

## 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,  $\rho_x$ , were made for 1653 trees representing 598 species, sampled from 87 sites across the Amazon basin. Measured values ranged from  $218 \text{ kg m}^{-3}$  for a *Cordia sagotii* (Boraginaceae) from Montagne de Tortue, French Guiana to  $1130 \text{ kg m}^{-3}$  for an *Aiouea* sp. (Lauraceae) from Caxiua, Central Pará, Brazil. Analysis of variance showed significant differences in average  $\rho_x$  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 constraints, 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

too (Elias and Potvin, 2003). Density,  $\rho$ , (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,  $\rho_w$ ) 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,  $\rho_x$ ). 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  $\rho_x$  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),  $\rho_x$  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  $\rho_x$  and  $\rho_w$  should be related (Swenson and Enquist, 2008; Sarmiento et al., 2009) as both reflect an individual species’ water transport strategy and



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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 constraints (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  $\rho_x$ . 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 been known that  $\rho_w$  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  $\rho_w$  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 successional stage (old-growth forest) and at the same elevation showed that in *várzea*  $\rho_w$  was higher than in igapó (Schöngart et al., 2005). At the community level, low  $\rho_w$  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  $\rho_x$  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  $\rho_x$  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  $\rho_w$  and  $\rho_x$  we hypothesised that  $\rho_x$  is a “plastic” trait that reflects both phylogenetic constraints and environmental gradients. We predict that individuals of species that are widespread across Amazonia will show an increase in  $\rho_x$  as the average-plot  $\rho_x$  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 exists 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](http://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 Caxiupana plots (Central Pará, Brazil) we sampled in two consecutive years (2002 and 2003) and since there was no statistical difference in  $\rho_x$  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 sub-sample (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  $\rho_x$  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 =  $619 \text{ kg m}^{-3}$ , mean lower branches =  $615 \text{ kg m}^{-3}$ ). The  $\rho_x$  values of trees sampled at Paracou followed a normal distribution, and included the range of densities measured for  $\rho_w$  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.

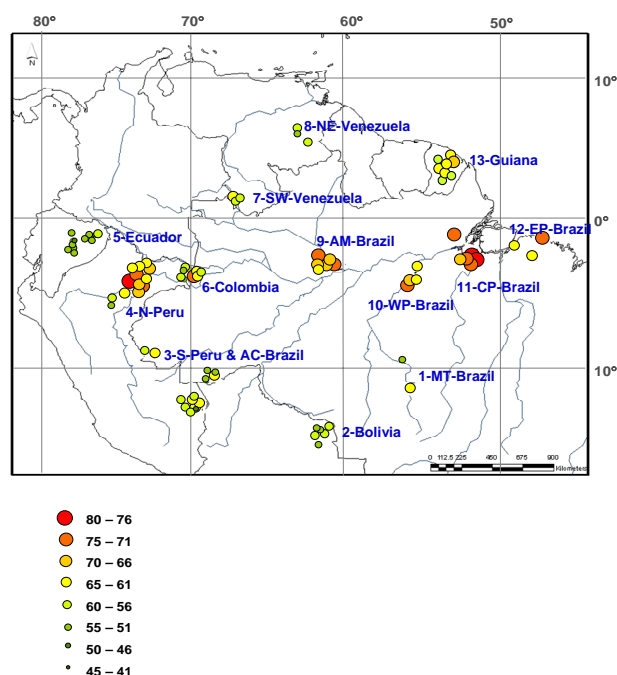
In order to assess the representativeness of the sampling strategy generally utilised across the Basin (usually only 20 trees per one hectare plot), we took advantage of the more comprehensive BRIDGE measurements to assess how representative this sampling strategy really was. Thus, for each comprehensively 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*.

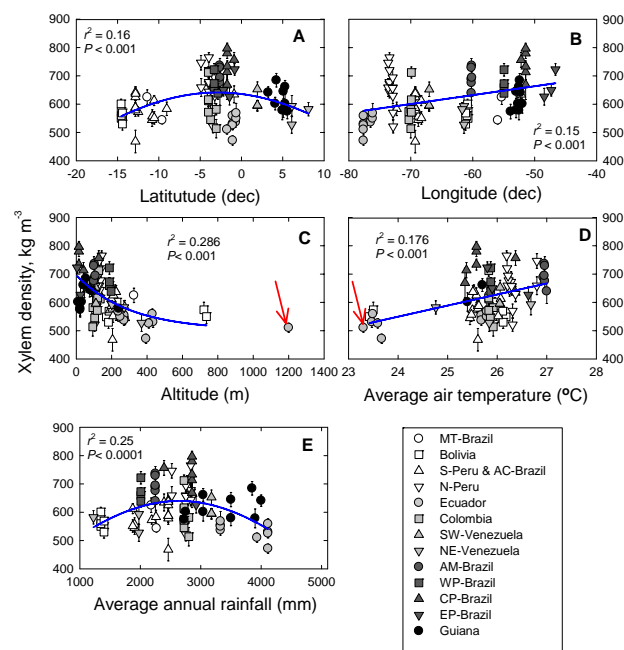
### 2.4 Xylem density determinations

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,  $\rho_x$ , for 87 forest plots across the Amazon basin. Each symbol represents one plot. Symbol size represents the arithmetic mean  $\rho_x$  ( $\text{kg m}^{-3}$ ). 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; 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,  $\rho_x$ , 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.

