# Disentangling the role of edaphic variability, flooding regime and topography of Amazonian white-sand vegetation

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## Abstract

**Question:** How much variation in plant community structure and composition can be predicted using soil, flooding and topography in white-sand vegetation of northern Amazonia?

**Location:** Brazil, northern Amazon, Roraima State, Viruá National Park (01°46′34″ N, 61°02′06″ W).

**Methods:** Data from 17, 1-ha permanent plots distributed across a 25 km$^2$ landscape within the Viruá National Park, northern Amazonia, was used to assess the soil, flooding and topography effects on tree species composition, diversity and structure. Our analyses were based on 16 599 trees (DBH $\geq$ 1 cm) belonging to 303 species. Principal components analysis (PCA) was used to reduce the dimensionality of soil variables, whereas dimensionality of floristic composition assemblage was reduced using non-metric multidimensional scaling (NMDS). Multiple regression analysis was used to test combined effects of soil, flooding and topography on floristic composition, diversity, basal area and tree density.

**Results:** Depending on the diameter class or the type of data (qualitative or quantitative), NMDS axis 1 explained 45–84% of total variation in species composition among plots. The first and second axes from PCA explained, respectively, 54.8% and 15.1% of the variation related to soil gradients. Soil texture and fertility (PCA axis 1) were the most important predictors of the variation in tree composition, diversity and structure for the three different size classes analysed (DBH $\geq$ 1 cm, 1 cm $\leq$ DBH $\leq$ 9.9 cm and DBH $\geq$ 10 cm). Overall, plots on more fertile clayey soils showed higher tree diversity and basal area than those on well-drained sandy soils. Although flooding had little effect on the tree community, the water level was higher in high-stature forests established on more clayey and fertile soils.

**Conclusions:** Even though soils in the study area are predominantly sandy and oligotrophic, our findings highlight the importance of soil in structuring plant communities of seasonally flooded white-sand vegetation at mesoscales in the Amazon Basin.

## Introduction

In the Amazon, the two most common forests types associated with flooding regimes are *Várzea* and *Igapó*, which are, respectively, forests flooded by white water (nutrient-rich) and black or clear water (nutrient-poor) river systems (Prance 1979; Kubitzki 1989). Many studies have shown that within these forest types, flooding is considered the major factor in determining the variation in structure and floristic composition, in which diversity decreases as flooding level (and/or timing) increases (e.g. Ferreira & Stohlgren 1999; Ferreira & Almeida 2005; Wittmann et al. 2006; Assis & Wittmann 2011). However, differences in soil fertility are considered the major

determinant of floristic composition between *Igapó* and *Várzea* forests as a result of differences in water chemical properties (Prance 1979; Wittmann et al. 2010).

Another vegetation type influenced by flooding is Amazonian white-sand forest, distributed on sandy and nutrient-poor soils, known in Brazil by the general term *Campinarana* (Veloso et al. 1991). The *Campinarana* vegetation is distributed in many environmental conditions over the Amazon Basin and varies from open grassland to dense forest (Prance 1996). In Central Amazonia, this vegetation type occupies small and fragmented areas surrounded by non-flooded *terra-firme* forest (Anderson 1981). However, in the Rio Negro basin, extensive plains are flooded due to poor drainage of sandy soils (spodzols; superficial rock beds) and water infiltration of periodically flooded river margins (Ab'saber 2002). In the floodplains, *Campinarana* and *Igapó* vegetation structure has been associated with such flooding or a rise in groundwater during wet seasons (Ferreira & Almeida 2005; Jirka et al. 2007). Thus, both vegetation types share the same ecological gradient of oligotrophy and flooding, with quite subjective limits between a variety of physiognomic classes, making it difficult to classify a vegetation area as *Campinarana* or *Igapó*. Indeed, the flora of these systems is phylogenetically linked (Kubitzki 1990).

In non-flooded and high diversity *terra-firme* Amazonian forests, several studies have shown that the distribution of plant species is associated with edaphic and topographic variability at different spatial scales (e.g. Ruokolainen & Tuomisto 2002; Tuomisto et al. 2003; Costa et al. 2005; Bohlman et al. 2008). Several hypotheses have been postulated to infer the magnitude of environmental effects – edaphic or hydrological – on the structure and floristic diversity of white-sand forests (Coomes & Grubb 1996; Prance 1996; Coomes 1997). In general, structural variation of white-sand vegetation can be related to flooding gradients (Vicentini 2004), with forests being replaced by open vegetation as flooding level increases or groundwater depth decreases. As a result, the vegetation can be influenced by ubiquitously homogeneous low-nutrient soils, leaving only variation in water levels (groundwater depth and/or flooding height) to determine the changes in floristic and structural patterns. There are still very few studies that have described the structure and tree species composition of white-sand *Campinaranas* (e.g. Vicentini 2004; Jirka et al. 2007; Fine et al. 2010; Stropp et al. 2011), and it is still unclear how flooding and other factors, such as soil texture and fertility, influence variation in vegetation structure and species composition.

Here, we investigated how much variation in structure, diversity and floristic composition of white-sand tree species can be predicted by soil, topography and flooding level over a spatial scale ranging from 1 to 5 km. Our main focus was to estimate the magnitude of these environmental variables on floristic and structural variation of white-sand forests in northern Amazonia.

