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Branch xylem density variations across the Amazon Basin

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Abstract. Xylem density is a physical property of wood that varies between individuals, species and environments. It reflects the physiological strategies of trees that lead to growth, survival and reproduction. Measurements of branch xylem density, ρ_x, were made for 1653 trees representing 598 species, sampled from 87 sites across the Amazon basin. Measured values ranged from 218 kg m^{-3} for a *Cordia sagotii* (Boraginaceae) from Mountagne de Tortue, French Guiana to 1130 kg m^{-3} for an *Aiouea* sp. (Lauraceae) from Caxiuana, Central Pará, Brazil. Analysis of variance showed significant differences in average ρ_x across regions and sampled plots as well as significant differences between families, genera and species. A partitioning of the total variance in the dataset showed that species identity (family, genera and species) accounted for 33% with environment (geographic location and plot) accounting for an additional 26%; the remaining "residual" variance accounted for 41% of the total variance. Variations in plot means, were, however, not only accountable by differences in species composition because xylem density of the most widely distributed species in our dataset 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 in a predictable manner. Within the analysed taxa, exceptions to this general rule seem to be pioneer species belonging for example to the *Urticaceae* whose branch xylem density is more constrained than most species sampled in this study. These patterns of variation of branch xylem density across Amazonia suggest a large functional diversity amongst Amazonian trees which is not well understood.

1   Introduction

Xylem tissue (wood) is a complex organic material composed of a matrix of hemicelluloses and lignin in which cellulose fibrils are embedded (Harada, 1965; Hamad, 2002; Pallardy and Kozlowski, 2007). It has a variety of functions in trees, such as structural support, actuation of the tree itself and of different organs (Niklas, 1992; Fratzl et al., 2008), long distance transport of water, inorganic ions, organic compounds and proteins from roots to leaves, and storage of water, carbohydrates and fat (Gartner, 1995; Smith and Shortle, 2001; Kehr et al., 2005). Wood also contains the majority of the carbon stored in a tree (Gartner, 1995). As the structure of xylem tissue changes as a result of environmental requirements and phylogenetic constrains, so does xylem function (Carlquist, 1975; Tyree and Ewers, 1991; Niklas, 1992; Gartner, 1995; Tyree and Zimmermann, 2002; Bass et al., 2004) and the quantity of stored carbon within this tissue

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too (Elias and Potvin, 2003). Density, ρ, (the ratio between oven-dry mass and fresh volume of xylem tissue) is one of the physical properties of wood (Kollmann and Côte, 1984) and provides an index of the balance between solid material (i.e. cell wall, parenchyma) and void (i.e. lumen of fibres, tracheids and conductive elements) of the xylem tissue. Therefore, changes in wood density are directly associated with structural variations at the molecular, cellular and organ levels. These structural differences are strongly correlated with the tree's mechanical properties (Givnish, 1986; Niklas, 1992; Gartner, 1995), water transport efficiency and safety (Hacke et al., 2001; Tyree and Zimmermann, 2002; Jacobsen et al., 2005; Holbrook and Zwieniecki, 2005; Pittermann et al., 2006), rates of carbon exchange (Tyree, 2003; Jacobsen et al., 2005; Ishida et al., 2008) and perhaps resistance to pathogens and herbivores (Rowe and Speck, 2005). Different species from different taxonomic, phylogenetic and architectural groups show convergence of these functional characteristics in response to the environment (Meinzer, 2003).

In this work we make the distinction between the density of the wood from the main trunk (here defined as wood density, ρ_w) normally measured at 1.3 m from the ground (possibly including both sapwood and heartwood that may have been air or oven-dried) and that of the sapwood or functional xylem of small (ca. 1.5 cm diameter) terminal branches of trees (here defined as xylem density, ρ_x). Xylem density is considered as a potential proxy for tree hydraulic architecture (water transport) (Stratton et al., 2000; Gartner and Meinzer, 2005; Meinzer et al., 2008). There is evidence supporting the idea that hydraulic architecture may limit tree performance in terms of transpiration, carbon exchange and growth, (Tyree, 2003; Meinzer et al., 2008). For example, there have been reports showing how ρ_x scales negatively with leaf gas exchange and water balance for neotropical forest trees with contrasting phenologies subjected to contrasting rainfall regimes (Santiago et al., 2004; Meinzer et al., 2008), for neotropical savannah trees (Bucci et al., 2004; Scholz et al., 2007), Hawaiian dry forests trees (Stratton et al., 2000) and Californian chaparral species (Pratt et al., 2007). For different environments (California chaparral, South African Mediterranean-type climate, Sonoran desert, Great Basin of central Utah) and for both gymnosperm and angiosperm trees and shrubs with distinct xylem structure (ring porous and diffuse porous), ρ_x scales positively with xylem resistance to cavitation and mechanical strength (Hacke et al., 2001; Pratt et al., 2007; Scholz et al., 2007; Jacobsen et al., 2007a, b; Dalla-Salda et al., 2008). It also, has been proposed that high density wood is necessary to avoid xylem implosion due to negative water tension inside xylem conduits (Hacke et al., 2001). These findings strongly suggest that xylem density could be used as a "trait" to predict the different physiological strategies of trees in tropical forests.

For any given species ρ_x and ρ_w should be related (Swenson and Enquist, 2008; Sarmiento et al., 2009) as both reflect an individual species' water transport strategy and

mechanical requirements (Asner and Goldstein, 1997; Wagner et al., 1998; Taneda et al., 2004). Nonetheless, there are many important structural and functional differences between branch and trunk wood as a result of different loading, hydraulic, architectural, and genetic constrains (Zobel and van Buijtenen, 1989; Gartner, 1995; Domec and Gartner, 2002; Cochard et al., 2005; Dalla-Salda et al., 2008). Trunk wood density may also be affected by factors in addition to those modulating ρ_x. For example, it may reflect differences in the storage of resins or variation in the storage of secondary compounds within bole heartwood over time, or intrinsic species-specific differences on wood density gradients within the main trunk (Wiemann and Williamson, 1988, 1989; Parolin, 2002; Knapic et al., 2008). In branches these additional effects may not occur, or at least not to the same extent.

It has long being known that ρ_w is a genetically conserved trait, and this characteristic has been used extensively in tree breeding (Zobel and van Buijtenen, 1989; Zobel and Jett, 1995; Yang et al., 2001). However, in plantations it is well known that for a given tree species, marked variations may also occur due to differences in genotype, climate, soil factors and management (Cown et al., 1991; Beets et al., 2001; Roque, 2004; Thomas et al., 2005). In neotropical forests, particularly in the Amazon basin, site-specific differences have been noticed when comparing the same species growing in different forests and/or site conditions (Wiemann and Williamson, 1989; Gonzalez and Fisher, 1998; Woodcock et al., 2000; Muller-Landau, 2004; Roque, 2004; Nogueira et al., 2005, 2007; Schöngart et al., 2005; Wittmann et al., 2006). A special case of complex systems seems to be the Amazonian floodplains. When comparing the same species growing on nutrient-rich white water floodplains (*várzea*) and nutrient-poor black water floodplains (*igapó*), Parolin (2002) and Parolin and Ferreira (2004) found higher ρ_w values in igapó forest. Such differences might have been due to the combined effect of forest successional stages (young successional stages in the *várzea* and old-growth forest in the igapó) and differences in soil nutrient availability. For *Macrolobium acciifolium* studied in both habitats at the same successesional stage (old-growth forest) and at the same elevation showed that in *várzea* ρ_w was higher than in igapó (Schöngart et al., 2005). At the community level, low ρ_w is often associated with one or a combination of high soil fertility, high rates of forest disturbance, early and secondary successional vegetation and/or high rates of tree growth and mortality, (Saldarriaga, 1987; Wiemann and Williamson, 1989; Enquist et al., 1999; Woodcock et al., 2000; Roderick and Berry, 2001; ter Steege and Hammond, 2001; Muller-Landau, 2004; Baker et al., 2004b; Nogueira et al., 2005; King et al., 2005, 2006; Erskine et al., 2005; Wittmann et al., 2006; Chao et al., 2008; Slik et al., 2008).

The Amazon Basin is 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 with contrasting species compositions and life history traits (ter Steege et al., 2000, 2006), geological origins (Fittkau et al., 1975; Quesada et al., 2009a), climates (Sombroek, 2001; Malhi et al., 2004b), and an enormous diversity of soils (Sombroek, 2000; Quesada et al., 2009b) exist within its boundary creating a mosaic of forests and vegetation types with such a floristic complexity the basis of which is still not well understood (Phillips et al., 2003). How and why species are distributed (Leigh et al., 2004; Pitman et al., 2008), what explains differential productivity (Malhi et al., 2004) and dynamic patterns across Amazonian regions (Phillips and Gentry, 1994; Phillips et al., 2002, 2004; Lewis et al., 2004; Baker et al., 2004a), how much carbon is being absorbed and released to the atmosphere (Grace et al., 1995; Phillips et al., 1998; Malhi et al., 2000, 2004, 2006; Clark, 2002), how Amazonian forests are responding to global change (Phillips, 1997; Cox et al., 2000; Laurance et al., 2004; Wright, 2005; Phillips et al., 2009) are some of the questions that have motivated this research (Lloyd et al., 2009). By studying ρ_x across Amazonia we hoped to gain insights into the understanding of the functioning of Amazonian forests and, for the first time, rigorously examine the importance of both environmental and genetic controls on a plant trait over large scales for the tropical forest biome. By analysing the geographic and taxonomic patterns of branch xylem density from different trees and forests across Amazonia, we address the following three questions:

1. Are there detectable patterns of ρ_x across Amazonia? If so, are those patterns related to taxonomic differences and/or to overall site conditions?