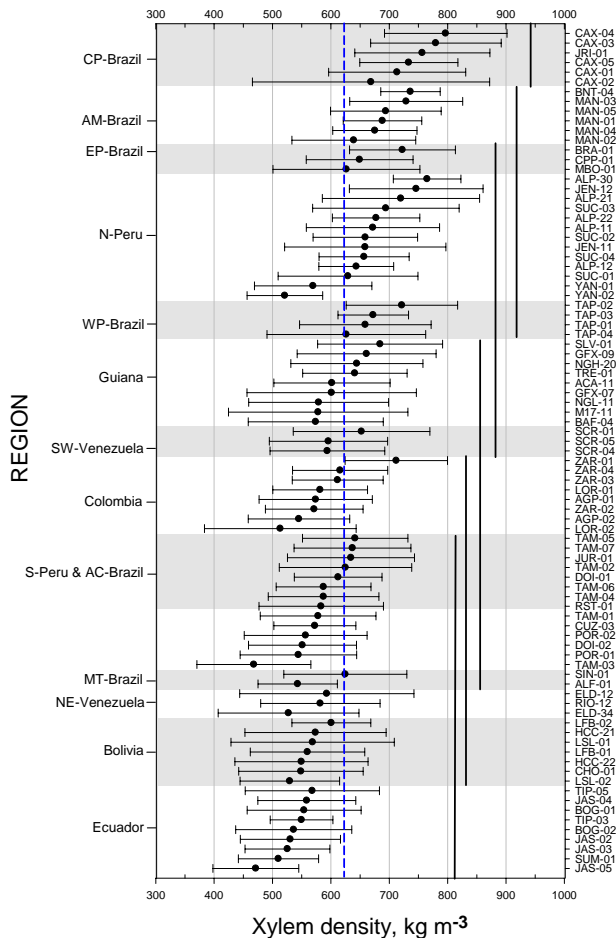
## 2.5 Statistical analysis

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

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

where  $\mu$  represents the overall mean of the dataset ( $619 \text{ kg m}^{-3}$ ); 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 ( $\varepsilon$ ) 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  $\rho_x$  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  $\rho_x$  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  $\rho_w$  values assimilated from a wide range of sources into the RAINFOR “wood density” database.

In order to determine the extent to which  $\rho_x$  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  $\rho_x$  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  $\rho_x$  followed normal distribution with mean and median values of  $619 \text{ kg m}^{-3}$  and  $612 \text{ kg m}^{-3}$ , respectively; normality test (StDev=0.124,  $N=1653$ ,  $AD=1.202$   $P<0.005$ ).