## Methods

### Study area

This study was conducted at Viruá National Park, located in the Caracaraí municipal district, Roraima State, Brazil (01°46'34" N, 61°02'06" W; Fig. 1 and Photo S1). According to Köppen classification, mean annual temperature is around 26 °C and mean annual rainfall is 1900 mm, with a dry season from November to April, during which monthly precipitation is <50 mm. The park occupies an area of approximately 227 000 ha, mostly lowlands (<150 m a.s.l.) with some residual hills of ca. 250 m a.s.l. The lowlands are usually dominated by poorly drained white-sand soils, and on the hills soils are clayish and lateritic. The vegetation at Viruá National Park includes white-sand forests and savannas, *Igapó* forests and dense rain forest (*terra-firme* forests) on the isolated hills. In the wet season, all plains become flooded. During the dry season, soil moisture is minimal, and savannas are frequently burned due to the increase in human activities around the park, but no fire has been reported in the study area since 2006, when the permanent plots were installed.

### Sampling design

A grid of 12.5-km trails, each separated by 1 km, covers an area of 25 km$^2$ within Viruá National Park. Thirty 1-ha permanent plots were established along the east–west trails at least 1 km from each other. These plots are long and narrow (250 m × 40 m) and follow the topographic contours, thereby maintaining a constant elevation, minimizing soil type and groundwater depth variation within plots (Magnusson et al. 2005). For this study, we selected 17 plots that were placed on sandy and flooded soils within the Viruá grid (Fig. 1). The 17 plots represent a vegetational gradient ranging from grasslands to tall forests. A hierarchical design was used to sample trees and palms (hereafter collectively called trees) in which diameter at breast height (DBH) was used to define the sampling area. Trees with DBH $\geq$ 30 cm were sampled in 1 ha (250 m × 40 m), while trees with DBH $\geq$ 10 cm and DBH $\geq$ 1 cm were sampled in 0.5 ha (250 m × 20 m) and 0.1 ha (250 m × 4 m). The DBH was measured to the nearest 1 mm at 1.3 m above the ground. All trees were mapped and marked with aluminium numbered tags. The data described here are part of the Research Program in Biodiversity (PPBio – http://ppbio.inpa.gov.br/) managed by the National Institute for the Amazon Research (INPA).
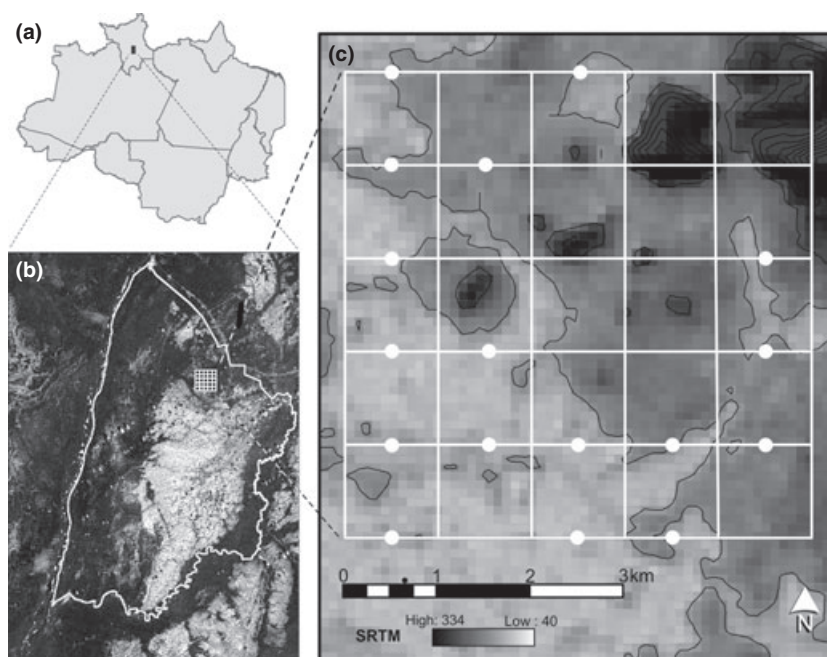
**Fig. 1.** Location of Viruá National Park whithin the Legal Brazilian Amazon (**a**) and the 25-km$^2$ grid system inside the Park (**b**). Dots on the trail system indicate the location of the 17 1-ha permanent plots (**c**).

### Botanical data

For species delimitation and identification, we collected specimens from November 2009 to May 2010 in the permanent plots. At least one individual of each species were collected per plot. Species delimitation was conducted by morphotyping specimens, and species identification was made by comparison with material deposited in the INPA herbarium. Specimens collected with flowers or fruits were deposited in the INPA herbarium (Appendix S1).

### Soil, flooding level and slope data

Six superficial soil subsamples (0–5-cm deep) were collected at 50-m intervals along the centre line of each plot, and these were mixed to form a composite sample per plot. Soil samples were dried at 105 °C, cleaned by removing stones and fine roots and then sieved (2-mm mesh size). Soil texture and pH were measured in the Soil Plant Thematic Laboratory of INPA and soil chemical measurements were carried out in the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) soil chemistry laboratory in Manaus. We used 12 soil variables (Appendix S2): clay, silt and sand (particles <0.002, 0.002–0.05 and 0.05–2.00 mm, respectively), pH, available phosphorus ($P^+$), $K^+$, $Ca^{2+}$, $Mg^{2+}$, $Fe^{2+}$, $Mn^{2+}$, $Zn^{2+}$, exchangeable aluminium ($Al^{3+}$).

