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Soil controls biomass and dynamics of an Amazonian forest through the shifting of species and traits

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Abstract The effects of soil on tree species composition and trait distributions in tropical forest, and how these interactions affect tree biomass and dynamics, are poorly understood because variation in soil is confounded with variation in climate over large areas. We excluded confounding due to climate by studying variation among 72 1-ha plots within 64 km^2, and minimized within-plot variation in soil and stand properties by using long narrow plots oriented along altitudinal contours in Reserva Ducke, Central Amazonia, Brazil. Soil variation caused shifts in tree species composition, which determined stand-level wood density. Soil clay content, cation exchange capacity, plot mean wood density and one-dimensional ordination of tree species composition explained about 40% of variation in tree biomass, 24% of variation in tree mortality and 18% of variation in coarse wood production. As pioneer species were not abundant, lower biomass and higher mortality on sandy soils is a consequence of dominance of species with low to medium wood density adapted to waterlogged and nutrient-poor sandy soils. Therefore, mesoscale variation in biomass and dynamics is caused by co-occurrence of species with similar traits in different parts of the edaphic gradient. Identification of mechanisms controlling tree biomass and dynamics in Amazonian forest will require better understanding of tree–soil physiologic interactions.

Introduction

The main determinants of variation in tree biomass and dynamics in Amazonian forests are still a matter of debate. Regional-scale studies are limited by correlations between climate variables (i.e., rainfall, dry season length and temperature), soil (texture and fertility) and stand properties (species composition, basal area, height and wood density), which make it difficult to identify causal factors underlying losses and accumulation of biomass (e.g., Baker et al. 2004, 2009; Malhi et al. 2004; Phillips et al. 2004; ter Steege et al. 2006; Baraloto et al. 2011; Quesada et al. 2012).

An East–West gradient of above-ground biomass and wood density in Amazonia has been related to changes in tree species composition (Baker et al. 2004). The most abundant genera in Eastern portions of Amazon basin (*Carapa, Lecythis, Aldina, Pentaclethra, Alexa, Dicorynia, Eperua, Catostemma, Mora* and *Dicymbe*) have higher wood density than those of Western part (*Iriartea, Attalea, Otoba, Oenocarpus, Pseudolmedia, Ficus, Clarisia, Sapium, Spondias* and *Cecropia*) (Chave et al. 2006; ter Steege et al. 2006). These differences explain about 45% of variation in above-ground biomass across Amazonia

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(Baker et al. 2004). Tree turnover rates and coarse wood production follow the same East–West gradient, with less dynamic and less productive forests on poorer soils of Eastern and Central Amazonia than on richer soils of Southern and Western parts of the basin (Phillips et al. 2004; Malhi et al. 2004; Quesada et al. 2012). These patterns are also associated with species substitution through the basin, with higher abundance of fast-growing and light-demanding taxa on richer soils of Western Amazonia (Chave et al. 2006; ter Steege et al. 2006). Nonetheless, fertility is associated with poor soil structure, which is related to other factors such as depth, aeration and porosity (Quesada et al. 2010). Species selection on richer and poorly structured soils favors those taxa with fast growth, fast maturation time and short lifespan, driving to more dynamic forests with higher growth, mortality and turnover rates but with smaller trees and lower biomass (Quesada et al. 2012). However, the East–West increase in soil fertility is strongly related to a decrease in dry season length and an increase in annual precipitation, making difficult to decouple the effects of soil from climate at large scale.

Correlations of soil and stand properties with climate can be avoided at mesoscales (0.1–100 km). Above-ground tree biomass is related to soil and topography at mesoscales in several sites in Amazonia (e.g., Castilho et al. 2006; Ferry et al. 2010). Also, effects of soil have been reported for wood density (Baraloto et al. 2011), tree mortality and recruitment, biomass change and coarse wood production (Castilho et al. 2010; Ferry et al. 2010; Toledo et al. 2011, 2012) and on tree- and palm-species composition (Valencia et al. 2004; John et al. 2007; Costa et al. 2009). Overall, biomass stocks and wood density are lower in forests on waterlogged sandy soils than on well-drained clayey soils, while tree mortality, recruitment and coarse wood production show an inverse pattern.

Although there are evidences about the effects of soil, wood density and associated changes in species composition on forest biomass and dynamics at both large and mesoscales, the contribution of these variables to variation in forest biomass and dynamics is poorly understood. Baraloto et al. (2011) determined the contribution of climate, soil, wood density and stand structure on tree above-ground biomass at medium and large scales in Peru and French Guyana. They controlled for the effect of climate and found little effect of soil or wood density on spatial distribution of biomass. The lack of influence of soil may be attributed to the site selection, which may have reduced the length of environmental gradients, and to plot shape (100 × 200 m). In undulating landscapes, such as those in Central Amazonia and the Guyana shield, square plots usually have different soil types in the same plot. Therefore, particularly at smaller scales, the effects of soil

properties through species composition and traits on biomass and forest dynamics are not elucidated.

Long, narrow plots that follow topographic contours have less within-plot soil variation and increase confidence in relationships with predictor variables (Magnusson et al. 2005). Here, we used data from 72 1-ha narrow plots oriented along topographic contours that were spread on 64 km^2 in Reserva Ducke to evaluate the influence of soil on stand properties (biomass, species composition and wood density) and processes (coarse wood production and tree mortality). We hypothesized that soil texture and fertility predict tree species composition and stand-level wood density, and thus determine mesoscale variation in above-ground tree biomass, tree mortality and coarse wood production.