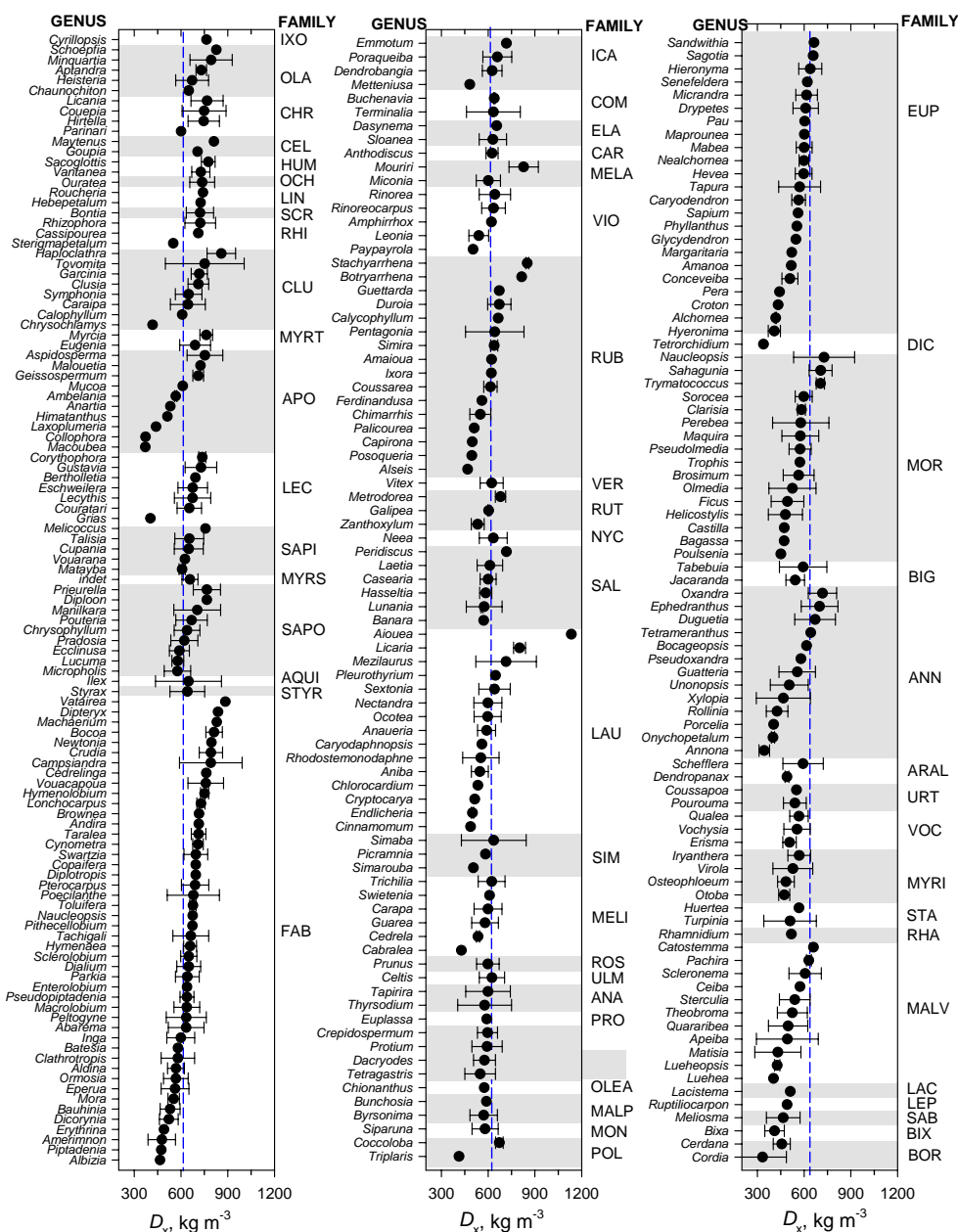
Of all the trees sampled, 95% (1568) had been identified to the family level, 89% (1475) to the genus level, and 72% (1199) to the species level. The trees sampled accounted for 60 families, representing 41% of the total number of families present in the neotropics (Mass and Westra, 1993) with 283 genera, 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*, *Minuartia 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  $\rho_x$  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  $\rho_x$  from North and South towards the Amazon River is apparent with high  $\rho_x$  being concentrated along the river itself. Plots located close to the Andes, North and South from the Amazon River tended to have the lowest  $\rho_x$ . For example, all plots in Ecuador, some in N-Perú, all in S-Perú and AC-Brazil and Bolivia had relatively low  $\rho_x$  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,  $\rho_x$  ( $\text{kg m}^{-3}$ ), between and within families. Each dot represents the average  $\rho_x$  of each genus. Left vertical axes represent genera, right vertical axes represent families and X-axis is the  $\rho_x$ . Grey and white shadows separate the families. Vertical dashed-blue line represents the mean  $\rho_x$  of the basin. Horizontal lines represent the Standard Deviation. Families in the Figure are sorted from high to low  $\rho_x$  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  $\rho_x$ : 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, AQU=Aquifoliaceae, STYR=Styracaceae, FAB=Fabaceae, ICA=Icacinaeae, 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  $\rho_x$  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  $0^\circ$  and  $-5^\circ$  while low density sites occurred in all the latitudinal range covered by this study:  $\approx 10^\circ$  to  $-15^\circ$  (Fig. 2a). Xylem density also tended to increase from West to East (Fig. 2b) as has been reported for  $\rho_w$  (Baker et al., 2004b; Chave et al., 2006; ter Steege et al., 2006). The western margin is marked by the low  $\rho_x$  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  $\rho_x$  than rest of forest plots in the same region (Region 12, Fig. 1). An inverse relationship between altitude and  $\rho_x$  (Fig. 2c) and a positive relationship with average air temperature (Fig. 2d) points to an effect of environmental conditions upon  $\rho_x$ . 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  $800 \pm 50 \text{ kg m}^{-3}$  ( $\pm$  standard deviation) at the dry experimental plot at Caxiua (Projeto Scafflor), CAX-04, with the nearby control plot CAX-03 being the second highest at  $780 \pm 120 \text{ kg m}^{-3}$ . 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  $\rho_x$  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  $\rho_x$  for the trees sampled within them. This shows that, although considerable plot-to-plot variation existed within regions (e.g. N-Peru and Colombia) large statistical differences between regions also existed ( $P < 0.001$ ). Of these, the

highest overall value was for CP-Brazil ( $754 \pm 126 \text{ kg m}^{-3}$ ,  $N=143$ ) which had significantly higher  $\rho_x$  (Tukey Test) than the rest of the regions while Ecuador had the lowest overall values ( $535 \pm 89 \text{ kg m}^{-3}$ ). Nevertheless, Ecuador did not differ significantly from Bolivia, S-Peru and AC-Brazil, MT-Brazil, and Colombia. Within some regions: PC-Brazil, PE-Brazil, N-Peru, PW-Brazil, Colombia, S-Peru, MT-Brazil and Ecuador, mean  $\rho_x$  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.

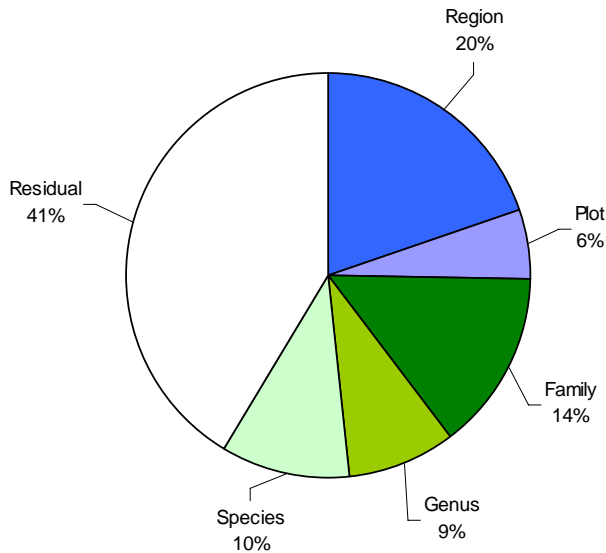
### 3.2 Taxonomic variation

In a similar manner to the Region/Plot analysis above, variation in  $\rho_x$  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  $\rho_x$  higher than the basin mean were *Olacaceae*, *Celastraceae*, *Chrysobalanaceae*, *Humiriaceae*, *Ochnaceae*, *Linaceae*, *Scrophulariaceae*, *Myrtaceae*, and *Lecythidaceae*. Families with lower  $\rho_x$  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  $\rho_x$  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*, *Colophora*, *Onychopetalum*, *Hyeronima*, and *Luehea*.