The groundwater level and the surface flooding level were recorded monthly using manual piezometers. Sandy soils in Viruá National Park have, at higher or lesser depths, an impermeable layer, cemented by organic matter and iron and aluminium compounds (spodic horizon). Due to the difficulty of drilling the ground in some areas, not all piezometers were installed to the same depth. For this reason, the maximum flood level was used to represent the hydrological variable, which also reflects the flooding time. Piezometer measurements were performed from September 2009 to December 2010. The slope measures were made with a clinometer at six points along the plot centre line, spaced 50 m apart. In this case, the slope of each plot was considered as the average of these six points.

### Data analysis

Principal components analysis (PCA) was used to reduce the dimensionality of the 12 top soil variables and define the main variables that explain the soil variation among the sampled plots. Before performing the PCA, soil variables were stantardized through division of the values by the standard deviation of each variable, to give equal weight to variables in the analysis.

Floristic composition was also reduced using the non-metric multidimensional scaling (NMDS) technique. Two types of ordination, one based on quantitative data (species density and dominance) and one on qualitative (species presence or absence) were performed for three diameter classes: (1) total community including all trees with DBH $\geq$ 1 cm; (2) adult trees, those with DBH > 10 cm; and (3), juvenile trees those with DBH < 10 cm. Therefore,

floristic composition data were analysed separately for three diameter classes and two data types (quantitative and qualitative). The first axis resulting from the NMDS was then used as a dependent variable in multiple regression models to test the effect of soil variables (obtained by PCA), flooding level and slope on species composition. Models of multiple regression analysis were also used to test these environmental effects on diversity (as measured by Fisher's diversity index), basal area and tree density. To account for multicollinearity, we calculated the tolerance of the independent variables in the multiple regression models. Tolerance values range from 0 to 1, and the lower the value the higher the multicollinearity among independent variables. Initially, all environmental variables (soil, flooding level and slope) were analysed in a single multiple regression model. However, tolerance values were relatively low for soil and slope data. Therefore, two multiple regression models were considered: (1) analysing soil and flooding level effects; (2) analysing flooding level and slope effects. In all cases, the tolerance values were above 0.9. The ordination analyses (PCA and NMDS) and the Fisher's diversity index were performed using PAST (Hammer et al. 2001) and multiple regression models were performed in SYSTAT 12.0 (Systat Inc., Evanston, IL, US).

## Results

### Floristic composition and vegetation structure

A total of 16 599 individuals (DBH $\geq$ 1 cm) were recorded in the 17 1-ha sample plots, distributed in 52 botanical families, 163 genera and 303 species (or morphotypes, see Appendix S1). The most abundant families were Rubiaceae (16.1% of all individuals, with 15 genera and 23 species), Chrysobalanaceae (12.5%, with four genera and 17 species), Annonaceae (5.5%, five and 12), Myrtaceae (5.3%; two and 11), and Lecythidaceae (3.8%, four and seven). These families together represented ca. 45% of all individuals recorded. The most abundant species were *Platycarpum egleri* (535 trees·ha$^{-1}$; Rubiaceae), *Duroia nitida* (306; Rubiaceae), *Virola surinamensis* (281; Myristicaceae), *Licania micrantha* (226; Chrysobalanaceae) and *Elvasia* cf. *canescens* (225, Ochnaceae).

Tree density (DBH $\geq$ 1 cm) between plots ranged from 854 to 14 642 ind·ha$^{-1}$, and basal area varied between 1.13 and 29.72 m$^2$·ha$^{-1}$. The species with larger DBH were *Buchenavia grandis* (88 cm; Combretaceae), *Maquira coriacea* (83.9 cm; Moraceae) and *Macrolobium* cf. *aciciifolium* (83.6 cm; Fabaceae).

### Tree community gradients

Independent of diameter class, the NMDS ordination axis explained 56–84% of the total variation in species composition among plots using qualitative data (Appendix S3). This ordination captures the patterns of the rarer species, because the more abundant species generally occur in most sites and therefore contribute little to the differences between sites. When quantitative matrices were used, the NMDS axis explained 51–56% (density) and 45–49% (dominance) of original tree community variation. The ordinations of quantitative data (density or cover) capture the patterns displayed by the most abundant species, as these will have the highest quantitative contribution to the differences between plots.

### Soil gradients and flooding regime

The first (PC1) and second (PC2) axes from PCA summarizing the 12 physical and chemical soil variables (Appendix S4) explained, respectively, 54.8% and 15.1% of the variation related to soil gradients. PC1 described a gradient positively correlated with clay and silt and negatively related to sand content. PC1 was also positively related to phosphorus (P$^+$), magnesium (Mg$^{2+}$), manganese (Mn$^{2+}$), iron (Fe$^{2+}$), zinc (Zn$^{2+}$), calcium (Ca$^{2+}$) and aluminium (Al$^{3+}$). Therefore, clayish soils had higher macro- and micronutrient availability, mainly P$^+$, Mg$^{2+}$ and Mn$^{2+}$. The second axis (PC2) mainly described a pH and exchangeable Al$^{3+}$ gradient. None of the individual soil components were highly correlated with the flooding level or slope, except Fe$^{2+}$ (Appendix S4).

In the dry season, no piezometers had water, and the groundwater remained below 2-m deep (Fig. 2). However, most plots suffered flooding above the soil surface during the rainy months (June to August). Therefore, flooding at this study site is closely associated with the precipitation regime. In the more sandy plots, flooding level was low (with a peak at 5 cm above the ground), while in the clayish soils, flooding level reached 70 cm above the ground. Although flooding level showed a high coefficient of variation, all plots presented water saturation during the same period.