Materials and methods

Study site – The study was carried out in Reserva Ducke, which is managed by the Instituto Nacional de Pesquisas da Amazônia (INPA). The 10,000-ha reserve is covered by relatively undisturbed "terra firme" tropical moist forest and is located on the periphery of the city of Manaus, Amazonas, Brazil (2°55′S, 59°59′W; Electronic Supplementary Material Appendix A1: Fig. A1). The forest has a closed canopy of 30–37 m tall, with emergent trees reaching 45 m and an understory with abundant acaulescent palms (Ribeiro et al. 1999).

Annual average temperature is 26 °C and the average annual rainfall is 2500 mm, with a dry season from July to September, during which monthly rainfall is often around 100 mm (Coordenação de Pesquisas em Clima e Recursos Hídricos–CPCRH–INPA, unpubl. data). Topography is undulated with altitude varying from 40 to 140 m above sea level (Ribeiro et al. 1999). The soils were originated from Tertiary fluvio-lacustrine deposits, which derived from the weathered Precambrian Guianan and Brazilian Shields (Chauvel et al. 1987). The oxisols ("Latossolo amarelo distrófico" in the Brazilian classification system after EMBRAPA 2006) predominate on plateaux, ultisols ("Argissolo vermelho amarelo distrófico") are more common on slopes, and spodosols ("Espodossolo cárbico hidromórfico") predominate in valleys, usually near water. These soils are acidic and poor in nutrients such as phosphorus, calcium, magnesium, sodium and potassium, while often high in aluminum (Chauvel et al. 1987; Castilho et al. 2006).

Experimental design – A grid of 18 8-km trails, each separated by 1 km, was installed in Reserva Ducke, encompassing 64 km^2. Between December 2000 and February 2003, 72 1-ha permanent plots were established along the east–west trails at least 1 km from each other (Electronic Supplementary Material Appendix A1: Fig. A1). These plots are narrow and long (40 × 250 m)

and follow topographic contours to maintain a constant elevation, minimizing within-plot variation in soil type and depth to the water table. A hierarchical design was used to sample trees and palms (collectively called trees) in which diameter at breast height (dbh) was used to define the sampling area (Magnusson et al. 2005; Castilho et al. 2006). In this study we used trees with dbh $\geq$10 cm sampled in 0.5 ha (20 $\times$ 250 m) and trees with dbh $\geq$30 cm, which were sampled in 1 ha (40 $\times$ 250 m). The dbh was measured to the nearest 1 mm at 1.3 m above ground. When deformities or buttresses were present, dbh was measured 50 cm above them, and the point of measurement was recorded. All trees were mapped and marked with aluminum numbered tags, and botanical vouchers were collected for identification and deposited at the Herbarium of the Instituto Nacional de Pesquisas da Amazônia (INPA).

A first census was carried out when plots were established between December 2000 and February 2003, a second was done between February 2003 and February 2005, and a third (though the time interval began in March 2005), between August 2006 and February 2008. The first census interval, between the first and second censuses, averaged 2 $\pm$ 0.03 years (mean $\pm$ standard deviation), and the second census interval, between the second and third census, was 3.1 $\pm$ 0.2 years (2.9–3.6 years). In the second census, all trees marked in the first census were measured again and recruits were inventoried, but in the third census we recorded only dead trees that had died between the second and third censuses. The total census interval between the first and third censuses averaged 5.1 $\pm$ 0.2 years (range: 4.9–5.8 years). Trees were defined as dead by the absence of leaves, sap and loss of bark. Stems which disappeared or those which were broken or had no sap below the point of measurement also were recorded as dead. In the second census (2003–2005), C. V. Castilho classified dead trees as standing or fallen, and in the third census (2005–2008), all dead trees $\geq$4 cm dbh, including those dead in the second census, were classified in the following modes of death (Toledo et al. 2012): (1) standing—dead trees with intact crown branches on their standing stem or with crown debris scattered in all directions around the tree stump; (2) uprooted—the root plate upturned with soil attached; (3) snapped—dead trees with a broken trunk and a downed stem on which crown branches were often attached; and (4) others—category used for trees that could not be located, i.e., those unidentifiable due to advanced stage of stem decomposition. We used data of trees (dbh $\geq$ 10 cm) inventoried in the first census and data of dead trees identified in the second and third census to calculate mortality rates per plot by mode of death and for all modes of death combined with the equation described by Sheil et al. (1995): $m = 1 - [1 - (N_0 - N_1)/N_0]^{1/t}$,

where m is given as percent of trees dead per year, N_0 and N_1 are the number of stems at the beginning and end of the time interval t ($\sim$5 years).