### 3.3 Partialling out geographical and taxonomic differences

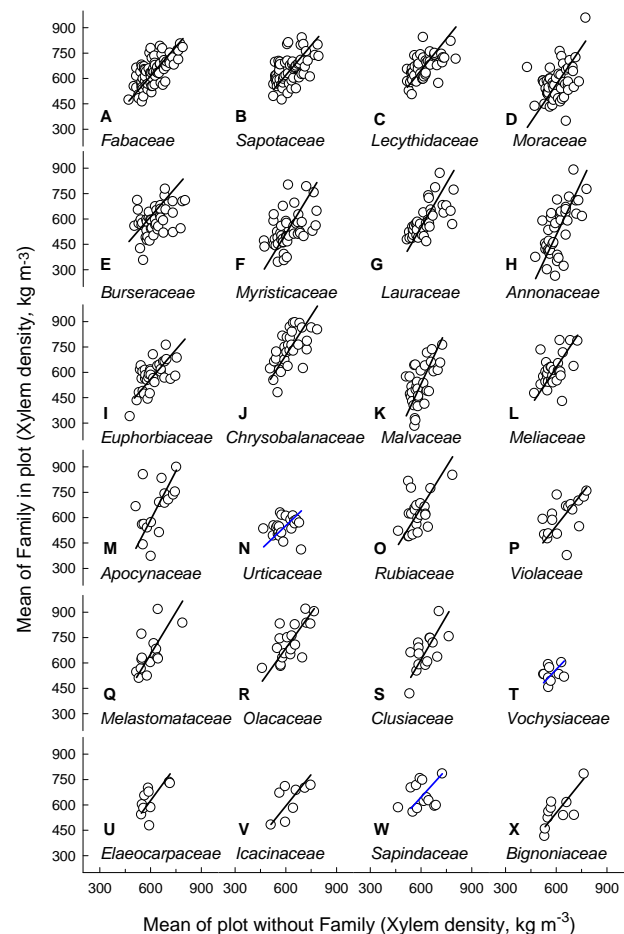
Results of this analysis are shown in Fig. 5. Taxonomic variance in  $\rho_x$  was inferred as 33% of the total variance in the dataset, with species and family accounting for 19% and genus *per se* accounting only for 9%. Taken together, the geographical parameters (region and plot) accounted for 26% 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.** Apportionment of the total variance of  $\rho_x$  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  $\rho_x$  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 where they were sampled as a function of the average density of all other trees sampled in the same plot. Our hypothesis had been that  $\rho_x$  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  $\rho_x$  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 were 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  $\rho_x$  of plot (X-axis) and mean  $\rho_x$  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

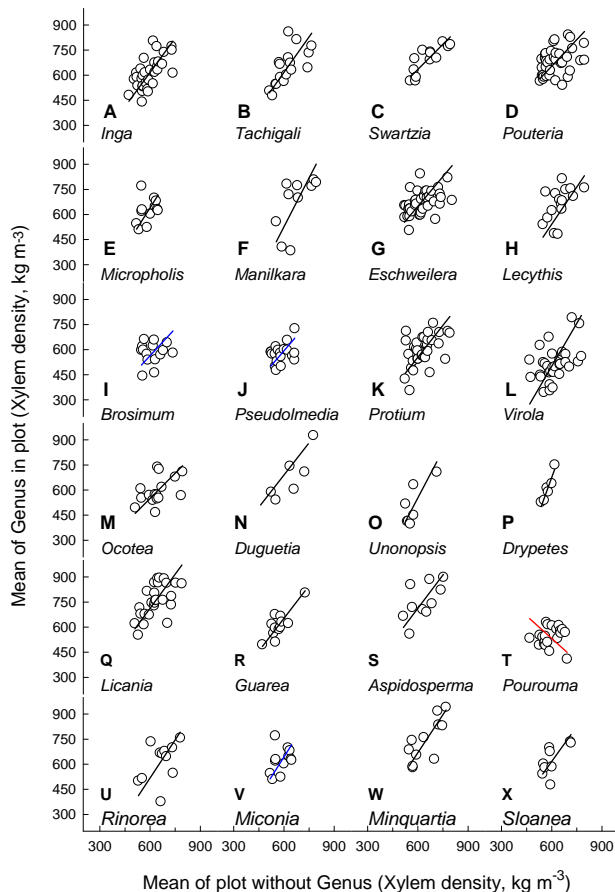


Fig. 6b. Continued.

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  $\rho_x$  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  $\langle \rho_x \rangle > \text{ca. } 550 \text{ kg m}^{-3}$ , 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.