### Effects of soil, flooding and slope on plant species composition

Independent of diameter class (DBH $\geq$ 1 cm, DBH $\geq$ 10 cm and DBH < 10 cm) and data type (density, dominance and presence/absence), soil characteristics and flooding level predicted 67–76% of the floristic variation (Table 1). However, only PC1 was significantly related to variation in species composition ($t > -7.02$, $P < 0.001$, for all DBH classes). Thus, the floristic distribution pattern captured by NMDS axes was mainly related to variations in soil texture and fertility (Fig. 3). The models using flooding level and slope explained only 12–22% of the
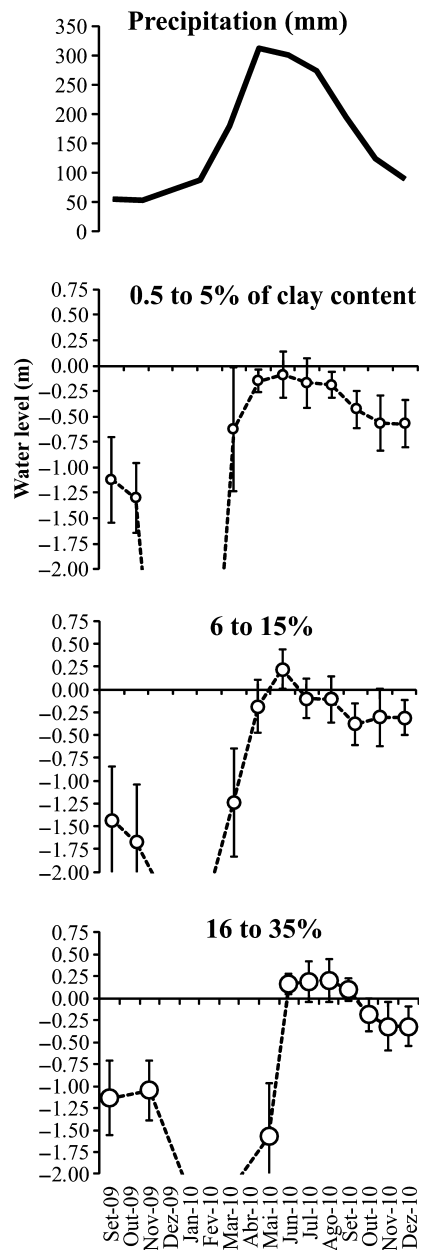
**Fig. 2.** Water level regime (mean ± SD) associated with seasonal precipitation throughout 1 yr. The values of the 17 plots were divided into three classes according to clay content in the sandy soils (0.5–5.0% – $n = 6$; 6–15% – $n = 6$; 16–35% – $n = 5$).

total variation in floristic composition (Table 1). In this case, only flooding level was related to species composition ($t > -2.50$, $P < 0.08$ for all DBH classes).

Some species were found only in more open, savanna-like physiognomies, such as *Pagamea coriacea*, *Euphronia guianensis*, *Ilex divaricata* and *Clusia* cf. *nitida*, which were associated with more sandy and less fertile

soils. These species were restricted to soils with a maximum of 6% clay content. On the other hand, species that reached larger diameters, such as *Maquira coriacea*, *Trymatococcus* sp. 1 and *Unonopsis* sp. 1, and understorey species, such as *Myrcia* cf. *cuprea*, *Strychnos* sp.1 and *Posocheria* cf. *latifolia* were associated with soils with higher nutrient availability and clayish texture (up to 35% clay content). *Mauritiella aculeata*, *Ouratea* cf. *discophora*, *Richeria grandis*, *Ruizterania retusa* and *Virola surinamensis* were considered soil generalists (Fig. 4a). Flooding was not a good predictor of floristic variation at the studied site, with most species occurring along the flooding gradient (Fig. 4b).

### Effects of soil, flooding and slope on diversity and vegetation structure

For total (DBH ≥ 1 cm) and adult (DBH ≥ 10 cm) communities, 55% and 67%, respectively, of the variation in diversity was explained by soil variables and flooding (Table 2). For both classes, tree diversity was positively related to PC1 ($t > 4.15$, $P < 0.002$), indicating higher diversity in the more clayish and fertile soils (Fig. 5a). Tree diversity was also negatively related to PC2 (soil pH variation; $t < -2.78$, $P < 0.08$), indicating higher diversity in more acidic soils (low pH). However, variation in pH was low, ranging from 4.2 to 5.1, and two plots drove the negative correlation between diversity and pH (Fig. 5b), suggesting that pH was not an appropriate variable to predict tree diversity in the white-sand forests studied. For juvenile trees (DBH < 10 cm), 39% of tree diversity variation was explained by soil texture ($t = 3.63$, $P = 0.003$), also indicating high diversity in the more clayish soils. Flooding level was also positively related to Fisher's α ($t = 2.37$, $P = 0.03$), indicating higher tree diversity in clayish and more fertile soils that also have higher flooding levels.