Wood density data – Taxonomic information was used to access wood density data compiled for Tropical South America in the Global Wood Density Database (Chave et al. 2009) available in the Dryad data repository at http://datadryad.org/ (Zanne et al. 2009). We carefully corrected all possible nomenclatural errors comparing every species name with information available in the Tropicos database (http://www.tropicos.org/). Genus or family-level wood density means were used in the absence of species-level information, and plot mean wood density at species level was used for those stems without any identification. We calculated plot mean wood density weighed by stem, basal area or species. Wood density calculated on stems or basal area basis gives more importance to abundant taxa while on species basis gives more weight to rare species. Further, basal area basis attributes more importance to species with higher contribution to biomass and coarse wood production (see Baker et al. 2004). In the 72 1-ha plots, 78.2% of 25,402 tagged stems with dbh $\geq$ 10 cm were identified to species, 92.5% to genus, 98.3% to family and 1.7% were not identified. Wood density was estimated based on species for 50% of stems, 91.6% based on genus, 98.3% based on family, and the 1.7% that could not be identified were given the plot mean wood density based on species. Plot mean wood density varied little for trees with dbh $\geq$ 10 cm and DBH $\geq$ 30 cm (Electronic Supplementary Material Appendix A2: Fig. A2). The mean estimated from number of stems (0.69 $\pm$ 0.01 g cm^{-3}, mean $\pm$ 95% CI) was slightly lower than estimates based on basal area (0.70 $\pm$ 0.011) and species (0.70 $\pm$ 0.012).

Soil and topographic data – Six superficial soil subsamples (0–5 cm deep) at 50-m intervals along the center line of each plot were collected with a hand-spade after removing superficial litter layer with a machete. Top soil was used since this layer holds larger portion of mineral fertility (see Quesada et al. 2011). The subsamples were mixed to form a composite sample per plot ($\sim$500 g of soil), which were transferred to laboratory. Soil samples were dried at 105 °C, cleaned by removing stones and fine roots, and then sieved (2-mm mesh size). Soil textural analyses were conducted at INPA, and nutrients analyses were conducted at EMBRAPA (Brazilian Agricultural Research Corporation) soil laboratory in Manaus. We mention here the methods for determination of four soil properties which were used in our analyses. Percentage of clay (particles < 0.002 mm) was estimated using the hydrometer method (Mathieu and Pieltain 1998). The ions K^+ and Na^+ were extracted from the soil samples using Mehlich 1 method (Nelson et al. 1953), while Ca^{2+} and Mg^{2+} were extracted with a concentrated 1 N KCl

solution. These ions were measured by atomic absorption spectrometry, and they were summed to express the cation exchange capacity (CEC).

A professional surveyor determined altitude (m.a.s.l.). Three points were georeferenced with a geodesic GPS and were used to determine the azimuth to start the projection of the trails. The altitudes of these points were used as reference to determine the altitude every 100 m along the trails with a theodolite (https://ppbio.inpa.gov.br/instalacao/grade). Slope was estimated with a clinometer at five points along the center line of the plot, and the mean slope was used for each plot (Castilho et al. 2006). Descriptive statistics (mean, SD and range) of soil and topographic variables are provided by Castilho et al. (2006).

In order to illustrate the differences in stand properties along the soil gradient, we used topographic classification (Toledo et al. 2012). Plots were classified as plateau, slope and valley using field observation and data on altitude, slope and percentage of clay. Plots with altitude ≥65 m a.s.l. and slope <12° were classified as on plateau, those with altitude <65 m and slope <12° were classified as in valleys, and plots with ground angle ≥12° were classified as on slopes. However, not all valleys are at low altitudes. Therefore, we compared this classification to subjective impressions obtained in the field. When doubt arose as to the classification, we applied an additional criterion using percentage of clay: plots on soils with clay <20% were classified as in valleys, those with clay ≥60% were on plateaus, and plots with clay between 20 and 60% were on slopes. Thus, 17 plots were classified as valley, 27 as plateaus and 28 as slopes.

Above-ground tree biomass estimates – Above-ground tree biomass was estimated using a Chave's pan-tropical allometric model (Chave et al. 2014), which estimates dry biomass directly from dbh, wood density and height. Tree height was estimated utilizing a model also developed by Chave et al. (2014), which uses dbh and a measure of environmental stress (E) calculated with measures of temperature seasonality, climatic water stress and precipitation seasonality. E was accessed from a 5×5 km resolution grid available at http://chave.ups-tlse.fr/pantropical_allometry.htm. We used Chave's biomass model to calculate coarse wood production over 2 years, between the first and second census. Production per plot area was estimated as differences in biomass due to growth of remaining living trees and inclusion of recruits. We avoided bias related to measurement errors excluding stems with growth ≥4 and <−0.2 cm year^{-1} (Chao et al. 2008).

Data analysis – We used percentage clay and cation exchange capacity (CEC) from superficial (0–5 cm deep) soil samples to assess the effect of soil texture and fertility on stand properties. Clay is a good descriptor of soil structure and is associated with fertility and waterlogging.

Overall, higher sodium, phosphorus, nitrogen and organic carbon contents are found in clayey soils, and clay is correlated with height above the nearest drainage (HAND), which is a strong surrogate for depth to the water table (Castilho et al. 2006; Toledo et al. 2012; Schietti et al. 2014). CEC is a strong predictor of soil mineral fertility because it is positively related to total phosphorus (Quesada et al. 2010) and a good predictor for variation in forest structure, dynamics and wood density (Quesada et al. 2012). We also used topographic positions (valley, slope and plateau) to illustrated differences in forest properties associated with soil clay content.