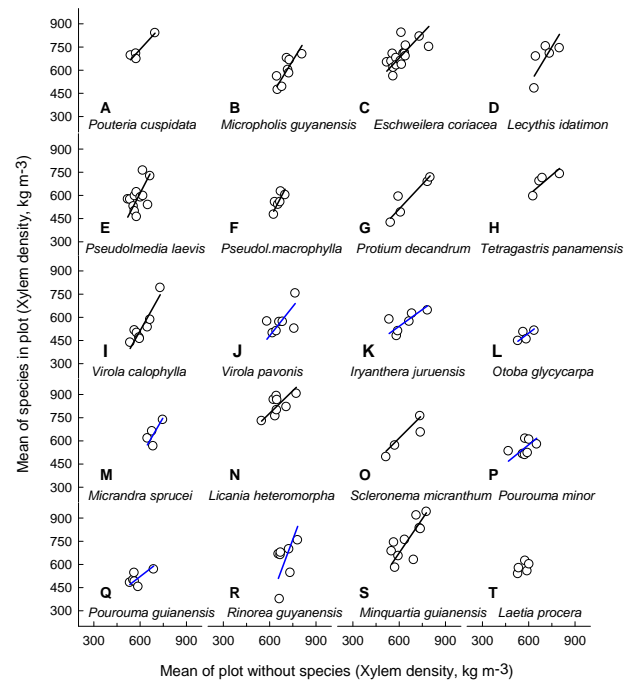


Fig. 6c. Continued

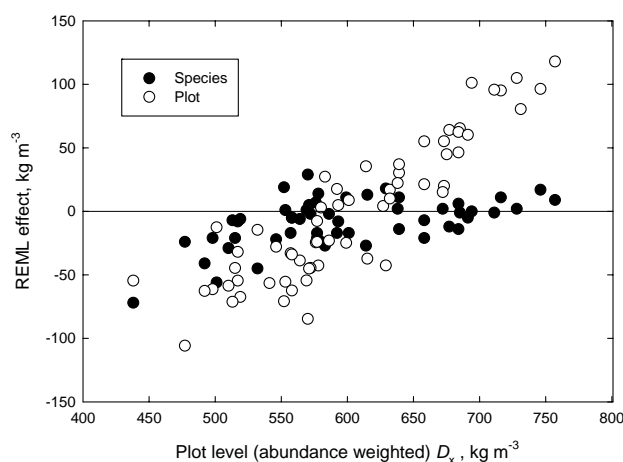
### 3.5 Phenotypic plasticity and index of variation

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 =  $0.29 \pm 0.13$ ,  $N=19$ ) was significantly higher (mean =  $0.15 \pm 0.07$ ,  $N=86$ ) 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  $\rho_w$  (Baker et al., 2004b; Chave et al., 2006; ter Steege, 2006).

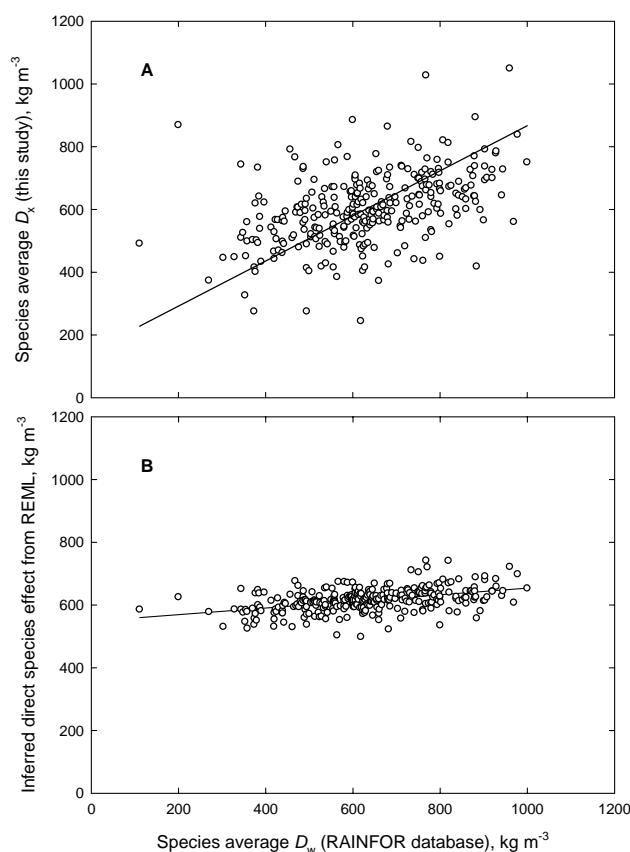
Regional variations of  $\rho_x$  could be explained by spatial patterns of climatic factors (Sombroek, 2001; Malhi and Wright, 2004), geomorphologic and geochemical conditions (Fittkau et al., 1975) as well as by the sorting of species across landscapes (ter Steege et al., 2006; Chave et al.,



**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  $\rho_x$  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),  $\rho_x$  observed varied by as much as  $400 \text{ kg m}^{-3}$  across sites. Moreover, this variation was systematic with different trees sampled within a given family/genus/species tending to have higher values of  $\rho_x$  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  $\rho_x$ ; 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  $\rho_x$  range by species with a characteristically lower  $\rho_x$  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  $\rho_w$  be predicted by knowledge of  $\rho_x$ ? We examined our species level means for  $\rho_x$  as a function



**Fig. 8.** The relationship between (A) observed species level values for xylem density ( $\rho_x$ ) obtained in the current study and species level mean values for wood density  $\rho_w$  obtained from the RAINFOR database and (B) deduced species level effects on  $\rho_x$  from the REML analysis of Eq. (1) and mean values of  $\rho_w$  from the RAINFOR database.