2. Are there differences in average values between forests and between different taxonomic groups?

3. Does the xylem density of particular species change across the basin according to the observed regional patterns?

Based on what it is known for ρ_w and ρ_x we hypothesised that ρ_x is a "plastic" trait that reflects both phylogenetic constrains and environmental gradients. We predict that individuals of species that are widespread across Amazonia will show an increase in ρ_x as the average-plot ρ_x increases and that the intra-specific variation of these common species is larger than the variations of different species growing in the same forest. There is evidence that substantial functional convergence exits between species from different phylogenetic and taxonomic groups in the same environment (Meinzer, 2003) and long term acclimatisation in response to the environment has been observed for xylem tissue (Hietz et al., 2005; Holste et al., 2006).

2 Methods

2.1 Study sites

Eighty-seven forest plots from across the Amazon basin were sampled, typically at the end of the rainy season, between January 2001 and December 2005. Two plots were sampled in Paracou, French Guiana in September 2007 and seven additional plots were sampled between May 2007 and September 2008 (see details below). The first 82 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 (Vinceti, 2003; Malhi et al., 2004; Phillips et al., 2004; Baker et al., 2004a, b). The additional seven plots form part of the BRIDGE, ANR project (http://www.ecofog.gf/Bridge/). 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

2.2.1 The RAINFOR protocol

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 for wood density sampling. On some occasions, such as when plots were unusually heterogeneous, as a consequence of topographic variations and/or shape (i.e. 1000×10 m) more trees were sampled (e.g. BOG-plots). For two of the Caxiuana plots (Central Pará, Brazil) we sampled in two consecutive years (2002 and 2003) and since there was no statistical difference in ρ_x for the two years, we combined all this data for the following analyses. When a plot was clearly composed of different defined landscapes, and each landscape was considered as an individual plot, on average 10 trees were sampled for each landscape (e.g. Jacaranda Plots, Km 34 Manaus, Brazil).

Trees were not chosen completely at random, sampling within each plot accounted for two factors. First, there was a selection of three to six contrasting areas (e.g. slopes, valleys, gaps, creeks, swamps) where these were present. Secondly, a professional tree climber then chose a "climbable tree" within the identified areas. Naturally, this "climbable tree" varied from climber to climber according to the technique employed and overall climbing skills. Nevertheless a general consideration was that from the "climbable tree", upper branches (exposed to light) of at least three neighbouring trees were reachable, either by moving himself from tree to tree or by using a clipper pole. In each plot we also sampled branches from low, middle and upper crown from a subsample (three to 5 trees) of the total number of trees sampled. These trees were selected on the basis of having three types of branches: upper canopy = exposed to light, middle = mid-light and lower = shaded.

2.2.2 The sampling strategy for the Guyaflux plots

For the Guyaflux plots, mostly lower branches from sub-canopy trees were sampled using a chain saw manipulated from the ground. To determine if data from lower branches introduces a bias in the data, we compared ρ_x of upper and lower branches from our sub-sample of 272 trees. We found no statistical differences between the density of branches from the two positions on the trees (ANOVA, $DF=1$, $F=0.18$, $P=0.674$, mean upper branches=619 kg m^{-3}, mean lower branches=615 kg m^{-3}). The ρ_x values of trees sampled at Paracou followed a normal distribution, and included the range of densities measured for ρ_w of 309 trees of a neighbouring plot. The composition of the trees sampled was also similar to the abundance distribution of the main families present in the Guyaflux plots (Jacques Beauchêne, BRIDGE unpublished data).

2.2.3 The BRIDGE protocol

For the BRIDGE protocol, the sampling strategy was basically the same: professional climbers selected "climbable trees" and from there moved across the canopy collecting upper branches from 70 to 100% of the trees present in the plots. From these branches 40 to 90% were used for xylem density determinations.

In order to assess the representativeness of the sampling strategy generally utilised across the Basin (usually only 20 trees per one hectare plot), we took advantage of the more comprehensive BRIDGE measurements to assess how representative this sampling strategy really was. Thus, for each comprehensively sampled BRIDGE plot we chose a sub-set of four clusters of five trees selected randomly across the sampled area (this also taking into account any topographic variability), comparing the estimated "plot level" values as calculated from these twenty trees only with the true plot mean.

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*; *Papilionaceae*, *Caesalpinaceae*, and *Mimosaceae* are included in the *Fabaceae*; *Cecropiaceae* in the *Urticaceae*; and *Flacourtiaceae* in the *Salicaceae*.

2.4 Xylem density determinations

A pair of consecutive 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
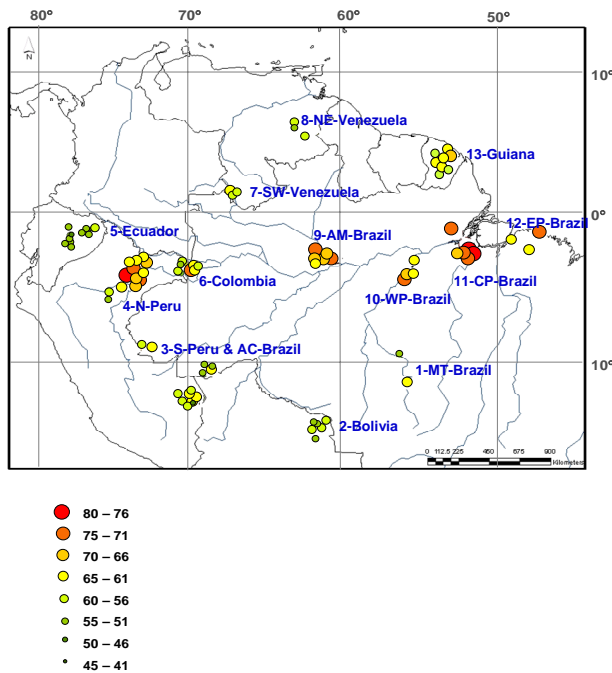
Fig. 1. Spatial pattern of branch xylem density, ρ_x, for 87 forest plots across the Amazon basin. Each symbol represents one plot. Symbol size represents the arithmetic mean ρ_x (kg m^{-3}). Coordinates were changed to avoid overlapping points in the map and are listed in Appendix A. Numbers in blue indicate the respective Region for each plot. 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. EP -Brazil-EP, 13. F-Guiana.

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 (the second sample was dried with the leaves and stored for possible further analysis) and its fresh volume calculated from its length and the average diameter of the two perpendicular 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) 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, ρ_x, was then determined as the dry mass divided by the green volume of the sample.
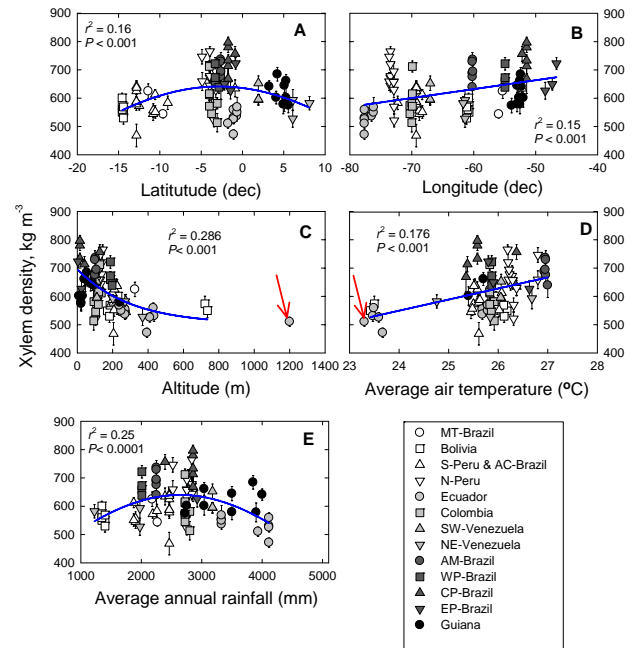

Fig. 2. The relationship between branch xylem density for all 87 forest plots and **(A)** latitude; **(B)** longitude; **(C)** altitude; **(D)** mean annual temperature; and **(E)** total annual precipitation. Vertical lines are the standard error of means. Red arrow indicates a data point has been excluded from the analysis. Point corresponds to SUM-01, a premontane forest in Ecuador.

2.5 Statistical analysis

Basic statistics shown in Figs. 1, 3 and 4 were performed with Minitab 15 (Minitab Inc.).

In order to apportion the variance within the dataset (Searle et al., 2006) into geographical and taxonomic components, we fitted a model according to

$$\rho_x = \mu + r/p + f/g/s + \varepsilon \tag{1}$$

where μ represents the overall mean of the dataset (619 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; we also sampled a more or less random (and incomplete) selection of Amazon families, genera and species. Variance partitioning for Fig. 5 was accomplished by applying Residual Error Maximum Likelihood (REML) analysis (Gilmour et al., 1995) employing GENSTAT Discovery Edition.
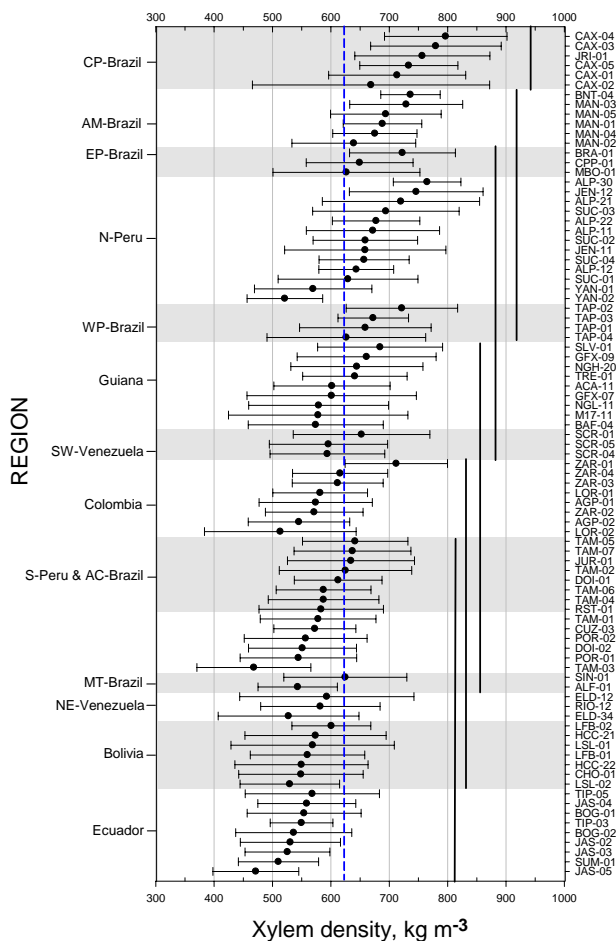
Fig. 3. Variation of ρ_x between and within regions. Regions and plots are indicated in the left and right axes, respectively. Horizontal lines represent the standard deviation. Vertical straight lines represent confidence limits defined using a Tukey test. Complementary information is given in Appendix B. Grey and white shadows separate the regions. Vertical dashed-blue line represents the mean ρ_x of the basin.

