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ORIGINAL ARTICLE

Floristic composition, structure and soil-vegetation relations in three white-sand soil patches in central Amazonia

Layon Oreste DEMARCHI[1,*], Veridiana Vizoni SCUDELLER[2], Livia Carvalho MOURA[3], Randolpho Gonçalves DIAS-TERCEIRO[1], Aline LOPES[1,4], Florian Karl WITTMANN[1,5], Maria Teresa Fernandez PIEDADE[1]

[1] Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo 2936, Aleixo, Manaus, AM, Brasil

[2] Universidade Federal do Amazonas – UFAM, Instituto de Ciências Biológicas – ICB, Av. General Rodrigo Otávio Jordão Ramos 3000, Aleixo, Manaus, AM, Brasil

[3] Universidade de Brasília – UnB, Departamento de Ecologia, Campus Darcy Ribeiro, Asa Norte, Brasília, DF, Brasil

[4] Universidade Nilton Lins, Av. Professor Nilton Lins 3259, Parque das Laranjeiras, Manaus, AM, Brasil

[5] Karlsruher Institut für Technologie – KIT, 76131 Karlsruhe, Germany

* Corresponding author: layon.lod@gmail.com

ABSTRACT

The Amazonian white-sand vegetation presents a set of unique features, such as the dominance of a few species, high endemism and low species richness, which differentiate it from other Amazonian forests. Soil parameters have long been recognized as the main drivers of white-sand vegetation (WSV) characteristics. However, how they influence the composition, richness and structure of this vegetation type is still poorly understood. In this study we investigated the variation in floristic composition between patches and the soil-vegetation relations in three central Amazonian WSV patches. We tested whether slight differences in soil properties are linked with differences in floristic composition, species richness and forest structure in adjacent patches. In each patch three plots of 50 x 50 m were sampled (a total of 2.25 ha). Soil samples were collected for each plot. The sampling cutoff for arboreal individuals was DBH ≥ 5 cm. We sampled a total of 3956 individuals belonging to 40 families and 140 species. In each patch only a few species were dominant, but the dominant species varied among patches. Differences among patches were significant, but plots in the same patch tended to have similar species composition. The variable sum of bases (SB) was directly related to species composition, however, species richness and forest structure were not related to soil parameters. Even small variations in soil parameters can change species composition in WSV, although these variations do not necessarily influence the richness and other structural parameters.

KEYWORDS: species richness, oligotrophic ecosystems, dominance, sum of bases

Composição florística, estrutura e relação solo-vegetação em três áreas de campinarana na Amazônia central

RESUMO

As campinaranas amazônicas apresentam uma série de características únicas, como a dominância de poucas espécies, alto grau de endemismos e baixa riqueza de espécies, que as diferenciam de outras formações florestais amazônicas. Parâmetros edáficos têm sido apontados como os principais responsáveis pelas características das campinaranas. Contudo, como estes parâmetros influenciam a composição, riqueza e estrutura deste tipo de vegetação ainda é pouco entendido. Neste estudo investigamos a variação estrutural, a composição florística e a relação solo-vegetação em três áreas de campinarana na Amazônia central, com intuito de testar se pequenas diferenças nos parâmetros edáficos do solo estão relacionados com diferenças na composição, riqueza e estrutura do componente arbóreo em áreas de campinarana adjacentes. Em cada área foram amostradas três parcelas de 50 x 50 m (totalizando 2.25 ha), com o critério de inclusão para os indivíduos de DAP ≥ 5 cm. Amostras de solo foram coletadas em cada parcela. O número total de indivíduos amostrados foi 3956, pertencendo a 40 famílias e 140 espécies. Em cada área poucas espécies foram dominantes, mas estas variaram entre as áreas. Diferenças entre as áreas foram significativas, porém parcelas da mesma área tenderam a ter composição florística similar. A variável soma de bases (SB) foi diretamente relacionada à composição de espécies; contudo, riqueza de espécies e estrutura florestal não foram relacionadas a nenhum dos parâmetros do solo amostrados. Concluimos que mesmo pequenas variações nos parâmetros edáficos do solo podem mudar a composição de espécies em campinaranas, embora esta variação não necessariamente influencie a riqueza e outros parâmetros estruturais da vegetação.