The variation in basal area for DBH ≥ 1 cm and DBH ≥ 10 cm classes could be explained by soil characteristics and flooding, which explained 41% and 66%, respectively (Table 2). Basal area was positively related to the texture and fertility soil PCA axis 1 ($t > 5.1$, $P < 0.063$) for both classes. Therefore, sandy and low fertility soils had lower basal areas (Fig. 5c). The models using flooding level and slope explained 18–28% of the variation in tree basal area for all diameter classes (Table 2), and only flooding was positively related with basal area ($t > 2.06$, $P < 0.06$; Fig. 5d), indicating that the sites with higher flooding levels have larger basal areas. Density was also positively related to flooding level ($t = 2.40$, $P = 0.032$), but only for the adult tree class (DBH ≥ 10 cm). Thus, plots with higher flooding levels had higher tree density.

**Table 1.** Results of the multiple regression analyses relating soil texture and fertility (PC1), soil pH (PC2), flood level (FL) and slope effects on the floristic gradient (NMDS1).

| | Model | Data type | Standard partial slope (b) | | | | $F$[†] | $P$ | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| | | | PC1 | PC2 | FL | Slope | | | |
| Total community DHB $\geq$ 1 cm | 1st | Density | **−0.86****** | 0.12 | −0.05 | | 15.07 | <0.001 | 0.72 |
| | | Dominance | **−0.86****** | 0.06 | −0.09 | | 16.31 | <0.001 | 0.74 |
| | | Pres./Abs. | **−0.85****** | 0.13 | −0.04 | | 14.12 | <0.001 | 0.71 |
| | 2nd | Density | | | **−0.58**** | 0.06 | 3.05 | 0.08 | 0.21 |
| | | Dominance | | | **−0.56**** | −0.01 | 3.04 | 0.08 | 0.21 |
| | | Pres./Abs. | | | **−0.58**** | 0.07 | 3.17 | 0.07 | 0.22 |
| Adult trees DHB $\geq$ 10 cm | 1st | Density | **−0.84****** | −0.12 | −0.03 | | 12.03 | <0.001 | 0.67 |
| | | Dominance | **−0.89****** | −0.07 | −0.10 | | 15.51 | <0.001 | 0.73 |
| | | Pres./Abs. | **−0.85****** | −0.11 | −0.01 | | 12.18 | <0.001 | 0.68 |
| | 2nd | Density | | | **−0.46*** | −0.10 | 2.07 | 0.17 | 0.12 |
| | | Dominance | | | **−0.52**** | −0.07 | 2.66 | 0.11 | 0.18 |
| | | Pres./Abs. | | | −0.37 | −0.15 | 1.52 | 0.26 | 0.06 |
| Juvenile trees DHB < 10 cm | 1st | Density | **−0.89****** | 0.13 | 0.01 | | 18.12 | <0.001 | 0.76 |
| | | Dominance | **−0.85****** | 0.06 | −0.09 | | 14.89 | <0.001 | 0.72 |
| | | Pres./Abs. | **−0.87****** | 0.18 | −0.02 | | 16.57 | <0.001 | 0.74 |
| | 2nd | Density | | | **−0.54**** | 0.08 | 2.49 | 0.12 | 0.17 |
| | | Dominance | | | **−0.51*** | 0.05 | 2.19 | 0.15 | 0.14 |
| | | Pres./Abs. | | | **−0.58**** | 0.13 | 3.10 | 0.07 | 0.22 |

First model: NMDS1 = PC1 + PC2 + FL; second model: NMDS1 = FL + Slope. Pres./Abs. = Presence or Absence.

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

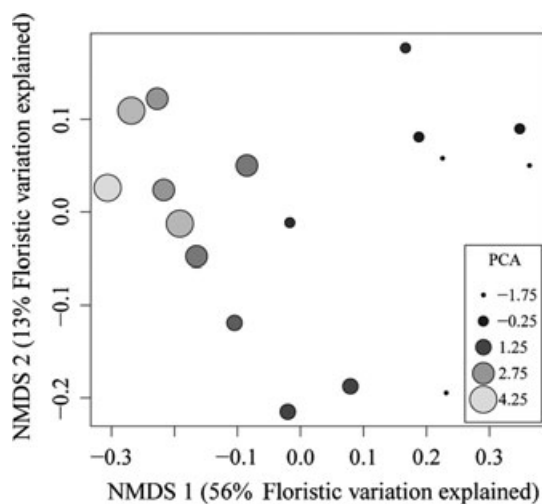†Three and 13 *df* in the first model; three and 13 *df* in the second model.



**Fig. 3.** NMDS ordination diagram of the 17 plots based on species abundance for trees $\geq$ 10 cm DBH related to the gradient of soil texture and fertility (PC axis 1).

## Discussion

### The importance of soil

Although soils of white-sand forests are predominantly sandy and oligotrophic, the floristic composition, tree diversity and vegetation structure were strongly related to variation in texture and fertility. Moreover, our findings showed that, regardless of the diameter class analysed, the effect of soil on floristic composition was higher than the other environmental variables examined (flooding and slope). The effect of soil fertility and texture on tree basal area was only significant for the adult diameter class (DBH $\geq$ 10 cm), and tree density was not related to the edaphic variables analysed, indicating that the distribution of small plants along the vegetation gradient was not susceptible to soil effects.