All Standard Major Axis line-fittings for Fig. 6a, b, c were undertaken using SMATR package (Warton et al., 2006). Mixed-effect modelling (Fig. 7) was carried out using "lmne" (Bates and Sarkar, 2007) and rank-based linear regression (Fig. 8) 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 to account for the possibility of "contaminated" data having been included in any of the ρ_w values assimilated from a wide range of sources into the RAINFOR "wood density" database.

In order to determine the extent to which ρ_x changed 1) in a given species within the same plot and between plots and 2) to estimate the variation within a given plot we calculated IPP (index of phenotypic plasticity) and IV (index of variation) respectively (Valladares et al., 2000). IPP and IV

were computed as the, absolute difference between the maximum value and the minimum value divided by the maximum value.

3 Results

We measured ρ_x of 1653 trees (see supplementary material: http://www.biogeosciences.net/6/545/2009/ bg-6-545-2009-supplement.zip) from 87 plots (Appendix A) across the Amazon basin. Data for ρ_x followed normal distribution with mean and median values of $619\,\mathrm{kg\,m^{-3}}$ and $612\,\mathrm{kg\,m^{-3}}$, respectively; normality test (StDev=0.124, N=1653, AD=1.202 P<0.005).

Of all the trees sampled, 95% (1568) had been identified to the family level, 89% (1475) to the genus level, and 72% (1199) to the species level. The trees sampled accounted for 60 families, representing 41% of the total number of families present in the neotropics (Mass and Westra, 1993) with 283 genera, and 598 species being sampled. The most common families sampled in our data set in order of abundance were *Fabaceae, Sapotaceae, Lecythidaceae, Moraceae, Burseraceae, Myristicaceae, Lauraceae, Annonaceae, Euphorbiaceae, Chrysobalanaceae,* with the most common genera being *Eschweilera, Pouteria, Protium, Inga, Licania, Virola, Pseudolmedia, Pourouma, Lecythis, Miconia.* The most common species were *Eschweilera coriacea, Pseudolmedia laevis, Rinorea guianensis, Tetragastris altissima, Minquartia guianensis, Pourouma guianensis, Pseudolmedia macrophylla, Lecythis persistens, Miconia poeppigii,* and *Pourouma minor.* At the family level we had 86 (5%) undetermined individuals. At the genus level we had 21 undetermined *Protium* sp., 18 *Pouteria* sp., 14 *Inga* sp., 11 *Ocotea* sp., 11 *Eschweilera* sp., 10 *Virola* sp. among others. The distribution of families and genera in our dataset represents well previous descriptions of floristic composition across Amazonia (Terborgh and Andresen, 1998; ter Steege et al., 2000, 2006).

3.1 Geographic variation

Arithmetic means of ρ_x for the 87 plots are shown in Fig. 1, which also shows our separation into 13 discrete geographical regions mainly determined by the proximity of plots. These regions are used for subsequent analysis.

From Fig. 1 a gradient of increasing ρ_x from North and South towards the Amazon River is apparent with high ρ_x being concentrated along the river itself. Plots located close to the Andes, North and South from the Amazon River tended to have the lowest ρ_x. For example, all plots in Ecuador, some in N-Perú, all in S-Perú and AC-Brazil and Bolivia had relatively low ρ_x compared to some plots in Colombia and N-Perú which were all at lower altitudes and closer to the Amazon River. Northern (NE-Venezuela, SW-Venezuela and Guiana) and Southern (Bolivia and MT-Brazil) regions
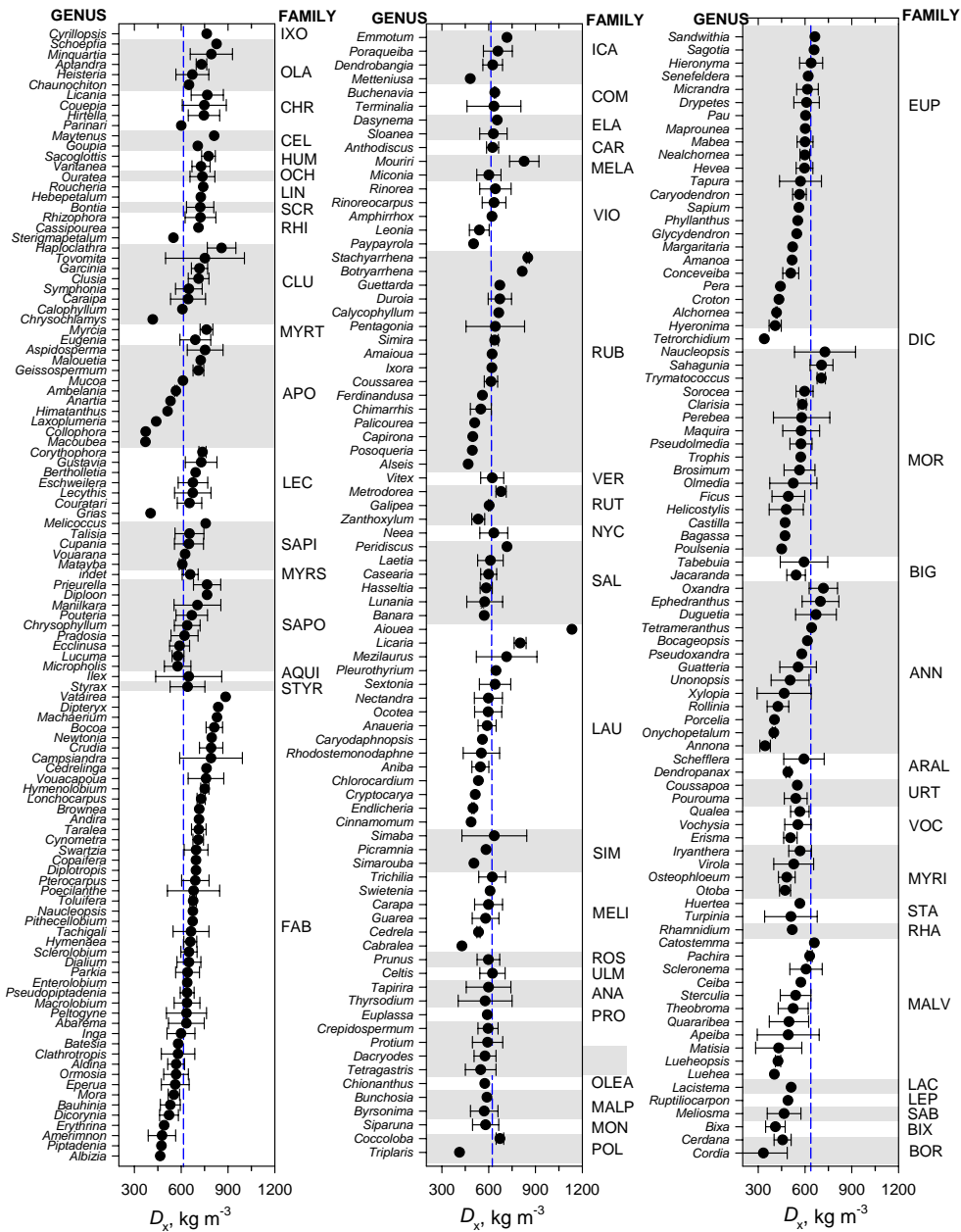
Fig. 4. Variation of xylem wood density, ρ_x (kg m^{-3}), between and within families. Each dot represents the average ρ_x of each genus. Left vertical axes represent genera, right vertical axes represent families and X-axis is the ρ_x. Grey and white shadows separate the families. Vertical dashed-blue line represents the mean ρ_x of the basin. Horizontal lines represent the Standard Deviation. Families in the Figure are sorted from high to low ρ_x from top-right (**A**) to left-bottom (**C**). The three panels (**A, B,** and **C**) represent one continuous Figure, divided only for purpose of presentation. Abbreviation of the families are listed below ρ_x: IXO=Ixonanthaceae, OLA=*Olacaceae*, CHR=*Chrysobalanaceae*, CEL=*Celastraceae*, HUM=*Humiriaceae*, OCH=*Ochnaceae*, LIN=*Linaceae*, SCR=*Scrophulariaceae*, RHI=*Rhizophoraceae*, CLU=*Clusiaceae*, MYRT=*Myrtaceae*, APO=*Apocynaceae*, LEC=*Lecythidaceae*, SAPI=*Sapindaceae*, MYRS=*Myrsinaceae*, SAPO=*Sapotaceae*, AQUI=*Aquifoliaceae*, STYR=*Styracaceae*, FAB=*Fabaceae*, ICA=*Icacinaceae*, COM=*Combretaceae*, ELA=*Elaeocarpaceae,* CAR=*Caryocaraceae*, MELA=*Melastomataceae*, VIO=*Violaceae*, RUB=*Rubiaceae*, VER=*Verbenaceae*, RUT=*Rutaceae*, NYC=*Nyctaginaceae*, SAL=*Salicaceae*, LAU=*Lauraceae*, SIM=*Simaroubaceae*, MELI=*Meliaceae*, ROS=*Rosaceae*, ULM=*Ulmaceae*, ANA=*Anacardiaceae*, PRO=*Proteaceae*, BUR=*Burseraceae*, OLEA=*Oleaceae*, MALP=*Malpighiaceae,* MON=*Monimiaceae*, POL=*Polygonaceae*, EUP=*Euphorbiaceae*, DIC=*Dichapetalaceae*, MOR=*Moraceae*, BIG=*Bignoniaceae*, ANN=*Annonaceae*, ARAL=*Araliaceae*, URT=*Urticaceae*, VOC=*Vochysiaceae*, MYRI=*Myristicaceae*, STA=*Staphyleaceae*, RHA=*Rhamnaceae*, MAL=*Malvaceae*, LAC=*Lacistemataceae*, LEP=*Lepidobotryaceae*, SAB=*Sabiaceae*, BIX=*Bixaceae*, and BOR=*Boraginaceae*.

