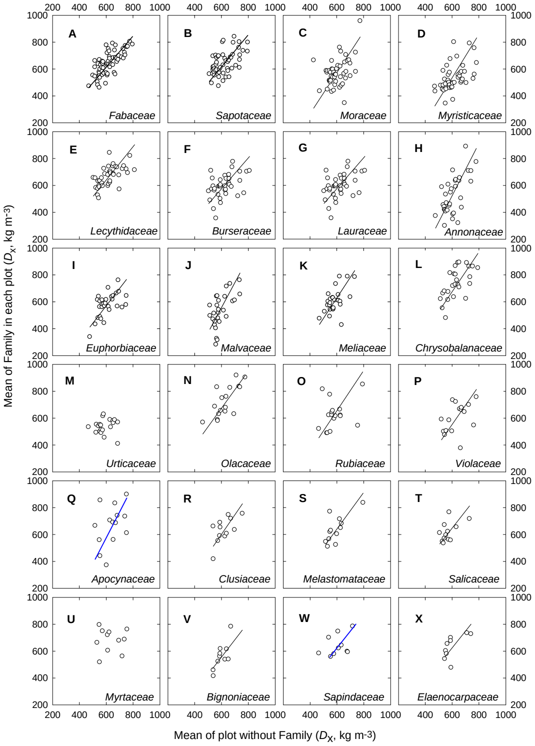

Fig. 5A. Relationships between mean D_x of plot (X-axis) and mean D_x of each family **(A)**, genera **(B)**, and species **(C)** within each plot. For each regression line a plot mean was calculated excluding the family, genera or species for which the analysis was done and plotted against the average of that family, genus or species. Families used in the analysis were collected at least in 6, genera 8 and species 6 plots. Regression lines in blue where not highly significant although follow the general trend. No regression lines in panels (A) M and U; (B) G and I; and (C) F, K, and M indicate that there were not significant relationships. Analysis were performed with SMATR. Mean of plot without species (D_x, kg m^{-3}).

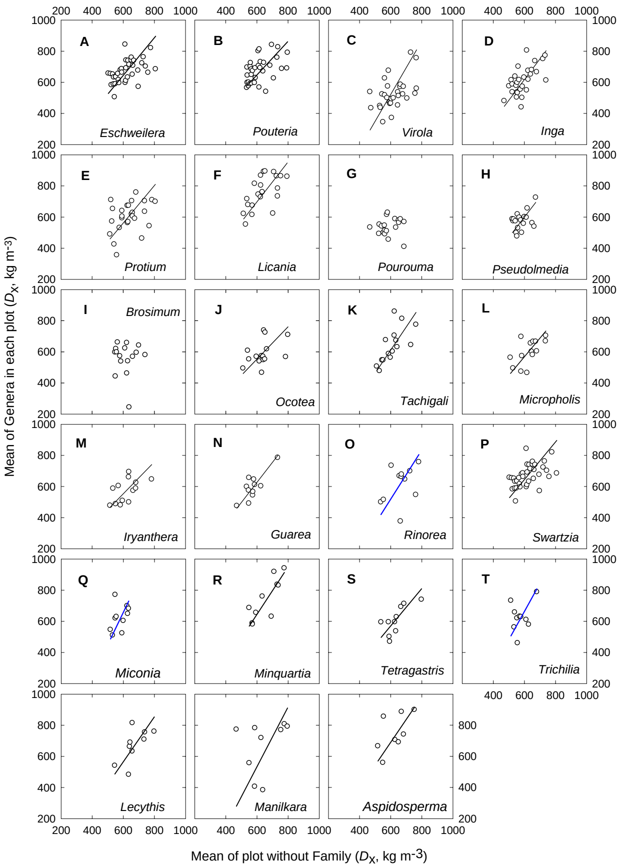

Fig. 5B. Mean of plot without species (D_x, kg m^{-3}).