We applied non-metric multidimensional scaling (NMDS) to reduce the dimensionality of tree species assemblage composition. Ordinations were performed in one and two dimensions on quantitative and presence–absence (qualitative) species data for trees with dbh ≥ 10 and ≥ 30 cm in order to determine whether the patterns are consistent across tree sizes. We used Bray–Curtis distance measure for quantitative and qualitative ordinations. Quantitative data were standardized through division of abundance of each species by the total abundance in each plot. Ordinations of quantitative data were used to describe the patterns showed by the most abundant species, while presence–absence ordinations reveals the patterns of the rarer species, because the more abundant genera tend to occur in most sites, thereby contributing little to the differences between sites. Only the results of one dimension are shown, since the solution for two dimensions captured a little more variation in the original distances. Furthermore, the quantitative and qualitative ordination axes were highly correlated ($r = -0.97$ and $r = -0.94$, $P < 0.001$, $df = 70$, for trees with dbh ≥ 10 cm and dbh ≥ 30 cm, respectively); therefore, we used only results from quantitative ordination in subsequent regression analyses.

In order to assess the distribution of species along the soil gradient of texture (clay) and fertility (CEC), we defined the most abundant species as those with ≥50 individuals (dbh ≥ 10 cm) in the 72 1-ha plots. Because of the strong relationships between species and soil clay content (see results), we separated the abundant species in two groups: those associated with sandy soil (≥50% of stems on soils with <15% of clay) and those associated with sandy–clayey soils (≥50% of stems on soils with ≥15% clay). We classified species according to growth form and successional status to evaluate biological differences between the two groups (Electronic Supplementary Material Appendix 3: Tables A3.1 and A3.2).

Using simple and multiple regressions, we tested our hypothesis that soil texture and fertility predict tree species composition and stand-level wood density, which in turn are able to explain the mesoscale variation in forest structure and dynamics. Firstly, we run a set of linear and

nonlinear (logistic exponential and quadratic models) regressions to describe the effects of soil predictors (clay content and CEC) on species composition and plot mean wood density (response variables) and the effect of species composition on plot mean wood density. Also, simple regressions were run to describe the relationships of biomass stock, tree mortality and coarse wood production with clay content, CEC, species composition and plot mean wood density. Multiple regressions were used to assess the combined effect of soil predictors, plot mean wood density and tree species composition (predictor variables) on biomass stocks, tree mortality and coarse wood production (response variables). Analyses were also undertaken for trees with dbh $\geq$ 10 cm and also with trees dbh $\geq$ 30 cm to determine whether the patterns are consistent for large trees alone. All analyses were run in the software R version 2.10.1 (R Development Core Team 2009), and the package vegan 2.0.1 (Oksanen et al. 2011) was used for ordinations and nlme 3.1.96 (Pinheiro et al. 2009) for nonlinear regressions.

Results

In the 72 1-ha plots, we found 904 species (Jackknife estimate: 1039 $\pm$ 23 species) distributed among 300 genera and 62 families from 25,402 stems $\geq$10 cm dbh. Most species were rare, with 88% having less than 1 individual per ha. The dominant families were Lecythidaceae (13.5% of all stems), Fabaceae (12.9%), Sapotaceae (11.9%), Burseraceae (7.6%), Moraceae (5.6%) and Chrysobalanaceae (5,4%), and the most abundant genera were *Eschweilera* (11%; Lecythidaceae), *Protium* (6.5%; Burseraceae), *Pouteria* (6.3%; Sapotaceae), *Licania* (3.9%; Chrysobalanaceae) and *Oenocarpus* (3.4%; Arecaceae). The dominant species were *Eschweilera truncata* A.C. Sm. (2.4%; Lecythidaceae), *E. coriacea* (DC.) S.A. Mori (2.4%), *Oenocarpus bataua* Mart. (2%; Arecaceae), *E. wachenheimii* (Benoist) Sandwith (1.8%) and *Protium hebetatum* D.C. Daly (1.7%; Burseraceae).

In the 72 1-ha plots, 78.2% of the stems with dbh $\geq$ 10 cm were identified to species, 92.5% to genus, 98.3% to family and 1.7% were not identified.