of species mean  $\rho_w$  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  $\rho_x$  for this study i.e. for the Amazon basin, ( $619 \text{ kg m}^{-3}$ ) is very similar to previous values reported for  $\rho_w$  for Amazonia. For example, Brown et al. (1984) estimated  $620 \text{ kg m}^{-3}$  as the average wood density of tropical America, Chave et al. (2006) reported  $650 \text{ kg m}^{-3}$  for Central and South America together and (Baker et al., 2004b) estimated  $620 \text{ kg m}^{-3}$  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  $\rho_w$  was attributed to genotype, in our case, variations in  $\rho_x$  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  $\rho_x$  and  $\rho_w$ , 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  $\rho_x$  (and by implication  $\rho_w$ ). For example we show that altitude is negatively correlated with  $\rho_x$  (Fig. 2c) and this effect has been suggested for  $\rho_w$  (Wiemann and Williamson, 1989; Chave et al., 2006). Temperature was also positively correlated with  $\rho_x$  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  $\rho_w$  (Hacke et al., 2000; Parolin, 2004; Parolin and Ferreira, 2004). In essence the REML species effect in Fig. 8b for  $\rho_x$  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  $\rho_x$  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  $\rho_x$  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<sup>-3</sup>; comparable to some of the slow-growth climax species observed.

Further evidence of the influence of site conditions on  $\rho_x$  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  $\rho_x$  were 722±87 kg m<sup>-3</sup> and 723±99 kg m<sup>-3</sup>, 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  $\rho_x$ . 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  $\rho_x$  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  $\rho_x$ , of the order we have found (for example from 750 kg m<sup>-3</sup> to 1130 kg m<sup>-3</sup>) 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  $\rho_x$ . High xylem density most likely is related to variation in resource availability and/or different site dependent soil physical characteristics and hydrological constraints.  $\rho_x$  is a trait that reflects environmental constraints (Cochard et al., 2008), and so aggregation of species according to  $\rho_x$  (ter Steege et al., 2006, for example) should also reflect environmental constraints imposed upon “species” of trees. We conclude that variations of  $\rho_x$  across basin reflect an enormous functional diversity among trees and Amazonian forests. Any change in  $\rho_x$  may reflect changes at various levels of organisation. For example, as  $\rho_x$  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  $\rho_x$  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  $\rho_x$  data was obtained. More precise coordinates will be available (Andersson 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 <i>T</i> (°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 I                                    | 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:<br>Varillal                                     | 6           | Colombia     | ZAR-01    | −4.01    | −69.91    | 130          | 25.6          | Caatinga               | M. C. Penuela and E. Alvarez   |
| EL Zafire:<br>Rebalse                                      | 6           | Colombia     | ZAR-02    | −4.00    | −69.90    | 120          | 25.6          | Seasonally flooded     | M. C. Penuela and E. Alvarez   |
| EL Zafire:<br>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<br>Oxisol                                       | 7           | SW-Venezuela | SCR-01    | 1.93     | −67.02    | 120          | 26.0          | Terra firme            | R. Herrera   |
| San Carlos<br>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<br>(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<br>(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,<br>plots G3 (ELD-03)<br>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:<br>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,<br>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,<br>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,<br>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   |
| Caxiuaná 3:<br>A (Control drought<br>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,<br>da Costa, L. de Sa, J. Grace,<br>P. Meir and Y. Malhi |
| Caxiuaná 4: B (Drought<br>experiment). Secaflor            | 11          | CP-Brazil    | CAX-04    | −1.73    | −51.46    | 15           | 25.6          | Terra firme            | S. Almeida, A. L.<br>da Costa, L. de Sa, J. Grace,<br>P. Meir and Y. Malhi                               |