tended to have lower ρ_x compared to regions paralleling Amazon River (some plots in N-Peru and Colombia, AM-Brazil, WP-Brazil, CP-Brazil, EP-Brazil). To explore this trend, plot coordinates (latitude and longitude), altitude, mean annual temperature, and mean annual rainfall (see Appendix A) were plotted against xylem density (Fig. 2). High density sites were located between 0° and −5° while low density sites occurred in all the latitudinal range covered by this study: ≈10° to −15° (Fig. 2a). Xylem density also tended to increase from West to East (Fig. 2b) as has been reported for ρ_w (Baker et al., 2004b; Chave et al., 2006; ter Steege et al., 2006). The western margin is marked by the low ρ_x of the Ecuadorian plots (Fig. 2b). These were the plots closest to the Andes with higher altitudes (Fig. 2c), lower annual mean temperatures (Fig. 2d), higher annual rainfall (Fig. 2e), and more fertile soils (Malhi et al., 2004; Quesada et al., 2008). The Eastern most plots, located in EP-Brazil include a mangrove forest which had higher ρ_x than rest of forest plots in the same region (Region 12, Fig. 1). An inverse relationship between altitude and ρ_x (Fig. 2c) and a positive relationship with average air temperature (Fig. 2d) points to an effect of environmental conditions upon ρ_x. Low density sites are found in the two extremes of the rainfall range (Fig. 2e). In the low rainfall range (Bolivia and NE-Venezuela for example) there are the Bolivian seasonally flooded (LSL-01 and LSL-02), liana (CHO-01) and gallery forests plots (HCC-21 and HCC-22) where soils may retain enough soil moisture thus high soil water potential during the dry season. In the rest of the Bolivian and Venezuelan forests, trees may have distinct mechanisms common in seasonal forests such as low density wood, high stem water storage capacity and/or deciduous leaves (Choat et al., 2005) to cope with prolonged drought. In the high rainfall range there are the low density Ecuadorian sites and the intermediate density Guiana plots.

Taking the Basin as a whole (no division into regions), statistically significant differences existed between plot means ($P<0.001$) ranging from $800\pm50\,\text{kg m}^{-3}$ ($\pm$ standard deviation) at the dry experimental plot at Caxiuana (Projecto Secaflor), CAX-04, with the nearby control plot CAX-03 being the second highest at $780\pm120\,\text{kg m}^{-3}$. These are both *terra firme* forests on acrisol soils with 80% sand in its upper layer (Quesada et al., 2009b). The lowest plot means were for TAM-03, a swamp forests in Tambopata, and JAS-05 a forest growing on recently deposited river sediments (fluvisol) in Jatun Sacha in Ecuador. Both these plots had a mean ρ_x of $470\,\text{kg m}^{-3}$. Data for all 87 plots are summarised in Appendix B.

Figure 3 gives means ($\pm$ standard deviations) for all plots, grouped according to region, with regions being presented sequentially from top to bottom according to the overall mean ρ_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 CP-Brazil ($754\pm126\,\text{kg m}^{-3}$, $N=143$) which had significantly higher ρ_x (Tukey Test) than the rest of the regions while Ecuador had the lowest overall values ($535\pm89\,\text{kg m}^{-3}$). Nevertheless, Ecuador did not differ significantly from Bolivia, S-Perú and AC-Brazil, MT-Brazil, and Colombia. Within some regions: PC-Brazil, PE-Brazil, N-Perú, PW-Brazil, Colombia, S-Perú, MT-Brazil and Ecuador, mean ρ_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. The most variable plots were TAP-04, CAX-02, M17-11 (IV=0.76, 0.76 and 0.73, respectively) with the least variable being BNT-04, YAN-02, ALP-12 and TAP-03 (IV=0.24, 0.27, 0.27, and 0.27, respectively). IV values for all the plots can be seen in Appendix B.

3.2 Taxonomic variation

In a similar manner to the Region/Plot analysis above, variation in ρ_x at the family and genera level is summarised in Fig. 4. Overall there were significant differences between the families sampled ($F=8.08$ $DF=57$ $P<0.001$). Families with ρ_x higher than the basin mean were *Olacaceae*, *Celastraceae*, *Chrysobalanaceae*, *Humiriaceae*, *Ochnaceae*, *Linaceae*, *Scrophulariaceae*, *Myrtaceae*, and *Lecythidaceae*. Families with lower ρ_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 ρ_x and include some of the most abundant families across the basin: *Fabaceae*, *Rubiaceae*, *Lauraceae*, *Sapotaceae*, *Apocynaceae* (Fig. 4). 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*, and *Machaerium*. The genera with the lowest densities were *Annona*, *Matisia*, *Tetrorchidium*, *Collophora*, *Onychopetalum*, *Hyeronima*, and *Luehea*.

3.3 Partialling out geographical and taxonomic differences

Results of this analysis are shown in Fig. 5. Taxonomic variance in ρ_x was inferred as 33% of the total variance in the dataset, with species and family accounting for 19% and genus *per se* accounting only for 9%. Taken together, the geographical parameters (region and plot) accounted for 26% of the total variation with 20% of this being attributable to between region variation (this represents the average variation between plots in any one region). Overall, the proportion of the variance in the dataset that remained unexplained was 41%. This is the "residual variance" reflecting tree-to-tree variation within individual species, perhaps as a result
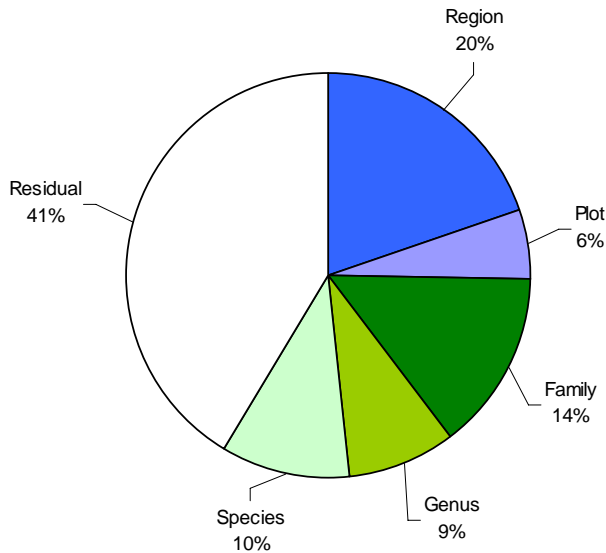
Fig. 5. Apportion of the total variance of ρ_x in the data set. The analysis includes only fully identified species (1198 individuals).

of architectural changes due to space constraints (Cochard et al., 2005), but also incorporating any measurement error. The analysis here differs from others (Baker et al., 2004b; ter Steege et al., 2006; Chave et al., 2006) 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 5 thus suggests that geographic location is as important as taxonomic identity in determining the value of ρ_x observed for any given tree but with considerable variation accountable for by neither. The first point is demonstrated further in Fig. 6, where we have taken the more widely abundant families (Fig. 6a) genera (Fig. 6b) and species (Fig. 6c) in our data set and plotted the average values observed in each of the plots were they were sampled as a function of the average density of all other trees sampled in the same plot. Our hypothesis had been that ρ_x of the most abundant families, genera and species across the basin would scale isometrically with the average of all other trees in the plot where they were found and thus we rationalised that ρ_x of individuals of the same species growing in different forests will reflect the mean values of the other trees in the same plot. Thus, we tested for a common slope amongst all the groups containing more than four observations at each taxonomic level. We found significant statistical indications that at the three levels there where common slopes, but in all cases the slopes fitted were significantly greater than 1.0: for families the common slope was 1.45, for genera 1.40 and for species 1.28 (Appendix C). We further tested for differences in elevation and shift across the SMA common slope and at the three levels there were significant shifts in elevation and along the common slopes. Notable exceptions did however exist for the *Urticaceae* (Fig. 6a,
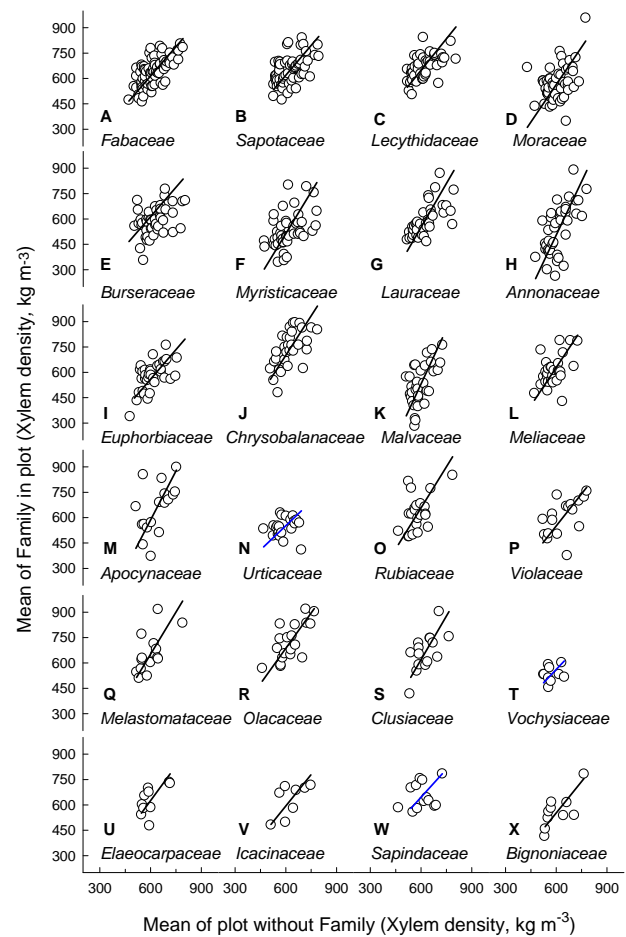
Fig. 6a. Pairwise relationships between mean ρ_x of plot (X-axis) and mean ρ_x of each family **(A)**, genera **(B)**, and species **(C)** within each plot. For each fitted line a plot mean was calculated excluding the family, genera or species for which the analysis was done and plotted against the average of that family, genus or species. Families used in the analysis were collected in at least 6 plots; genera in at least 8 plots and species in at least 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. All analysis were performed using SMATR.