NMDS ordination captured 73 and 55% of variation in the original Bray-Curtis associations among plots in one dimension for quantitative data for trees with dbh $\geq$ 10 cm and dbh $\geq$ 30 cm, respectively. Soil clay content explained 81% of variation in species composition of trees with dbh $\geq$ 10 cm (Fig. 1a) and 79% of trees with dbh $\geq$ 30 cm using nonlinear models (Electronic Supplementary Material Appendix A4: Fig. A4a and Appendix A5: Table A5). For these plots with clay content <15% (N = 21 plots), linear models with clay content as the
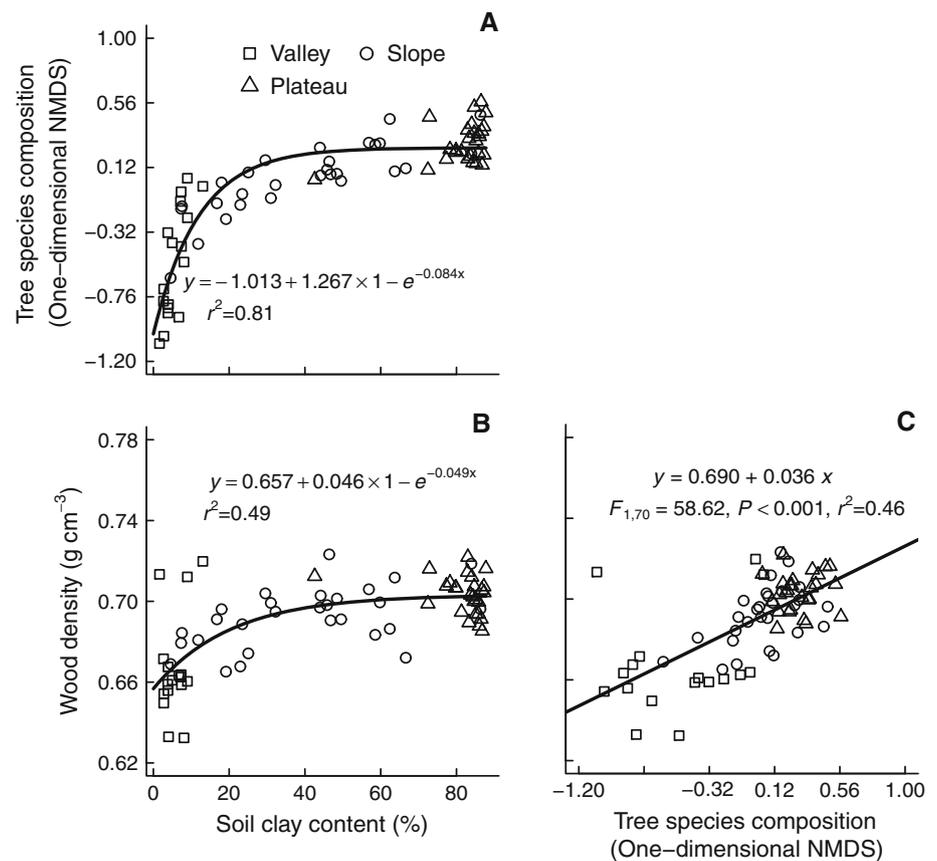
predictor variable explained more than 50% of variation in species composition (Electronic Supplementary Material Appendix 4: Fig. A4b and c).

From the 168 most abundant species, 21 had distributions restricted to waterlogged sandy soils and 147 species were predominantly found on sandy–clayey soils (Electronic Supplementary Material Appendix 3). Low- to medium-wood-density species (<0.7 g cm^{-3}, sensu Melo et al. 1990) were more frequent on sandy soils (67%) than on sandy–clayey soils (48%), and the only abundant pioneer species found on sandy soils was *Pourouma ovata* Trécul (Electronic Supplementary Material Appendix 3: Table A3.1). On sandy soils, the palm *Oenocarpus bataua* Mart., and the eudycotiledons *Chrysophyllum sanguinolentum* (Pierre) Baehni and *P. ovata* Trécul were the most abundant species ($\geq$5 stems ha^{-1}) with low to medium wood density, and *Eperua duckeana* Cowan was the most abundant high-wood-density species (>0.7 g cm^{-3}). On sandy–clayey soils, 12 species were very abundant, and the three most abundant with high wood density were *Eschweilera truncata* A.C. Sm., *E. wachenheimii* (Benoist) Sandwith and *E. coriacea* (DC.) S.A. Mori. *Protium hebetatum* D.C. Daly and *O. bacaba* Mart. were the most abundant species with low to medium wood density (Electronic Supplementary Material Appendix 3: Table A3.2).

Wood density increased from stands on sandy soils in valleys to clayey soils on plateaus. Soil clay content explained 49, 55, and 39% of variation in plot mean wood density of trees with dbh $\geq$ 10 cm, based on stem, basal area and species, respectively (Fig. 1b and Electronic Supplementary Material Appendix A5: Fig. A5a and b). For trees with dbh $\geq$ 30 cm, the same pattern was observed, and clay explained 46% of variation in wood density based on stems, 52% based on basal area, and 26% based on species (Electronic Supplementary Material Appendix A5: Fig. A5c-e). Tree species composition explained 46% of variation in plot mean wood density for trees with dbh $\geq$ 10 cm (Fig. 1c and Electronic Supplementary Material Appendix A5: Table A5) and 43% for trees with dbh $\geq$ 30 cm (Electronic Supplementary Material Appendix A5: Table A5), indicating that species turnover accounts for larger portion of spatial variation in wood density.

Tree species composition, soil clay content, cation exchange capacity (CEC) and plot mean wood density on stem basis together explained 33% of variation in biomass of trees with dbh $\geq$ 10 cm (multiple regressions—MR: $F_{4,67}$ = 8.43, P < 0.001; Table 1). When plot mean wood density on basal area (MR: $F_{4,67}$ = 10.43, P < 0.001) and species (MR: $F_{4,67}$ = 6.74, P < 0.001) basis were used, 39 and 29% of variation were explained in the models, respectively. For large trees (dbh $\geq$ 30 cm), the predictor

Fig. 1 Relationships of **a** tree species composition (one-dimensional NMDS of quantitative data) and **b** plot mean wood density (stem basis) with soil clay content and **c** plot mean wood density with tree species composition for trees with dbh $\geq$ 10 cm in 72 1-ha plots in Reserva Ducke

Panel A: $y = -1.013 + 1.267 \times 1 - e^{-0.084x}$, $r^2 = 0.81$

Panel B: $y = 0.657 + 0.046 \times 1 - e^{-0.049x}$, $r^2 = 0.49$

Panel C: $y = 0.690 + 0.036\ x$, $F_{1,70} = 58.62$, $P < 0.001$, $r^2 = 0.46$

variables explained 23, 25 and 23% of variation in biomass using wood density on stem, basal area and species basis, respectively (MR: $F_{4,67} > 5$, $P = 0.001$) (Electronic Supplementary Material Appendix A6: Table A6). Above-ground tree biomass was lower on sandy soils in valleys and increased on clayey soils on plateaus (Fig. 2a). Plots with lower mean wood density in valleys showed lower stocks of biomass than plots on plateaus with higher wood density (Fig. 2b).