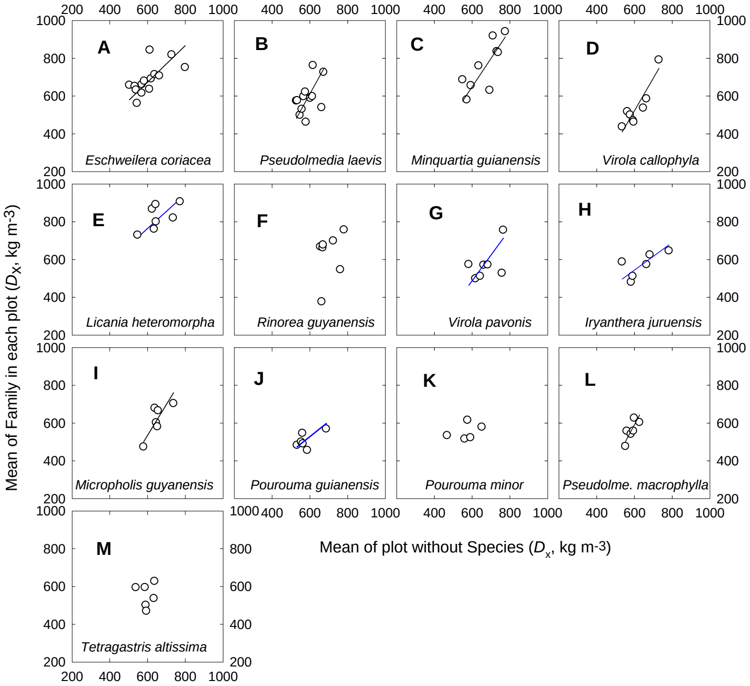

Fig. 5C. Mean of plot without species (D_x, kg m^{-3}).

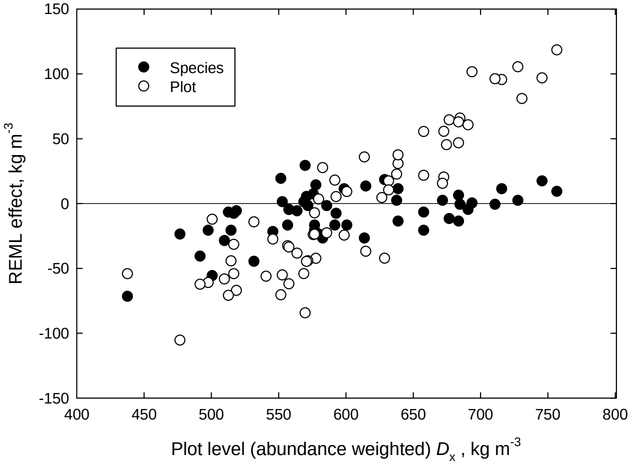

Fig. 6. Plot level (abundance weighted) D_x, kg m^{-3}.

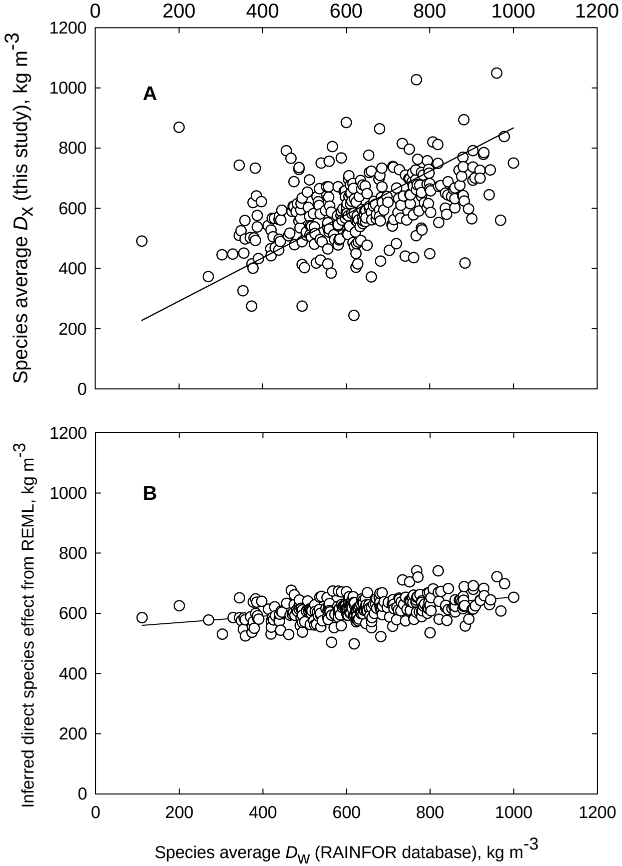

Fig. 7. The relationship between **(a)** observed species level values for xylem density (D_x) obtained in the current study and species level mean values for wood density D_w obtained from the RAINFOIR database and **(b)** deduced species level effects on D_x from the REML analysis of Eq. (1) and mean values of D_w from the RAINFOR database.