panel T), that consist mostly of pioneer species (Whitmore, 1989). Non-significant relationships might be related to the "pioneer" character of the examined species i.e. *Pourouma minor*, *Pourouma guianensis* and also related to the reduced number of observations. Detailed outputs of all the analyses are given in Appendix C.

3.4 Geographical and taxonomic contributions to stand level differences

In order to evaluate the extent to which overall plot-to-plot variation might be caused by geographical or taxonomic

Fig. 6b. Continued.

Fig. 6c. Continued

3.5 Phenotypic plasticity and index of variation

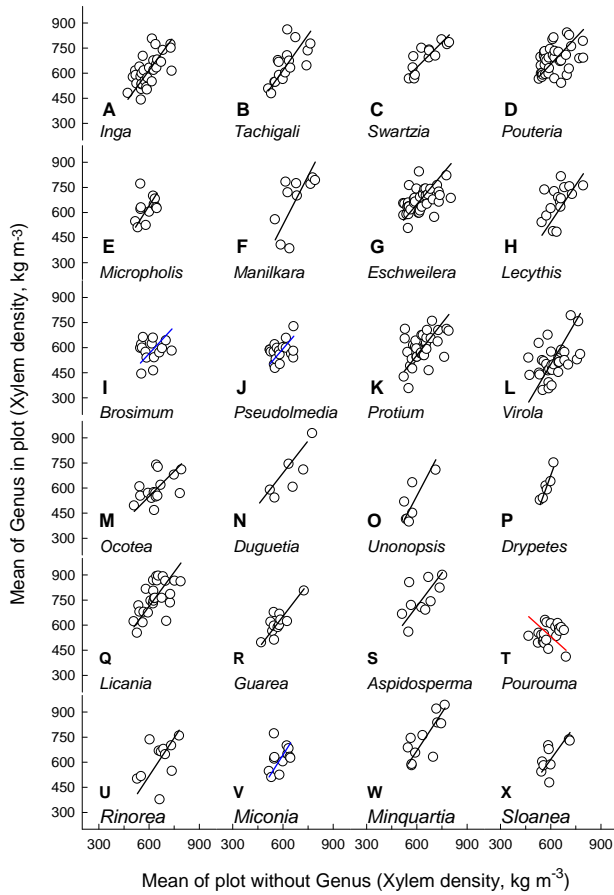In order to determine the intra-specific variation we compared the IPP of the same species collected several times within one plot and over several plots. The IPP of individual species collected in more than two plots (mean=0.29±0.13, N=19) was significantly higher (mean=0.15±0.07, N=86) than the variation of the same species collected more than twice within one plot (DF=1, F=16.24, P <0001). IPP values are given in Appendix D.

4 Discussion

Our results show that there are significant variations of branch xylem density across Amazonia with regional and local patterns and with considerable plasticity observed 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 the Basin patterns of branch xylem density may not be only explained by patterns of species composition and abundance as has previously been considered to be the case for ρ_w (Baker et al., 2004b; Chave et al., 2006; ter Steege, 2006).

Regional variations of ρ_x could be explained by spatial patterns of climatic factors (Sombroek, 2001; Malhi and Wright, 2004), geomorphologic and geochemical conditions (Fittkau et al., 1975) as well as by the sorting of species across landscapes (ter Steege et al., 2006; Chave et al.,

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 ρ_x for that plot according to the observed abundance of each species within it, denoted here as $\langle\rho_x\rangle$. 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 $\langle\rho_x\rangle$ in Fig. 7. This analysis shows that by far the most of the variation in $\langle\rho_x\rangle$ was accountable in terms of plot-to-plot differences, with the plot effects increasing almost linearly with $\langle\rho_x\rangle$ 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 $\langle\rho_x\rangle$> ca. 550 kg m^{-3}, although declining slightly thereafter. We treated our plot term as a fixed effect for the analysis in Fig. 7 (as opposed to a random effect in Fig. 5), as this permitted us to allow for different plots to have different intrinsic variances consistent with differences in topography and soils heterogeneity between the various plots. This also removed a slight bias in the residuals which was present when treating the r/p term as random.
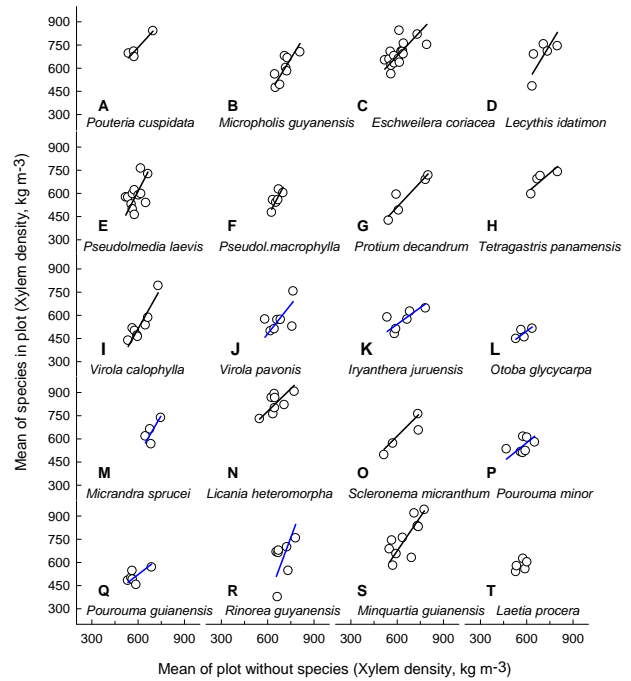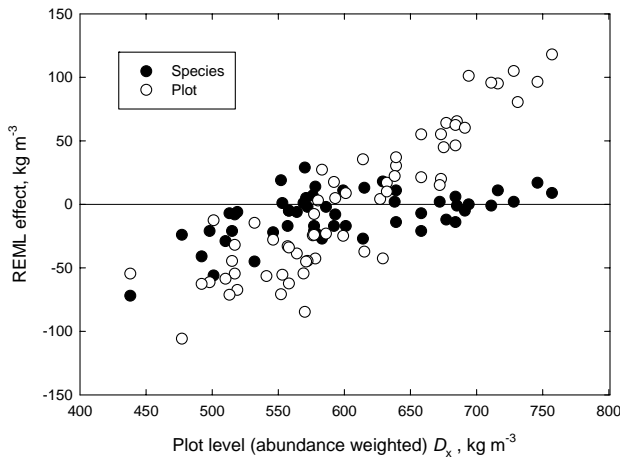
Fig. 7. The contribution of estimated plot effects (the r/p term of Eq. (1) and estimated genotypic effects (the $f/g/s$ term of Eq. (1) to stand level variations in wood density.

2006). Local differences may be associated to topographic and physiognomic variations along with soil chemical and physical properties. In plantations it is well known that the addition of nutrients (e.g. N and/or P) reduces wood density (Beets et al., 2001; Wang and Aitken, 2001; Thomas et al., 2005) and plots paralleling the Andes generally have higher soil P availability than those paralleling the Amazon River (Quesada et al., 2009b). Patterns of ρ_x across Amazonia support the idea that species are not randomly distributed across landscapes but follow the "habitat tracking" hypothesis (Ackerly, 2003). For example, irrespective of the taxonomic level examined (Fig. 6), ρ_x observed varied by as much as $400 \, \mathrm{kg \, m^{-3}}$ across sites. Moreover, this variation was systematic with different trees sampled within a given family/genus/species tending to have higher values of ρ_x along with other trees in the same plot (and vice versa). At each taxonomic level there was a common slope which was steeper than one, indicating that, at least for the widespread species examined in this study there exists considerable phenotypic plasticity in ρ_x; i.e. there is long term acclimation and thus adaptation of the xylem tissue to any given environment. That the slopes in Fig. 6 fitted through SMA are consistently greater than 1.0, suggests a continual replacement of species towards the maximum end of their ρ_x range by species with a characteristically lower ρ_x under the same growth conditions. Additional evidence for widespread plasticity comes from the REML variance partitioning of Fig. 5 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.