For trees with dbh $\geq$ 10 cm, species composition, soil clay content, CEC and plot mean wood density explained 19, 20 and 24% (for models using wood density based on stems, basal area and species, respectively) of variation in mortality for all modes of death combined (MR: $F_{4,67} > 4$, $P < 0.01$; Table 1). The predictor variables explained 17, 15 and 20% (using wood density based on stems, basal area and species, respectively) of variation in snapping mortality (MR: $F_{4,67} > 3$, $P < 0.05$), and 16, 19 and 23% in uprooting mortality (MR: $F_{3,67} > 3$, $P < 0.05$). For trees with dbh $\geq$ 30 cm, 12% (MR significant only with wood density on stem basis: $F_{4,67} = 2.23$, $P = 0.08$) of variation in mortality for all modes of death combined and 18, 19 and 16% (using wood density based on stems, basal area and species, respectively) in uprooting mortality (MR:

$F_{4,67} > 3$, $P < 0.05$) were explained by those variables, but there were no significant effects for snapping mortality or standing mortality (MR: $F_{4,67} < 1.5$, $P > 0.25$; Electronic Supplementary Material Appendix A6: Table A6). Tree mortality was higher on sandy soils in valleys and decreased in clayey soils on plateaus (Fig. 2d), and was negatively related to plot mean wood density (Fig. 2e).

Tree species composition, soil clay content, CEC and plot mean wood density on stem or basal area or species basis together explained 18% of variation in coarse wood production of trees with dbh $\geq$ 10 cm (MR: $F_{4,67} > 3.5$, $P < 0.05$; Table 1). Coarse wood production of trees with dbh $\geq$ 30 cm have 18, 16 and 19% of its variation explained by the predictors when using wood density on stem, basal area and species basis, respectively (MR: $F_{4,67} > 3$, $P < 0.05$) (Electronic Supplementary Material Appendix A6: Table A6). Coarse wood production increased with soil fertility (Electronic Supplementary Material Appendix 5: Table A5), but relationships with species composition, plot mean wood density and clay were not significant in simple regressions. By the inspection of the partials from the multiple regression models, it was possible to observe that only the effect of clay and CEC were consistent.

Table 1 Results of multiple regressions relating above-ground biomass, tree mortality and coarse wood production of trees with dbh $\geq$ 10 cm with tree species composition described by one-dimensional NMDS ordination on abundance data, plot mean wood density on stem, basal area or species basis, soil clay content and cation exchange capacity (CEC)

Response variable	Wood density weight	Standard partial slope (b)						
		NMDS	Wood density	Clay	CEC	$F_{4,67}$	P	R^2
Above-ground biomass	Stem	−0.47**	0.45***	0.43*	0.25*	8.43	<0.001	0.33
	Basal area	−0.55***	0.64****	0.31	0.29**	10.49	<0.001	0.39
	Species	−0.50**	0.29*	0.60***	0.18	6.74	<0.001	0.29
Tree mortality (all modes of death combined)	Stem	−0.26	−0.20	−0.01	−0.02	3.86	0.007	0.19
	Basal area	−0.22	−0.29	0.04	−0.03	4.12	0.005	0.20
	Species	−0.15	−0.39**	0.00	−0.05	5.37	0.001	0.24
Standing mortality	Stem	−0.30	0.15	−0.02	−0.06	1.19	0.322	0.07
	Basal area	−0.28	0.03	0.06	−0.11	1.00	0.414	0.06
	Species	−0.27	0.00	0.07	−0.11	0.99	0.417	0.06
Snapping mortality	Stem	−0.49**	−0.24	0.37	−0.03	3.46	0.013	0.17
	Basal area	−0.50**	−0.15	0.32	0.00	3.02	0.024	0.15
	Species	−0.40*	−0.34**	0.34	−0.05	4.25	0.004	0.20
Uprooting mortality	Stem	0.24	−0.32*	−0.32	0.01	3.2	0.018	0.16
	Basal area	0.30	−0.46**	−0.23	−0.02	3.9	0.007	0.19
	Species	0.37	−0.48***	−0.34	−0.01	4.95	0.002	0.23
Coarse wood production	Stem	0.44**	0.12	−0.71***	0.51***	3.57	0.011	0.18
	Basal area	0.50**	−0.13	−0.56**	0.43***	3.56	0.011	0.18
	Species	0.41*	0.14	−0.68***	0.51****	3.65	0.009	0.18

The b shows the magnitude and nature of the effect of the predictive variables on response variables

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$

Discussion

Soil indirectly determines spatial variation in tree biomass by limiting the distribution of tree species and thereby defining stand-level traits, such as wood density, which directly affects biomass estimates and storage at local and regional scales in Amazonia (Baker et al. 2004; Castilho et al. 2006; Ferry et al. 2010; Baraloto et al. 2011). Moreover, species composition and stand-level wood density of large trees (dbh $\geq$ 30 cm), which contribute to 60% of above-ground tree biomass in Reserva Ducke (Castilho et al. 2006) were highly related to soil texture (clay content) and fertility (cation exchange capacity).