PALAVRAS-CHAVE: riqueza de espécies, ecossistemas oligotróficos, dominância, soma de bases

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INTRODUCTION

The Amazonian region is formed by a mosaic of landscapes with different floristic compositions. Each landscape diversity is related to a variety of habitat characteristics and species preferences (Pitman *et al.* 2001; Coronado *et al.* 2009; Junk *et al.* 2011). It is estimated that Amazonian forests contain between 12,500 and 16,000 tree species (Hubbell *et al.* 2008; ter Steege *et al.* 2013). The formations designated as white-sand vegetation (WSV) or campinarana (Veloso *et al.* 1991) constitute a peculiar phytophysiognomy in the Amazon region. Soils beneath white-sand vegetation are composed of heavily leached white-sand of very low fertility (Heyligers 1963; Anderson 1981; Luizão *et al.* 2007; Mendonça *et al.* 2015); the woody vegetation is scleromorphic and relatively poor in tree species compared to other Amazonian ecosystems (Vicentini 2004; Stropp *et al.* 2011,), but rich in endemisms (Janzen 1974; Anderson *et al.* 1975; Anderson 1981; Boubli 2002; Fine *et al.* 2010; Adeney *et al.* 2016; Fine and Baraloto 2016; Guevara *et al.* 2016).

Estimates of white-sand vegetation cover ranged from 64,000 km^2 (Braga 1979) to 400,000 km^2 (Prance and Daly 1989). However, more accurate mapping techniques with remote sensing suggest that the coverage might be larger, since surveys of the Negro River basin alone (where continuous areas of white-sand vegetation are common) estimated its coverage to be 104.000 km^2 (Junk *et al.* 2011), and the most recent estimate of white-sand vegetation coverage in the Amazon basin is 334,879 km^2 (Adeney *et al.* 2016). In many other Amazonian regions, white-sand vegetation distribution is isolated and island-like, a result of the fragmented nature of the distribution of the sandy soils on which this vegetation type occurs (Prance 1996).

The structure of white-sand vegetation varies from grassland and open areas, dominated by herbaceous plants, to open shrub and dense-canopy forest physiognomies (Veloso *et al.* 1991; IBGE 2012). Many white-sand soils have an underlying hardpan, where any increase in precipitation can quickly elevate the groundwater level, subjecting plants to waterlogging or hydric saturation periods (Richardt *et al.* 1975; Kubitzki 1989a; Franco and Dezzeo 1994). Because of this characteristic, some authors emphasize the comparatively high floristic similarity between white-sand vegetation and Amazonian black-water seasonally-flooded forest (igapó) (Kubitzki 1989a; Kubitzki 1989b; Damasco *et al.* 2013).

Oligotrophic soils and hydric saturation have been considered the main drivers of white-sand vegetation characteristics (Heyligers 1963; Pires and Prance 1985; Franco and Dezzeo 1994; Tiessen *et al.* 1994; Sobrado 2009), since they work as strong environmental filters for tree species establishment and distribution (Targhetta *et al.* 2015; Adeney *et al.* 2016). Studies show that white-sand vegetation areas with higher hydric saturation may present lower species richness and smaller individuals (Bongers *et al.* 1985; Franco and Dezzeo 1994; Targhetta *et al.* 2015), although under certain edaphic and topographic conditions hydric saturation may provide less adverse conditions for species establishment, thereby these conditions might have a positive effect on species richness and diversity (Damasco *et al.* 2013). Though soil properties are directly influenced by hydric saturation, soil texture and fertility have been considered the main factors causing structural and floristic variation of white-sand vegetation (Tiessen *et al.* 1994; Coomes and Grubb 1996; Coomes 1997; Damasco *et al.* 2013). However, there are few studies that investigated the role of small differences in soil nutrient concentration within this oligotrophic ecosystem.

To investigate the relationships between soil parameters and the composition and structural characteristics of the woody plant assemblage, three isolated patches of white-sand vegetation surrounded by upland forest (*terra-firme*) forest were studied to address the following questions: (1) are the patches different in assemblage composition and (2) if so, are such differences linked to soil characteristics?

MATERIAL AND METHODS

Study Area

WSV was studied in three areas within the Tupé Sustainable Development Reserve (SDR Tupé, Figure 1), located on the left margin of the Negro River, approximately 30 km west of the city of Manaus, in the state of Amazonas, Brazil. The SDR Tupé covers an area of 11.973 ha and, together with other protected areas, forms an important mosaic of protected habitats in the central Brazilian Amazon. The average annual rainfall in the region is 2,100 mm, with a well defined rainy season (165-300 mm $month^{-1}$) from November to May, and a dry season (<65 mm $month^{-1}$) from July to September. The average temperature is 27 °C, ranging between 18 °C and 37 °C throughout the year, and average relative humidity is around 85% (Radam Brasil 1978). The study area is inserted in the Igarapé Tarumã-mirim basin (a tributary of the Rio Negro). This region is largely covered by WSV areas, which are distributed in patches. The vegetation of the SDR Tupé is predominantly upland forest (*terra-firme*), with black water river floodplains forest (*igapó*) dominating the narrow riverine floodplain (Scudeller *et al.* 2005).