Since wood density is an important parameter in estimating forest carbon stocks (Baker, 2004a) one question to answer was: can ρ_w be predicted by knowledge of ρ_x? We examined our species level means for ρ_x as a function
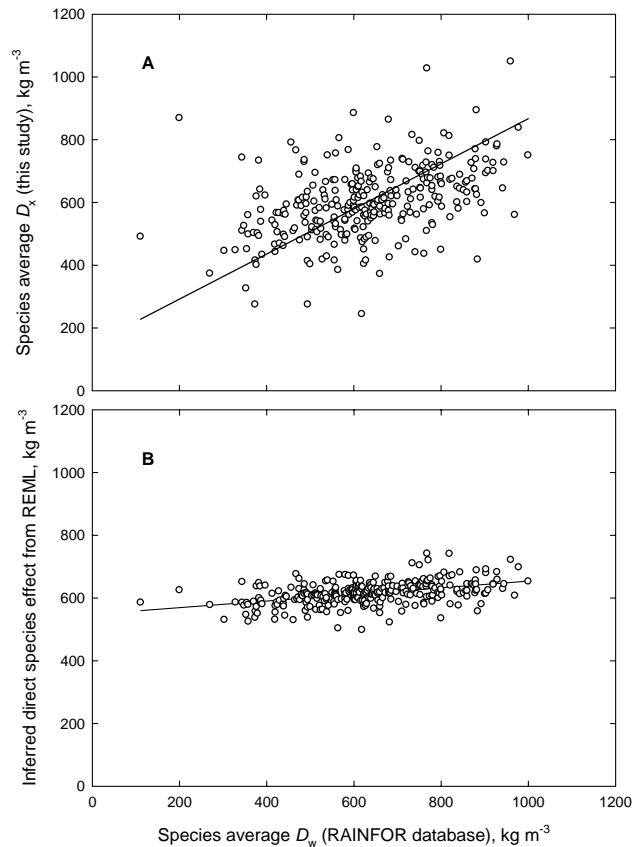
Fig. 8. The relationship between (**A**) observed species level values for xylem density (ρ_x) obtained in the current study and species level mean values for wood density ρ_w obtained from the RAINFOIR database and (**B**) deduced species level effects on ρ_x from the REML analysis of Eq. (1) and mean values of ρ_w from the RAINFOR database.

of species mean ρ_w using an expanded database (RAINFOR wood density data base) from that presented in Baker et al. (2004b). We found a reasonably good relationship (Fig. 8a). Similar results have been shown for Puerto Rican (Swenson and Enquist, 2008), Colombian (Juliana Agudelo and Pablo Stevenson, unpublished data) and Guiana forest species (Sarmiento et al., 2008). It is worth noting that the average ρ_x for this study i.e. for the Amazon basin, ($619 \, \mathrm{kg \, m^{-3}}$) is very similar to previous values reported for ρ_w for Amazonia. For example, Brown et al. (1984) estimated $620 \, \mathrm{kg \, m^{-3}}$ as the average wood density of tropical America, Chave et al. (2006) reported $650 \, \mathrm{kg \, m^{-3}}$ for Central and South America together and (Baker et al., 2004b) estimated $620 \, \mathrm{kg \, m^{-3}}$ as the overall species-level mean for Amazonia.

As reflected in Fig. 8b, our results do, however, differ from Baker et al. (2004b) and Chave et al. (2006) in that whilst all of their variation in ρ_w was attributed to genotype, in our case, variations in ρ_x are also attributable to both site

and genetic variations. 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) and thus, if there is some equivalence between ρ_x and ρ_w, what has previously been interpreted as a solely genetic effect for the latter, may in fact be partly a geographic (site and regional) effect: this being attribute to variations in climate, and soils. 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 ρ_x (and by implication ρ_w). For example we show that altitude is negatively correlated with ρ_x (Fig. 2c) and this effect has been suggested for ρ_w (Wiemann and Williamson, 1989; Chave et al., 2006). Temperature was also positively correlated with ρ_x as shown in Fig. 2d. The physical basis of this effect of temperature on wood density (water viscosity decreases as temperature increases) has been proposed by Roderick and Berry (2001) and has been experimentally supported by Thomas et al. (2004). There is also evidence that physical and chemical properties of soils may have an influence ρ_w (Hacke et al., 2000; Parolin, 2004; Parolin and Ferreira, 2004). In essence the REML species effect in Fig. 8b for ρ_x represents the inferred value that each species would have were it to be found on some sort of "overall average site".

It is also worth noting that, in contrast to the general trend, long-lived pioneer species (Whitmore, 1989) within the *Urticaceae* often associated to gap colonisation, secondary vegetation and/or late stages of forest succession, showed little tendency to exhibit variation in ρ_x across the sites where they were found (Fig. 6a, panel T, respectively). This brings the question of whether species showing little phenotypic plasticity and intermediate ρ_x values are present in sites where the majority of trees have relative low xylem density. These species when found in *terra firme* old grow forests (this study) may be more restricted to specific edaphic and microclimatic conditions that sustain colonisation and fast growth (i.e. gaps with enough water supply from the soil, nutrients, optimal temperature, not too much wind, sufficient light). This is because if they where in a high density site (stressful conditions) they could not cope with the environment. Also, species such as *Pourouma minor* and *P. guianensis*, which are generally considered low-density, fast-growing species did not have the lowest branch densities in our study; xylem density varied from 410 to 690 kg m^{-3}; comparable to some of the slow-growth climax species observed.

Further evidence of the influence of site conditions on ρ_x of trees comes from our own data. In a Mangrove forest in East Pará, Brazil (EP-Brazil, BRA-01, Appendix A) only two species were sampled (10 individuals per species) *Avicennia germinans* and *Rhizophora mangle* which mean ρ_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 converged to an almost identical high ρ_x. Mangroves are well known for having special water dynamics, fluctuating salinity, low oxygen concentration in the soil, and particular soil chemical and physical characteristics (Lovelock et al., 2006a). These environmental factors constrain tree water relations, gas exchange and growth (Lovelock et al., 2006b).

As suggested from experimental studies done on different species from different environments, high ρ_x is an adaptive response to severe environmental conditions such as drought (Dalla-Salda et al., 2008), high temperature (Thomas et al., 2004), porous soils (Hacke et al., 2000), poor nutrient conditions and long periods of high floods (Beets et al., 2001; Wang and Aitken, 2001; Thomas et al., 2005; Wittmann et al., 2006). For Amazonian species it is difficult to imagine that high ρ_x, of the order we have found (for example from 750 kg m^{-3} to 1130 kg m^{-3}) are directly associated with extreme drought conditions – those regions of the Amazon where severe water stress is most likely to occur are those regions with a long dry season i.e. Bolivia, parts of Venezuela, Guiana, and East Brazil. These regions were characterised by low and intermediate ρ_x. High xylem density most likely is related to variation in resource availability and/or different site dependent soil physical characteristics and hydrological constraints. ρ_x is a trait that reflects environmental constrains (Cochard et al., 2008), and so aggregation of species according to ρ_x (ter Steege et al., 2006, for example) should also reflect environmental constraints imposed upon "species" of trees. We conclude that variations of ρ_x across basin reflect an enormous functional diversity among trees and Amazonian forests. Any change in ρ_x may reflect changes at various levels of organisation. For example, as ρ_x increases, microfibril angle, cell wall thickness, modulus of elasticity and resistance to cavitation also increase, but hydraulic efficiency and rates of gas exchange decrease. Additional studies on these subjects, particularly how variations in ρ_x relates to other plant physiological characteristics (e.g. Fyllas et al., 2009) are needed to better understand the functional diversity of Amazonian trees.

Appendix A

Description of forests plots from which ρ_x data was obtained. More precise coordinates will be available (Andersoson et al., 2009) 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 West. ** not a permanent plot, samples were taken from trees around the Eddy covariance tower, – data not available. Additional information of plots can be found in: (Malhi et al., 2002, 2003; Baker et al., 2004; Vinceti, 2003).

Table A1.

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. Silveira
Alta Foresta	1	MT-Brazil	ALF-01	−9.60	−55.94	255	25.6	Terra firme	M. Silveira
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. Arroyo
Huanchaca Dos, plot2	2	Bolivia	HCC-22	−14.57	−60.75	735	25.1	Gallery	L. Arroyo
Las Londras, plot 1	2	Bolivia	LSL-01	−14.41	−61.14	170	25.9	Seasonally flooded	L. Arroyo
Las Londras, plot 2	2	Bolivia	LSL-02	−14.41	−61.14	170	25.9	Seasonally flooded	L. Arroyo
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 Amazónico, 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
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, clayey	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
Sucusari C	4	N-Peru	SUC-03	−3.25	−72.93	110	26.4	Seasonally flooded	O. Phillips, A. Monteagudo
Sucusari 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, T. DiFiore
Bogi 2	5	Ecuador	BOG-02	−0.70	−76.47	270	26.0	Terra firme	N. Pitman, 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

Table A1. Continued.