This is the first study showing consistent changes in stand-level wood density related to soil gradients without the confounding effect of climatic variation in Amazonia. Most mesoscale studies were not designed to control within-plot soil variation, which has probably weakened estimates of the effects of soil on wood density (e.g., Baraloto et al. 2011). Higher wood density in clayey soils and lower in sandy soils is caused by shifts in tree community composition driven by soil. Linear changes in species composition in plots with less than 15% of clay indicate that soil waterlogging is also playing an important

role in the distribution of species. In fact, the soil hydrological model, HAND, explained 80% of variation in species composition of trees in these plots (Schietti et al. 2014). Palms in Reserva Ducke also followed a similar pattern, changing linearly in composition up to 50 m from water courses (Costa et al. 2009). The high frequency of the palm *O. bataua* Mart. contributes to low stand-level wood density on sandy soils, but the relationship between plot mean wood density and clay is insensitive to the exclusion of palms (49% of variation explained with palms and 50% without palms), indicating that changes in tree species are shaping stand-level wood density. Also, successional status differed little between sandy and sandy–clayey soils, so lower wood density on valleys does not appear to be a consequence of higher frequency of fast-growing and light-demanding species in Reserva Ducke, though such species are believed to be important in determining mean biomass in other Amazonian sites (Quesada et al. 2012; Ferry et al. 2010). As canopy and subcanopy old-growth species were dominant in all soil types, convergent selection of species with similar traits (ter Steege and Hammond 2001) appears to be the main determinant of differences in stand-level wood density along the soil gradient.
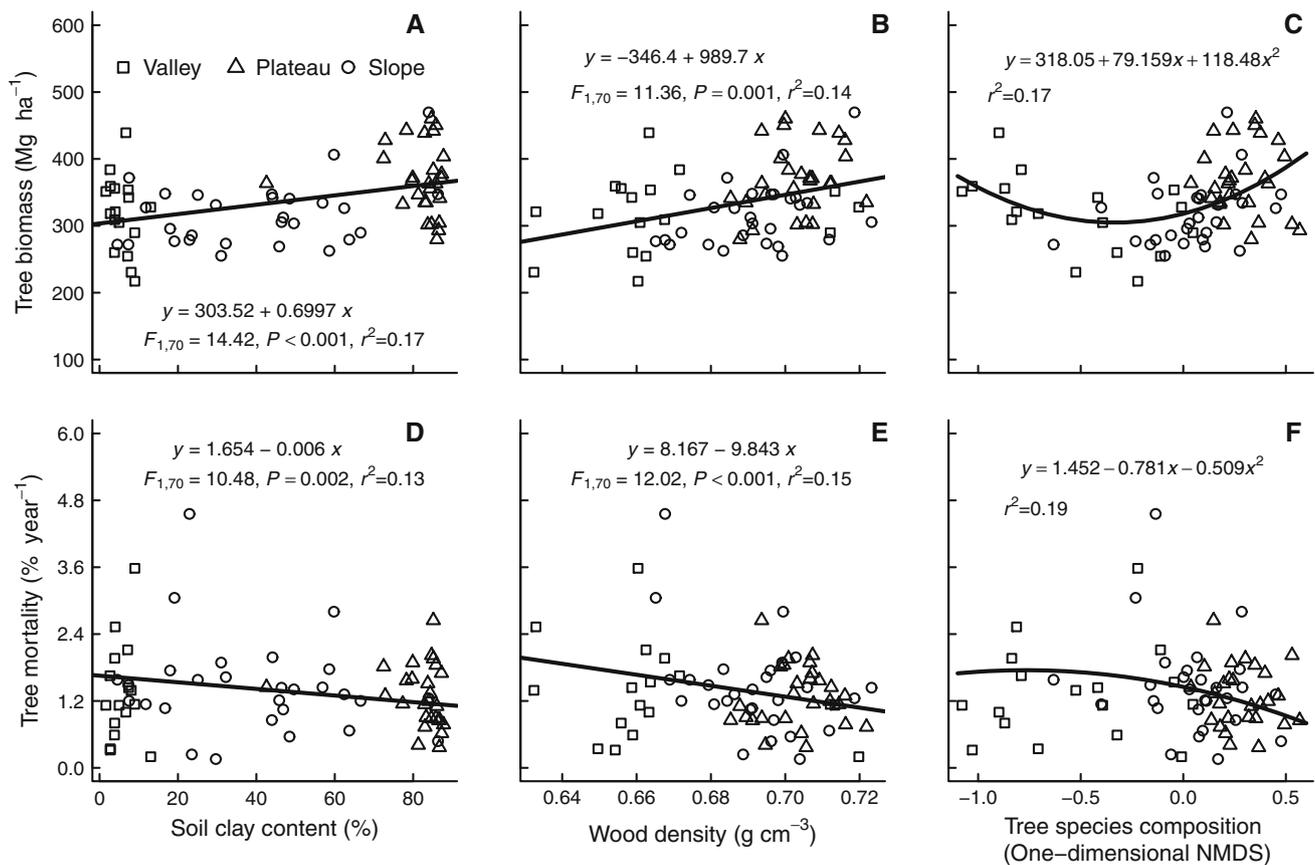
Fig. 2 Relationships of **a–c** above-ground tree biomass and **d–e** tree mortality of trees (dbh ≥ 10 cm) with soil clay content, plot mean wood density (stem basis) and tree species composition (one-dimensional NMDS of quantitative data) in 72 1-ha plots in Reserva Ducke. Tree biomass was calculated using Chave et al. (2014) equation, and mean wood density was calculated on a stem basis