In general, Amazonian sandy and oligotrophic environments are associated with low-stature forests and low diversity vegetation (Prance 1975; Anderson 1981; Coomes 1997; Vicentini 2004; Stropp et al. 2011). On the other hand, clayish soils with higher nutrient availability are linked to higher diversity and biomass (Coomes & Grubb 1996; Givnish 1999; Laurance et al. 2010; Stropp et al. 2011). At the local and mesoscales, empirical studies have shown that soil influences the spatial distribution of above-ground live biomass (Laurance et al. 1999; Castilho et al. 2006) and plant species composition (Costa et al. 2005; Bohlman et al. 2008). In this study, tree diversity and basal area in white-sand forests were positively related to soil texture and fertility, indicating less diversity and low basal area in extremely sandy soils. Thus, soil variations at the mesoscale substantially determine the physiognomic gradient of seasonally flooded white-sand forests. Sandy
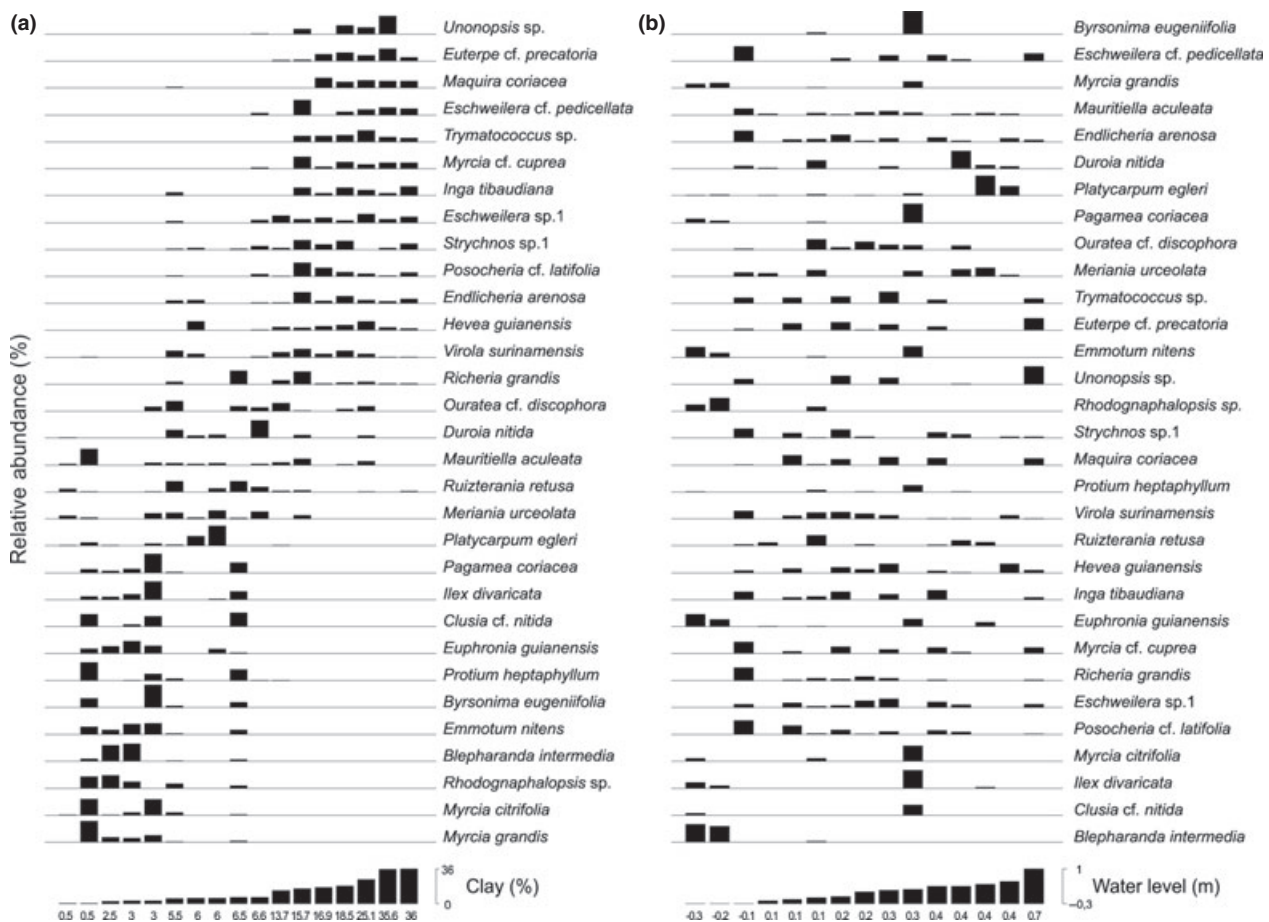
**Fig. 4.** Main tree species distribution along the (**a**) soil texture gradient represented by clay content, and (**b**) gradient flooding surface represented by the maximum flooding level.

soils that have a higher clay content allow more nutrient retention, such as P$^+$, K$^+$, Ca$^{2+}$ and Mg$^{2+}$. Phosphorus availability tends to be critically limiting to plant growth (Sollins 1998) and may influence vegetation structure, tree diversity and floristic composition of the studied white-sand forests. In this case, nutritional restriction determines the occasionally less diverse and non-forest formations, such as the grasslands and savannas in this study. The high-stature physiognomy in this study, which slightly differs from *Igapó* forests (*sensu* Kubitzki 1989), are established on more fertile clayey soils that harbour the largest plant biomass and higher tree diversity (see below).