Plot Name and Description	Region Code	Region	Plot Code	latitude	longitude	Altitude (m)	Mean T (°C)	Forest Type	Principal Investigator
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
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
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 Hutyra, Wofsy, de Camargo, Vieira	10	WP-Brazil	TAP-04	−2.85	−54.96	73	26.5	Terra firme	S. Saleska, Hammond-Pyle,
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). Secaflor	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, da Costa, L. de Sa, J. Grace, P. Meir and Y. Malhi
Caxiuana 4: B (Drought experiment). Secaflor	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
Bragança	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
Acarouany, A11	13	Guiana	ACA-11	4.08	52.69	30	–	Terra firme	C. Baraloto, J. Chave
BAFOG, B4	13	Guiana	BAF-04	5.55	53.88	22	–	Terra firme	C. Baraloto, J. Chave
Guyaflux 7	13	Guiana	GFX-07	–	–	–	–	Flooded	D. Bonal
Guyaflux 9	13	Guiana	GFX-09	–	–	–	–	Terra firme	D. Bonal
Montagne Tortue, M1711	13	Guiana	M17-11	4.94	52.54	240	–	Terra firme	C. Baraloto, J. Chave
Nouragues-20H, NH20	13	Guiana	NGH-20	5.07	53.00	76	–	Terra firme	C. Baraloto, J. Chave
Nouragues-11L, NL11	13	Guiana	NGL-11	5.07	53.00	22	–	Terra firme	C. Baraloto, J. Chave
Saut Lavilette, LV1	13	Guiana	SLV-01	4.22	52.41	54	–	Terra firme	C. Baraloto, J. Chave
Tresor, T1	13	Guiana	TRE-01	3.24	52.28	87	–	Terra firme	C. Baraloto, J. Chave

Appendix B

Analysis of variance for each region. In the first column, the number below the name of the region is the mean followed by the standard deviation in parenthesis of that region. DF=degrees of freedom; F=statistical values, P=probability, N=number of samples, SE=standard error of mean, StDev=Standard deviation. IV=index of variation and plots size are also given; * after plot code means "significantly different" (Tukey test) and ** "not a permanent plot".

Appendix C

Pairwise relationships between average plot ρ_x and average ρ_x of family (Table C1), genera (Table C2) and species (Table C3). Slope of the SMA, Pearson's R correlation coefficient, sig the significance of the correlation, and n the number of cases used, sig: ****<0.001, ***<0.01, **<0.05, *<0.1, ns=not significant.

Table B1.

Region/Country	DF	F	P	Plot Code	Plot size (ha)	N	Mean (kg m^{-3})	SE Mean	St Dev	IV
CP-Brazil										
754 (126)	5	4.32	0.001	CAX-02*	1	15	669	52	203	0.757
				CAX-05	0.25	19	733	19	84	0.341
				CAX-01	1	20	740	37	166	0.505
				JRI-01	1	20	757	26	116	0.483
				CAX-03*	1	38	788	18	112	0.489
				CAX-04*	1	32	797	19	105	0.489
AM-Brazil										
702 (082)	5	2.11	0.74	MAN-02*	1	6	639	43	106	0.327
				MAN-04	1	10	675	23	72	0.277
				MAN-01	1	13	688	19	67	0.275
				MAN-05**		20	694	21	95	0.401
				MAN-03	1	9	729	32	97	0.295
				BNT-04*	1	21	736	11	51	0.240
EP-Brazil										
668 (109)	3	4.58	0.014	MBO-01	1	18	627	30	126	0.605
				CPP-01	1	20	649	21	92	0.490
				BRA-01*	1	20	723	20	91	0.333
	12	4.89	< 0.001	YAN-02*	1	8	521	23	65	0.268
				YAN-01*	1	17	570	24	101	0.459
				SUC-01*	1	19	629	28	120	0.411
				ALP-12	0.4	9	644	21	64	0.272
				SUC-04	1	20	657	17	77	0.308
				JEN-11	1	19	659	32	138	0.549
				SUC-02	1	16	659	22	90	0.346
				ALP-11	0.44	10	672	36	114	0.372
				ALP-22	0.44	12	678	22	75	0.312
				SUC-03	1	18	694	30	125	0.512
				ALP-21	0.48	6	720	55	135	0.373
				JEN-12*	1	20	746	26	115	0.414
				ALP-30*	1	12	765	17	58	0.281
WP-Brazil										
663 (114)	3	3.07	0.032	TAP-04*	4	33	627	24	136	0.758
				TAP-01	1	16	659	28	113	0.541
				TAP-03	1	20	673	14	60	0.272
				TAP-02*	1	19	722	22	96	0.405
SW-Venezuela										
610 (106)	2	2.35	0.102	SCR-04	1	26	594	19	98	0.487
				SCR-05	1	34	596	17	101	0.561
				SCR-01	1	21	653	26	117	0.471
Guiana										
620 (123)	8	2.42	0.017	BAF-04	1	20	574	26	116	0.535
				M17-11	1	21	578	34	154	0.725
				NGL-11	1	20	579	27	120	0.5
				GFX-07	0.5	20	601	32	145	0.691
				ACA-11	1	20	602	22	100	0.514
				TRE-01	1	20	641	20	90	0.391
				NGH-20	1	20	645	25	113	0.499
				GFX-09	0.42	28	661	23	119	0.542
				SLV-01*	1	20	684	24	107	0.427

Table B1. Continued.

Region/ Country	DF	F	P	Plot Code	Plot size (ha)	N	Mean (kg m^{-3})	SE Mean	St Dev	IV
S-Peru and AC-Brazil										
589 (100)	13	2.90	0.001	TAM-03*	0.58	6	468	40	98	0.395
				CUZ-03	1	23	573	15	70	0.399
				TAM-01	1	22	578	21	99	0.511
				TAM-04	0.42	15	588	25	95	0.379
				TAM-06	0.96	21	588	18	81	0.387
				TAM-02	1	19	625	26	114	0.545
				TAM-07	1	20	637	22	100	0.479
				TAM-05	1	20	642	20	90	0.375
				POR-01	1	19	545	23	100	0.571
				DOI-02	1	18	551	22	93	0.534
				POR-02	1	20	557	24	105	0.568
				RST-01	1	20	583	24	107	0.591
				DOI-01	1	18	613	18	75	0.386
				JUR-01	1	13	634	30	109	0.559
MT-Brazil										
575 (093)	1	9.55	0.004	ALF-01*	1	26	543	13	68	0.475
				SIN-01*	1	17	625	26	105	0.478
NE-Venezuela										
568 (125)	2	1.29	0.284	ELD-34	0.5	16	528	30	121	0.625
				RIO-12	0.5	19	582	24	102	0.527
				ELD-12	0.5	16	593	37	149	0.615
Bolivia										
561 (106)	6	0.74	0.62	LSL-02	1	16	530	21	85	0.525
				CHO-01	1	18	549	25	107	0.540
				HCC-22	1	21	550	25	114	0.481
				LFB-01	1	18	560	23	98	0.495
				LSL-01	1	14	569	37	140	0.602
				HCC-21	1	20	574	27	121	0.615
				LFB-02	1	16	601	17	68	0.355
Colombia										
593 (105)	7	8.00	< 0.001	ZAR-02	1	20	572	19	84	0.441
				ZAR-03	1	18	612	18	78	0.346
				ZAR-04	1	20	616	18	82	0.380
				ZAR-01*	1	20	712	20	88	0.372
				LOR-02	1	16	513	33	130	0.355
				AGP-02	1	20	545	19	87	0.5
				AGP-01	1	20	574	22	97	0.565
				LOR-01	1	17	582	20	81	0.602
Ecuador										
535 (089)	8	2.32	0.021	JAS-05*	1	20	472	16	74	0.424
				SUM-01	1	18	510	16	69	0.432
				JAS-03	1	19	526	17	73	0.388
				JAS-02	1	21	531	19	86	0.464
				BOG-02	1	33	536	17	100	0.572
				TIP-03	1	20	550	12	54	0.385
				BOG-01	1	44	554	15	98	0.593
				JAS-04	0.92	22	559	18	84	0.472
				TIP-05	1	11	568	35	115	0.490

Table C1.

Family	n	R^2	sig	Slope	Slope 95% CI	Interc	Interc 95% CI
Fabaceae	73	0.439	****	1.155	(0.968 1.377)	−0.078	(−0.205 0.050)
Sapotaceae	61	0.253	****	1.176	(0.941 1.470)	−0.086	(−0.252 0.080)
Moraceae	52	0.160	***	1.477	(1.142 1.911)	−0.322	(−0.557 −0.087)
Lecythidaceae	48	0.342	****	1.239	(0.977 1.573)	−0.095	(−0.282 0.092)
Myristicaceae	48	0.144	***	1.645	(1.254 2.158)	−0.473	(−0.754 −0.191)
Burseraceae	46	0.169	***	1.165	(0.886 1.532)	−0.140	(−0.344 0.064)
Lauraceae	41	0.252	***	1.729	(1.311 2.279)	−0.485	(−0.791 −0.178)
Annonaceae	39	0.410	****	2.112	(1.640 2.721)	−0.760	(−1.093 −0.426)
Euphorbiaceae	35	0.359	****	1.271	(0.961 1.682)	−0.199	(−0.421 0.023)
Malvaceae	33	0.318	****	2.160	(1.603 2.910)	−0.767	(−1.160 −0.373)
Chrysobalanaceae	31	0.364	****	1.556	(1.154 2.097)	−0.232	(−0.529 0.065)
Meliaceae	30	0.231	***	1.504	(1.078 2.099)	−0.272	(−0.573 0.028)
Urticaceae	22	0.009	ns	0.951	(0.607 1.490)	−0.018	(−0.281 0.245)
Rubiaceae	22	0.229	**	1.618	(1.086 2.410)	−0.313	(−0.702 0.075)
Olacaceae	19	0.474	***	1.393	(0.969 2.002)	−0.149	(−0.476 0.178)
Apocynaceae	17	0.277	**	1.930	(1.228 3.033)	−0.572	(−1.150 0.006)
Violaceae	17	0.277	**	1.266	(0.805 1.990)	−0.208	(−0.593 0.176)
Melastomataceae	15	0.388	**	1.656	(1.053 2.606)	−0.342	(−0.812 0.128)
Clusiaceae	15	0.406	**	1.714	(1.096 2.678)	−0.409	(−0.908 0.090)
Sapindaceae	13	0.058	ns	1.101	(0.601 2.019)	−0.015	(−0.450 0.420)
Vochysiaceae	10	0.035	ns	1.049	(0.504 2.183)	−0.068	(−0.551 0.416)
Elaeocarpaceae	10	0.404	**	1.371	(0.757 2.482)	−0.197	(−0.718 0.325)
Bignoniaceae	10	0.529	**	1.242	(0.728 2.118)	−0.193	(−0.619 0.233)
Icacinaceae	8	0.403	ns	1.239	(0.609 2.521)	−0.149	(−0.755 0.456)

Table C2.