| Caxiuaná 5:<br>Eddy tower                                  | 11          | CP-Brazil    | CAX-05    | −1.72    | −51.46    | 15           | 25.6          | Terra firme            | S. Almeida,<br>L. de Sa, J. Grace, P.<br>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<br>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  $\rho_x$  and average  $\rho_x$  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/<br>Country        | DF   | F       | P       | Plot<br>Code | Plot size<br>(ha) | N   | Mean<br>(kg m <sup>-3</sup> ) | SE<br>Mean | St<br>Dev | IV    |
|---------------------------|------|---------|---------|--------------|-------------------|-----|-------------------------------|------------|-----------|-------|
| CP-Brazil<br>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<br>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<br>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<br>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<br>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<br>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/<br>Country                | DF | F    | P       | Plot<br>Code | Plot size<br>(ha) | N  | Mean<br>(kg m <sup>-3</sup> ) | SE<br>Mean | St<br>Dev | IV    |
|-----------------------------------|----|------|---------|--------------|-------------------|----|-------------------------------|------------|-----------|-------|
| S-Peru and AC-Brazil<br>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<br>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<br>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<br>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<br>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<br>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                  | <i>n</i> | <i>R</i> <sup>2</sup> | sig  | Slope | Slope 95% CI  | Interc | Interc 95% CI   |
|-------------------------|----------|-----------------------|------|-------|---------------|--------|-----------------|
| <i>Fabaceae</i>         | 73       | 0.439                 | **** | 1.155 | (0.968 1.377) | −0.078 | (−0.205 0.050)  |
| <i>Sapotaceae</i>       | 61       | 0.253                 | **** | 1.176 | (0.941 1.470) | −0.086 | (−0.252 0.080)  |
| <i>Moraceae</i>         | 52       | 0.160                 | ***  | 1.477 | (1.142 1.911) | −0.322 | (−0.557 −0.087) |
| <i>Lecythidaceae</i>    | 48       | 0.342                 | **** | 1.239 | (0.977 1.573) | −0.095 | (−0.282 0.092)  |
| <i>Myristicaceae</i>    | 48       | 0.144                 | ***  | 1.645 | (1.254 2.158) | −0.473 | (−0.754 −0.191) |
| <i>Burseraceae</i>      | 46       | 0.169                 | ***  | 1.165 | (0.886 1.532) | −0.140 | (−0.344 0.064)  |
| <i>Lauraceae</i>        | 41       | 0.252                 | ***  | 1.729 | (1.311 2.279) | −0.485 | (−0.791 −0.178) |
| <i>Annonaceae</i>       | 39       | 0.410                 | **** | 2.112 | (1.640 2.721) | −0.760 | (−1.093 −0.426) |
| <i>Euphorbiaceae</i>    | 35       | 0.359                 | **** | 1.271 | (0.961 1.682) | −0.199 | (−0.421 0.023)  |
| <i>Malvaceae</i>        | 33       | 0.318                 | **** | 2.160 | (1.603 2.910) | −0.767 | (−1.160 −0.373) |
| <i>Chrysobalanaceae</i> | 31       | 0.364                 | **** | 1.556 | (1.154 2.097) | −0.232 | (−0.529 0.065)  |
| <i>Meliaceae</i>        | 30       | 0.231                 | ***  | 1.504 | (1.078 2.099) | −0.272 | (−0.573 0.028)  |
| <i>Urticaceae</i>       | 22       | 0.009                 | ns   | 0.951 | (0.607 1.490) | −0.018 | (−0.281 0.245)  |
| <i>Rubiaceae</i>        | 22       | 0.229                 | **   | 1.618 | (1.086 2.410) | −0.313 | (−0.702 0.075)  |
| <i>Olcaceae</i>         | 19       | 0.474                 | ***  | 1.393 | (0.969 2.002) | −0.149 | (−0.476 0.178)  |
| <i>Apocynaceae</i>      | 17       | 0.277                 | **   | 1.930 | (1.228 3.033) | −0.572 | (−1.150 0.006)  |
| <i>Violaceae</i>        | 17       | 0.277                 | **   | 1.266 | (0.805 1.990) | −0.208 | (−0.593 0.176)  |
| <i>Melastomataceae</i>  | 15       | 0.388                 | **   | 1.656 | (1.053 2.606) | −0.342 | (−0.812 0.128)  |
| <i>Clusiaceae</i>       | 15       | 0.406                 | **   | 1.714 | (1.096 2.678) | −0.409 | (−0.908 0.090)  |
| <i>Sapindaceae</i>      | 13       | 0.058                 | ns   | 1.101 | (0.601 2.019) | −0.015 | (−0.450 0.420)  |
| <i>Vochysiaceae</i>     | 10       | 0.035                 | ns   | 1.049 | (0.504 2.183) | −0.068 | (−0.551 0.416)  |
| <i>Elaeocarpaceae</i>   | 10       | 0.404                 | **   | 1.371 | (0.757 2.482) | −0.197 | (−0.718 0.325)  |
| <i>Bignoniaceae</i>     | 10       | 0.529                 | **   | 1.242 | (0.728 2.118) | −0.193 | (−0.619 0.233)  |
| <i>Icacinaeae</i>       | 8        | 0.403                 | ns   | 1.239 | (0.609 2.521) | −0.149 | (−0.755 0.456)  |