### The indirect flooding effect

The magnitude of flooding effects on tree composition, structure and diversity was lower than the effect of soil texture and fertility. Moreover, when combined with soil variables in the same model, the influence of flooding level was overwhelmed by the high effects related to soil texture and fertility. In this study, the surface water level increases

from the savanna-like vegetation, on extremely sandy soils, to forested areas on the more clayish soils, where tree diversity and vegetation structure were higher. In contrast, studies conducted in flooded forests (*Igapó* and *Várzea*) showed a negative correlation between diversity and flooding level (Junk et al. 1989; Ferreira 1997; Ferreira & Prance 1998; Ferreira & Stohlgren 1999; Koponen et al. 2004; Wittmann et al. 2006). However, much studied *Igapó* and *Várzea* forests are generally located in perennial rivers that have well-defined flood pulses. We hypothesize that the edaphic gradient in white-sand vegetation covers a range of physical and chemical properties that are more variable than in forests seasonally flooded by lateral inundation of major rivers.

Although we used short-term flooding data, which may be not representative of the long-term variation in flooding level or groundwater depth, the overall hydrological regime of white-sand vegetation at Viruá National Park is strongly related to annual rainfall seasonality (both extreme wet and dry seasons; see Fig. 2). Thus, unusual inter-annual variation of the

**Table 2.** Results of the multiple regression analyses relating soil texture and fertility (PC1), soil pH (PC2), flood level (FL) and slope effects on tree diversity (Fisher's index), tree basal area ($m^2 \cdot ha^{-1}$) and tree density (ind·$ha^{-1}$).

| | Model | Standard Partial Slope (b) | | | | $F^{\dagger}$ | P | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| | | PC1 | PC2 | FL | Slope | | | |
| Diversity Fisher's Index | | | | | | | | |
| DBH $\geq$ 1 cm | 1st | **0.77*** | **−0.33*** | −0.09 | | 7.10 | 0.005 | 0.55 |
| | 2nd | | | 0.35 | −0.14 | 0.87 | 0.46 | <0.001 |
| DBH $\geq$ 10 cm | 1st | **0.69**** | **−0.42*** | 0.09 | | 11.17 | 0.001 | 0.67 |
| | 2nd | | | **0.55*** | −0.32 | 3.19 | 0.07 | 0.22 |
| DBH < 10 cm | 1st | **0.69*** | −0.30 | −0.10 | | 4.16 | 0.031 | 0.39 |
| | 2nd | | | 0.30 | −0.13 | 0.62 | 0.55 | <0.001 |
| Tree Basal Area | | | | | | | | |
| DBH $\geq$ 1 cm | 1st | **0.46*** | −0.01 | 0.40 | | 4.49 | 0.025 | 0.41 |
| | 2nd | | | **0.63*** | −0.13 | 3.96 | 0.045 | 0.28 |
| DBH $\geq$ 10 cm | 1st | **0.75**** | 0.03 | 0.18 | | 10.62 | 0.001 | 0.66 |
| | 2nd | | | **0.55*** | −0.14 | 2.62 | 0.11 | 0.18 |
| DBH < 10 cm | 1st | −0.08 | −0.15 | 0.39 | | 0.90 | 0.47 | <0.001 |
| | 2nd | | | **0.51*** | −0.05 | 2.16 | 0.15 | 0.13 |
| Tree Density | | | | | | | | |
| DBH $\geq$ 1 cm | 1st | −0.24 | −0.22 | 0.42 | | 1.16 | 0.36 | 0.03 |
| | 2nd | | | 0.37 | −0.08 | 0.99 | 0.39 | <0.001 |
| DBH $\geq$ 10 cm | 1st | 0.37 | 0.01 | 0.36 | | 2.63 | 0.10 | 0.25 |
| | 2nd | | | **0.57*** | −0.16 | 2.90 | 0.09 | 0.20 |
| DBH < 10 cm | 1st | −0.28 | −0.28 | 0.41 | | 1.20 | 0.35 | 0.04 |
| | 2nd | | | 0.35 | −0.07 | 0.83 | 0.46 | <0.001 |

First model: Y = PC1 + PC2 + FL; second model: Y = FL + Slope.

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

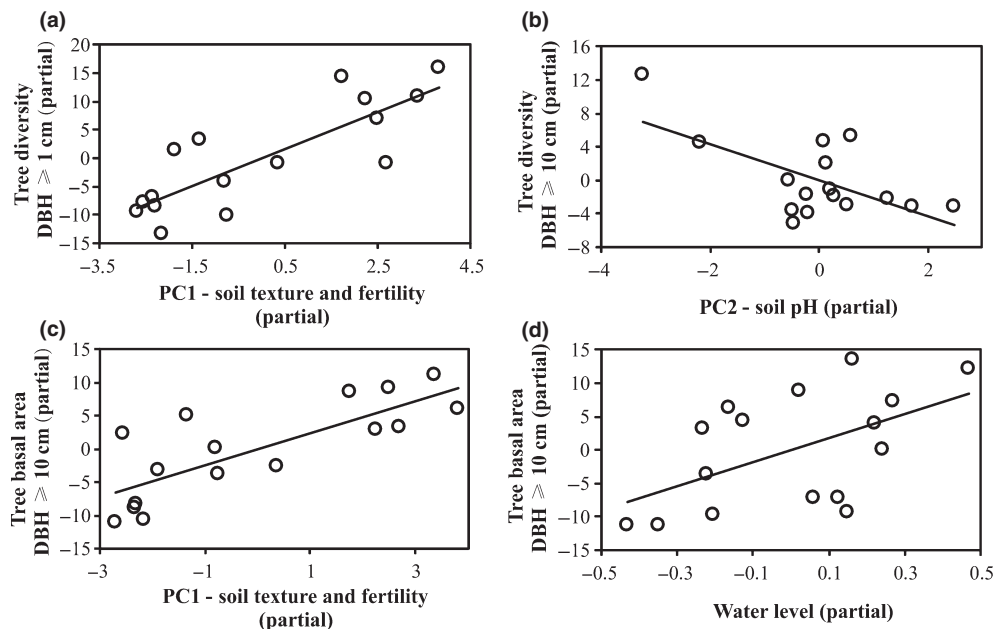†Three and 13 df in the first model; two and 13 df in the second model.