Physiological constraints, imposed by nutrient availability and soil waterlogging, affect the distribution of tree species (e.g. Clark et al. 1999; John et al. 2007). Nutrient variation within Reserva Ducke is low (see Castilho et al. 2006), and all soil types are poor (Chauvel et al. 1987), suggesting that tree species are adapted to such constraints. However, long-term experiments have demonstrated that addition of nitrogen and potassium increases tree biomass production in primary (Wright et al. 2011) and secondary forests (Siddique et al. 2010). Soil nitrogen in Reserva Ducke increased with clay content and probably contributes to the accumulation of biomass in clayey soils on plateaus. Even though nitrogen is directly cycled by the vegetation, positive feedback may facilitate establishment of emergent species of high-density wood, which account for most of the biomass. Soil waterlogging and depth to the water table are other important constraints for species distributions, but the effects are difficult to separate from soil since soil properties are highly correlated with depth to water table (Schietti et al. 2014). Abrupt changes in species composition in valley plots suggest that waterlogging is the most important factor in this habitat since water excess

decreases oxygen, selecting tree species adapted to anoxic or hypoxic soil. However, for many tropical tree species, water shortage is the most limiting factor (Condit et al. 2004; Engelbrecht et al. 2007), and high-wood-density species are believed to be more resistant to cavitation (Hacke et al. 2001), so regular or extreme droughts may select species with high wood density in sites with low soil water availability (Condit et al. 1995; Engelbrecht et al. 2007), restricting taxa with low wood density to humid areas. Selection due to rainfall seasonality may be higher in habitats with waterlogged soils, such as swamps or humid slopes (Condit et al. 1995; Engelbrecht et al. 2007), which are often dominated by species with low wood density (Ferry et al. 2010; this study). Further, as economy in wood construction may allow investments in stilt and buttressed roots, increasing resistance to stem buckling (Young and Perkocha 1994) and light wood species achieve greater resistance to breakage at lower construction cost (Anten and Schieving 2010; Larjavaara and Muller-Landau 2010), these characteristics may be preferentially selected for more dynamic environments, such as valleys in Reserva Ducke.

The negative relationship between tree mortality and wood density in this study has been found at the community and species level (e.g., Nascimento et al. 2005; Chao et al. 2008; Kraft et al. 2010). This pattern also follows the soil texture gradient, with higher mortality on sandy than on clayey soils (Toledo et al. 2011, 2012). Trunks with low wood density are more susceptible to breakage (Chao et al. 2009), which is concordant with the negative relationship between snapping mortality and plot mean wood density. However, recent studies have contradicted such ideas, showing that the same strength to support tree weight is achieved by a low-wood-density trunk with lower construction cost than by one with higher wood density (Anten and Schieving 2010). The relationships between wood density, mortality, resistance to cavitation and susceptibility to pathogens have also been argued. Low wood density is believed to be less resistant to drought-induced xylem implosion (Hacke et al. 2001; Jacobsen et al. 2005), but liquid transport is performed by only a small portion of the trunk tissue mass, which casts doubts on whether selection for liquid transport would affect the density of the whole trunk (Larjavaara and Muller-Landau 2010). Further, wood with low density is more susceptible to pathogen attacks (Romero and Bolker 2008), but pathogen avoidance by increase of secondary compounds and decrease of surface in tree species with high wood density have not been studied (Larjavaara and Muller-Landau 2010). Larjavaara and Muller-Landau (2010) proposed that species with low wood density, such as pioneers, prioritize short-term gains over long-term costs, thereby not only evolving low wood density, but also low trunk and xylem resistance and low concentration of protective substances in the wood. In Reserva Ducke, uprooting mortality was also negatively related to wood density, but must be a direct effect of soil waterlogging weakening the root system and decreasing root-soil adherence. Uprooting contributed only 14% to total tree mortality, while snapping mortality contributed 26% (Toledo et al. 2012). Standing mortality (which accounts for more than 50% of tree deaths) is not related to soil, so stem breakage is the main cause of differences in mortality along the soil gradient and is more frequent among tree species with low to medium wood density.

We showed that soil indirectly affects forest biomass and dynamics by controlling species distribution and consequently affecting stand-level traits. A direct effect of soil fertility may restrict biomass accumulation in valleys predominated by sandy soils which hold low concentrations of exchangeable bases and total available phosphorus, which are good predictor of forest dynamics (see Quesada et al. 2010, 2012). Poor soil anchorage also increases tree mortality by uprooting independent of wood density or associated traits in valleys (Toledo et al. 2012). Poor soil structure

is a strong predictor of forest structure and dynamics acting as a species filtering toward a forest with higher rates of growth, mortality, turnover, but low stocks of biomass (Quesada et al. 2012). We conclude that mesoscale variation in biomass and dynamics is a result of selection of species with similar traits in homogeneous edaphic conditions. Physiologic interactions between trees and soil need more detailed investigation to allow us to understand why and how sites with nutrient-poor and waterlogged sandy soils host tree species of low wood density.

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