Table C2.

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

Table C3.

| Species                         | <i>n</i> | <i>R</i> <sup>2</sup> | sig | Slope | Slope 95% CI  | Interc | Interc 95% CI   |
|---------------------------------|----------|-----------------------|-----|-------|---------------|--------|-----------------|
| <i>Pouteria cuspidata</i>       | 4        | 0.891                 | *   | 1.091 | (0.450 2.645) | 0.081  | (−0.574 0.736)  |
| <i>Micropholis guyanensis</i>   | 8        | 0.627                 | **  | 1.631 | (0.916 2.906) | −0.444 | (−1.080 0.192)  |
| <i>Eschweilera coriacea</i>     | 17       | 0.369                 | **  | 1.060 | (0.694 1.621) | 0.043  | (−0.244 0.329)  |
| <i>Lecythis idatimon</i>        | 5        | 0.458                 | ns  | 1.649 | (0.544 5.004) | −0.486 | (−2.062 1.090)  |
| <i>Pseudolmedia laevis</i>      | 12       | 0.214                 | ns  | 1.938 | (1.074 3.495) | −0.549 | (−1.262 0.164)  |
| <i>Pseudolmedia macrophylla</i> | 6        | 0.603                 | *   | 1.912 | (0.867 4.214) | −0.560 | (−1.542 0.421)  |
| <i>Protium decandrum</i>        | 5        | 0.851                 | *   | 1.067 | (0.551 2.063) | −0.126 | (−0.634 0.381)  |
| <i>Tetragastris panamensis</i>  | 4        | 0.663                 | ns  | 0.857 | (0.226 3.250) | 0.090  | (−0.963 1.144)  |
| <i>Virola calophylla</i>        | 8        | 0.812                 | **  | 1.786 | (1.173 2.720) | −0.558 | (−1.035 −0.082) |
| <i>Virola pavonis</i>           | 7        | 0.282                 | ns  | 1.259 | (0.531 2.985) | −0.275 | (−1.104 0.555)  |
| <i>Iryanthera juruensis</i>     | 6        | 0.465                 | ns  | 0.719 | (0.295 1.754) | 0.111  | (−0.360 0.581)  |
| <i>Otoba glycyarpa</i>          | 4        | 0.472                 | ns  | 0.752 | (0.162 3.489) | 0.046  | (−0.917 1.010)  |
| <i>Micrandra sprucei</i>        | 4        | 0.536                 | ns  | 1.724 | (0.394 7.544) | −0.541 | (−3.005 1.923)  |
| <i>Licania heteromorpha</i>     | 8        | 0.423                 | *   | 0.972 | (0.483 1.958) | 0.195  | (−0.289 0.679)  |
| <i>Scleronema micranthum</i>    | 4        | 0.842                 | *   | 0.999 | (0.359 2.779) | −0.018 | (−0.799 0.762)  |
| <i>Pourouma minor</i>           | 7        | 0.138                 | ns  | 0.811 | (0.320 2.051) | 0.089  | (−0.411 0.589)  |
| <i>Pourouma guianensis</i>      | 6        | 0.383                 | ns  | 0.770 | (0.300 1.980) | 0.060  | (−0.430 0.549)  |
| <i>Rinorea guyanensis</i>       | 7        | 0.162                 | ns  | 2.698 | (1.077 6.756) | −1.261 | (−3.252 0.731)  |
| <i>Minquartia guianensis</i>    | 10       | 0.554                 | **  | 1.473 | (0.875 2.479) | −0.209 | (−0.739 0.321)  |
| <i>Laetia procera</i>           | 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  $\rho_x$  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<br>(g cm <sup>-3</sup> ) | Min<br>(g cm <sup>-3</sup> ) | IPP<br>(within) | IPP<br>(between) |
|---------------------------------|--------|---|------------------------------|------------------------------|-----------------|------------------|
| <i>Aldina kunhardtiana</i>      | SCR-04 | 2 | 0.594                        | 0.491                        | 0.174           | 0.118            |
|                                 | SCR-01 | 2 | 0.579                        | 0.543                        |                 |                  |
| <i>Brosimum lactescens</i>      | SUC-03 | 2 | 0.655                        | 0.628                        | 0.212           | 0.099            |
|                                 | TAM-01 | 3 | 0.613                        | 0.516                        |                 |                  |
| <i>Eperua falcata</i>           | GFX-09 | 4 | 0.733                        | 0.387                        | 0.473           | 0.300            |
|                                 | GFX-07 | 4 | 0.589                        | 0.513                        |                 |                  |
| <i>Erisma uncinatum</i>         | CHO-01 | 2 | 0.533                        | 0.489                        | 0.107           | 0.074            |
|                                 | LFB-01 | 2 | 0.509                        | 0.476                        |                 |                  |
| <i>Eschweilera coriacea</i>     | 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                        |                 |                  |
| <i>Inga laurina</i>             | AGP-01 | 2 | 0.659                        | 0.573                        | 0.225           | 0.057            |
|                                 | LSL-01 | 3 | 0.726                        | 0.669                        |                 |                  |
|                                 | CUZ-03 | 2 | 0.584                        | 0.563                        |                 |                  |
| <i>Lecythis idatimon</i>        | CAX-01 | 2 | 0.803                        | 0.706                        | 0.194           | 0.118            |
|                                 | CPP-01 | 2 | 0.731                        | 0.647                        |                 |                  |
| <i>Lecythis persistens</i>      | 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                        |                 |                  |
| <i>Manilkara bidentata</i>      | CAX-03 | 2 | 0.858                        | 0.796                        | 0.182           | 0.117            |
|                                 | JRI-01 | 2 | 0.837                        | 0.702                        |                 |                  |
| <i>Miconia poeppigii</i>        | LSL-01 | 3 | 0.685                        | 0.493                        | 0.354           | 0.290            |
|                                 | LSL-02 | 7 | 0.632                        | 0.443                        |                 |                  |
| <i>Minquartia guianensis</i>    | CAX-04 | 4 | 1.079                        | 0.844                        | 0.271           | 0.156            |
|                                 | JRI-01 | 4 | 0.869                        | 0.787                        |                 |                  |
| <i>Otoba glycycarpa</i>         | JAS-04 | 2 | 0.516                        | 0.496                        | 0.166           | 0.078            |
|                                 | YAN-01 | 2 | 0.487                        | 0.430                        |                 |                  |
| <i>Oxandra asbeckii</i>         | SLV-01 | 2 | 0.851                        | 0.759                        | 0.186           | 0.144            |
|                                 | GFX-09 | 7 | 0.845                        | 0.693                        |                 |                  |
| <i>Pourouma guianensis</i>      | 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                        |                 |                  |
| <i>Pseudolmedia laevis</i>      | 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                        |                 |                  |
| <i>Pseudolmedia macrophylla</i> | 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                        |                 |                  |
| <i>Qualea paraensis</i>         | LFB-02 | 2 | 0.638                        | 0.497                        | 0.221           | 0.136            |
|                                 | LSL-02 | 2 | 0.607                        | 0.575                        |                 |                  |
| <i>Rinorea guianensis</i>       | 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                        |                 |                  |
| <i>Tetragastris altissima</i>   | CAX-01 | 2 | 0.645                        | 0.449                        | 0.350           | 0.163            |
|                                 | DOI-01 | 4 | 0.649                        | 0.461                        |                 |                  |
|                                 | 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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