**Fig. 5.** Partial regressions testing for the effects of gradients of texture and soil fertility (**a** and **c**), soil pH (**b**) and maximum flood level (**d**) on tree diversity and tree basal area. Flood level partials correspond to the second model (see Table 2).

maximum flood level may exist over several years (e.g. more or less extended flooding periods), but we argue that the variation in flooding regime would be the same among all plots. Due to the rainfall seasonality, most of plots suffered surface flooding during the wet season. Among the high-stature physiognomies, flooding can also be associated with rising levels of tributary streams and undefined drainage lines in the wet season. On the other hand, flooding in low-stature forests is shallower due to poor drainage.

In soils with a clay content of more than 15%, the flooding level reached maximum values and the water remained longer above the surface. Besides the influence of soil gradient on vegetation composition, it could also act on the soil saturation time and flood level in the studied white-sand forests. It is worth noting that not all white-sand forests of the Rio Negro basin are flooded, as many areas are located on sandy uplands where groundwater may raise but not emerge during the wet season (Coomes & Grubb 1996; Jirka et al. 2007). We believe that the flood gradient in our study site is characterized by two extremes: (1) sandy interfluves where the poor soils are highly leached by the groundwater oscillations; and (2) white-sand forests located where flooding is a result of intermittent stream formation and shallow drainage lines, which allow the input of sediment and nutrient retention in soil.

### The floristic composition gradient

The Amazonian white-sand forests are characterized by low tree diversity and the occurrence of specialized tree species on nutrient-poor soils (Anderson 1981; Prance 1996). In this study, *Byrsonima eugeniifolia*, *Blepharanda intermedia*, *Clusia* cf. *nitida*, *Emmotum nitens*, *Euphronia guianensis*, *Ilex divaricata*, *Pagamea coriacea*, *Platycarpum egleri*, *Myrcia citrifolia* and *M. grandis* were restricted to the extremely sandy and unfertile soils and the more savanna-like physiognomies. As a result, such species can be considered highly specialized in sandy soils and less demanding above the nutritional limits necessary for successful establishment. Tolerant species on sandy soils allocate more resources to defence against herbivory than to growth (Fine et al. 2004, 2006). Thus, in soils with a higher clay and nutrient availability, tolerant species to nutritional scarcity may be quickly suppressed by those that invest most resources in growth. However, some tree species found in the savanna-like vegetation were also common in forested physiognomies, such as *Calophyllum brasiliense*, *Duroia nitida*, *Manilkara bidentada*, *Mauritiella aculeata*, *Meriania urceolata*, *Protium heptaphyllum*, *Richeria grandis* and *Ruizterania retusa*. In extremely sandy soils, these species were stunted, possibly in response to nutritional stress; however, in forested areas they reached the canopy.

The strong relationship between soil features and floristic distribution may suggest that an environmental filter related to physiological ability to tolerate the nutritional scarcity may act on species establishment. On the other hand, the need to tolerate flood stress is a common condition along the studied gradient. Despite the fact that flooding level had little influence on the floristic gradient, typical tree species of *Igapó* forests, such as *Exollodendrum coriaceum*, *Gustavia augusta*, *Licania apetala*, *Leptolobium nitens* and *Parkia discolor* (Kubitzki 1987; Ferreira & Prance 1998; Ferreira & Almeida 2005), were sampled in plots with the highest flooding levels, emphasizing that there is no clear distinction between white-sand and *Igapó* forests. The floristic patterns not only depend on the plants' ability to survive under flooding conditions, but also on the ability to withstand low water availability (Parolin et al. 2010). During the dry season, evapotranspiration increases and soil moisture decreases causing limitations to tree growth (Prance 1979; Parolin et al. 2010; Parolin & Wittman 2010). As a result, tree species established on savanna-like physiognomies suffer higher water scarcity in relation to forest environments because the soil is sandier and more porous, and, hence, has lower capacity to retain water. In contrast, clayish soils allow increased moisture retention, which is available to plants during the dry season, when the monthly precipitation is <100 mm. Thus, the species metabolic performance will depend not only on flooding stress, but also on ability to tolerate the dry season (Parolin et al. 2010). We highlight that plant physiological performance during the dry and wet seasons should be investigated in order to enhance the discussion about flooding effects on vegetation composition.

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** List of all species and morphospecies and their respective densities, basal area and voucher numbers collected in the 17 1-ha plots at the Viruá National Park.

**Appendix S2.** Topography, flood level and 12 soil variables measured in 17 sandy soil plots of the PPBio grid, located at Viruá National Park, Brazil.

**Appendix S3.** Variance percentage explained by two axes generated from non-metric multidimensional scaling (NMDS) for different data types and size classes.

**Appendix S4.** Correlation of 12 soil variables (0–15 cm depth) with two axes generated from principal components analysis (PCA), flood level and slope.

**Photo S1.** Photo of white-sand vegetation, exemplifying the savanna-like physiognomy, located in the floodplains of Viruá National Park, northern Amazonia.

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