Genera	n	R^2	sig	Slope	Slope 95% CI	Interc	Interc 95% CI
Eschweilera (Lec)	40	0.252	***	1.1907	(0.8995 1.5761)	−0.063767	−0.277379 0.149845
Pouteria (Sap)	37	0.141	*	1.0595	(0.7748 1.4489)	0.020563	(−0.190905 0.232031)
Ocotea (Lau)	34	0.211	**	1.2725	(0.9289 1.743)	−0.208803	(−0.468646 0.05104)
Virola (Myri)	33	0.111	*	1.7147	(1.2218 2.4065)	−0.528158	
Inga (Fab)	32	0.409	****	1.3688	(1.0315 1.8165)	−0.20076	(−0.435863 0.034343)
Licania (Chry)	26	0.351	***	1.3635	(0.9772 1.9024)	−0.103841	(−0.399524 0.191843)
Pseudolmedia (Mor)	19	0.114	ns	1.1711	(0.7358 1.8638)	−0.109588	(−0.441129 0.221952)
Tachigali (Fab)	17	0.446	**	1.4143	(0.949 2.1075)	−0.227317	(−0.58844 0.133806)
Micropholis (Sap)	16	0.385	**	1.3497	(0.8732 2.0863)	−0.255261	(−0.637631 0.12711)
Lecythis (Lec)	16	0.267	*	1.5616	(0.9731 2.5062)	−0.345006	(−0.843226 0.153214)
Ocotea (Lau)	16	0.22	*	1.0082	(0.6196 1.6406)	−0.055156	(−0.386934 0.276623)
Pourouma (Urt)	16	0	ns	−0.8993	(−1.552 −0.5211)	1.071904	(0.763112 1.380696)
Brosimum (Mor)	15	0.012	ns	1.0845	(0.6164 1.9082)	−0.086202	(−0.485705 0.313302)
Swartzia (Fab)	13	0.683	****	1.0007	(0.6943 1.44240	0.036976	(−0.210473 0.284425)
Guarea (Meli)	12	0.678	***	1.3031	(0.8822 1.9248)	−0.148985	(−0.447886 0.149916)
Miconia (Mel)	12	0.119	ns	1.5847	(0.8517c2.9483)	−0.307446	(−0.925763 0.310871)
Rinorea (Vio)	11	0.192	ns	1.5168	(0.8044c2.8599)	−0.392198	(−1.081057 0.29666)
Minquartia (Ola)	11	0.588	**	1.5207	(0.9535c2.4253)	−0.243791	(−0.72481 0.237228)
Tetragastris	11	0.274	*	1.5604	(0.8521c2.8575)	−0.410824	(−1.056808 0.23516)
Manilkara (Sap)	10	0.401	*	1.9426	(1.0712c3.5229)	−0.635196	(−1.464367 0.193974)
Aspidosperma (Apo)	10	0.368	*	1.3236	(0.7193c2.4354)	−0.081181	(−0.627278 0.464915)
Sloanea (Ela)	9	0.46	*	1.3939	90.7523c2.583)	−0.219332	(−0.776561 0.337897)
Unonopsis (Ann)	7	0.598	*	1.8996	(0.9658c3.7363)	−0.586441	(−1.386101 0.213218)
Duguetia (Ann)	6	0.699	*	1.4467	(0.717c2.9192)	−0.246887	(−0.96251 0.468736)
Drypetes (Eup)	6	0.888	**	2.7519	(1.7565c4.3114)	−0.976167	(−1.713112 −0.239221)

Table C3.

Species	n	R^2	sig	Slope	Slope 95% CI	Interc	Interc 95% CI
Pouteria cuspidata	4	0.891	*	1.091	(0.450 2.645)	0.081	(−0.574 0.736)
Micropholis guyanensis	8	0.627	**	1.631	(0.916 2.906)	−0.444	(−1.080 0.192)
Eschweilera coriacea	17	0.369	**	1.060	(0.694 1.621)	0.043	(−0.244 0.329)
Lecythis idatimon	5	0.458	ns	1.649	(0.544 5.004)	−0.486	(−2.062 1.090)
Pseudolmedia laevis	12	0.214	ns	1.938	(1.074 3.495)	−0.549	(−1.262 0.164)
Pseudolmedia macrophylla	6	0.603	*	1.912	(0.867 4.214)	−0.560	(−1.542 0.421)
Protium decandrum	5	0.851	*	1.067	(0.551 2.063)	−0.126	(−0.634 0.381)
Tetragastris panamensis	4	0.663	ns	0.857	(0.226 3.250)	0.090	(−0.963 1.144)
Virola calophylla	8	0.812	**	1.786	(1.173 2.720)	−0.558	(−1.035 −0.082)
Virola pavonis	7	0.282	ns	1.259	(0.531 2.985)	−0.275	(−1.104 0.555)
Iryanthera juruensis	6	0.465	ns	0.719	(0.295 1.754)	0.111	(−0.360 0.581)
Otoba glycycarpa	4	0.472	ns	0.752	(0.162 3.489)	0.046	(−0.917 1.010)
Micrandra sprucei	4	0.536	ns	1.724	(0.394 7.544)	−0.541	(−3.005 1.923)
Licania heteromorpha	8	0.423	*	0.972	(0.483 1.958)	0.195	(−0.289 0.679)
Scleronema micranthum	4	0.842	*	0.999	(0.359 2.779)	−0.018	(−0.799 0.762)
Pourouma minor	7	0.138	ns	0.811	(0.320 2.051)	0.089	(−0.411 0.589)
Pourouma guianensis	6	0.383	ns	0.770	(0.300 1.980)	0.060	(−0.430 0.549)
Rinorea guyanensis	7	0.162	ns	2.698	(1.077 6.756)	−1.261	(−3.252 0.731)
Minquartia guianensis	10	0.554	**	1.473	(0.875 2.479)	−0.209	(−0.739 0.321)
Laetia procera	5	0.259	ns	1.050	(0.304 3.627)	−0.015	(−0.957 0.927)

Appendix D

Index of phenotypic plasticity within and between plots. N is
the number of individual in each plot, Max and Min are the
maximum and minimum ρ_x of each species within one plot.
IPP within is the average IPP within plots, IPP between takes
the max and min of each species occurring in different plots.

Table D1.

Species	Plot	N	Max (g cm^{-3})	Min (g cm^{-3})	IPP (within)	IPP (between)
Aldina kunhardtiana	SCR-04	2	0.594	0.491	0.174	0.118
	SCR-01	2	0.579	0.543		
Brosimum lactescens	SUC-03	2	0.655	0.628	0.212	0.099
	TAM-01	3	0.613	0.516		
Eperua falcata	GFX-09	4	0.733	0.387	0.473	0.300
	GFX-07	4	0.589	0.513		
Erisma uncinatum	CHO-01	2	0.533	0.489	0.107	0.074
	LFB-01	2	0.509	0.476		
Eschweilera coriacea	CAX-04	2	0.823	0.679	0.304	0.108
	MBO-01	2	0.750	0.631		
	CAX-02	2	0.744	0.670		
	CPP-01	3	0.722	0.709		
	LOR-01	2	0.683	0.638		
	AGP-01	2	0.659	0.573		
Inga laurina	LSL-01	3	0.726	0.669	0.225	0.057
	CUZ-03	2	0.584	0.563		
Lecythis idatimon	CAX-01	2	0.803	0.706	0.194	0.118
	CPP-01	2	0.731	0.647		
Lecythis persistens	TRE-01	3	0.784	0.686	0.657	0.287
	NGL-11	2	0.782	0.690		
	GFX-07	2	0.705	0.269		
Manilkara bidentata	CAX-03	2	0.858	0.796	0.182	0.117
	JRI-01	2	0.837	0.702		
Miconia poeppigii	LSL-01	3	0.685	0.493	0.354	0.290
	LSL-02	7	0.632	0.443		
Minquartia guianensis	CAX-04	4	1.079	0.844	0.271	0.156
	JRI-01	4	0.869	0.787		
Otoba glycycarpa	JAS-04	2	0.516	0.496	0.166	0.078
	YAN-01	2	0.487	0.430		
Oxandra asbeckii	SLV-01	2	0.851	0.759	0.186	0.144
	GFX-09	7	0.845	0.693		
Pourouma guianensis	HCC-22	4	0.611	0.406	0.301	0.158
	LFB-01	2	0.595	0.498		
	CHO-01	2	0.505	0.495		
	HCC-21	2	0.484	0.427		
Pseudolmedia laevis	LFB-02	2	0.670	0.507	0.419	0.179
	CUZ-03	4	0.652	0.560		
	BOG-02	2	0.607	0.544		
	LFB-01	3	0.503	0.389		
Pseudolmedia macrophylla	LFB-01	2	0.647	0.468	0.277	0.141
	TAM-02	2	0.633	0.574		
	TAM-04	3	0.599	0.492		
	TAM-01	2	0.545	0.537		
Qualea paraensis	LFB-02	2	0.638	0.497	0.221	0.136
	LSL-02	2	0.607	0.575		
Rinorea guianensis	CAX-03	2	0.773	0.742	0.419	0.120
	TAP-01	4	0.723	0.632		
	TAP-02	2	0.713	0.686		
	TAP-03	5	0.712	0.646		
	CAX-01	2	0.645	0.449		
Tetragastris altissima	DOI-01	4	0.649	0.461	0.350	0.163
	POR-01	2	0.629	0.560		
	POR-02	6	0.530	0.421		
	RIO-12	2	0.512	0.489		

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