Vegetation sampling

Three white-sand forest patches (A, B and C) were selected within the SDR Tupé. The patches were 40 to 100 ha in size and were surrounded by *terra-firme* and/or *igapó* forest. In each patch three 50 x 50 m plots were established, totalling 0.75 ha per patch, and 2.25 ha among the three patches. To avoid sampling transitional areas between WSV and surrounding forest formations, all plots were allocated in the central part of each white-sand forest patch, with a distance of 100 to 180 m among sampling plots within patches, and a distance of 3.5 to 4 km among patches.

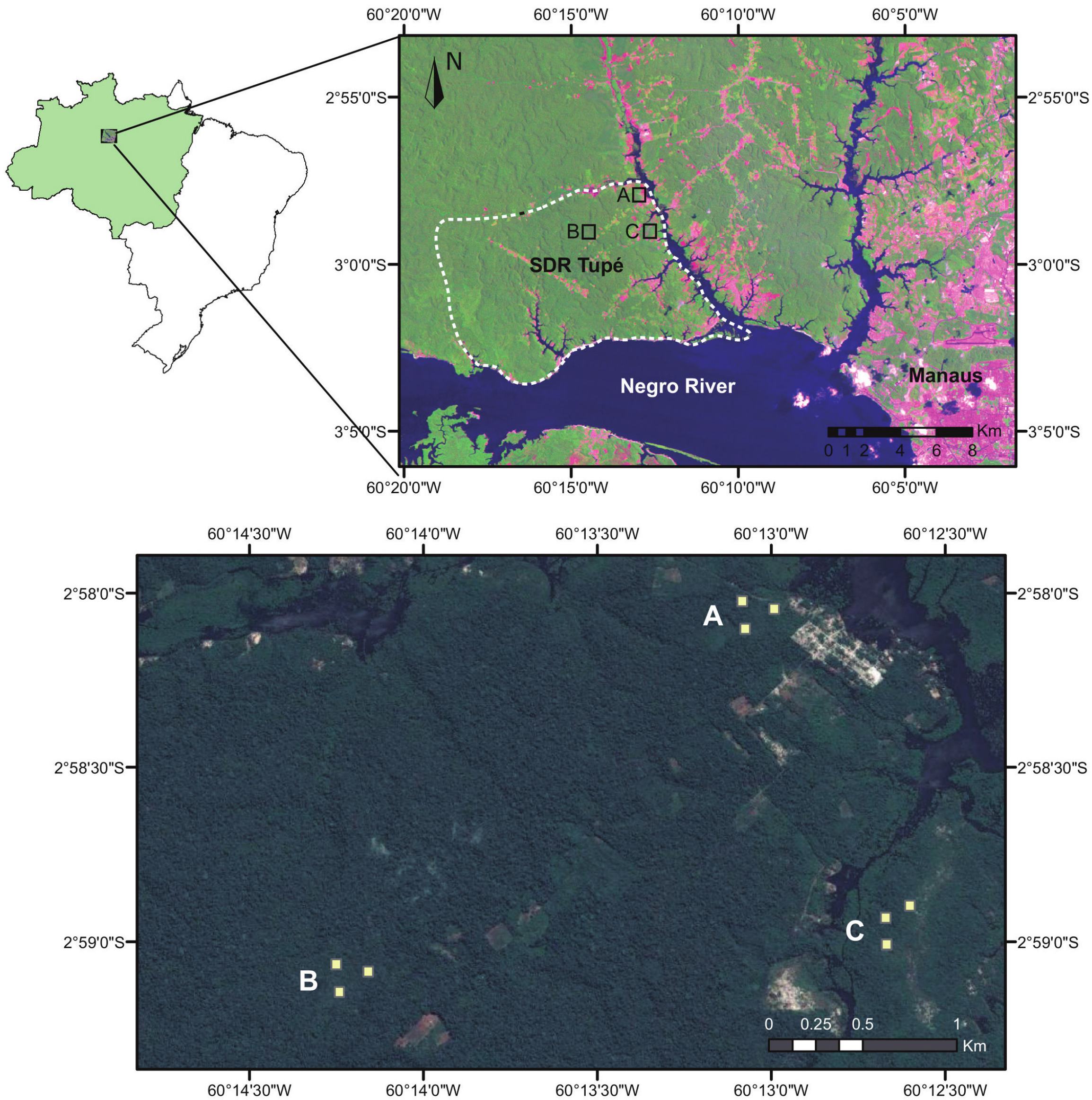

Figure 1. Map locating the white-sand forest patches studied (A, B and C) within the limits of the Tupé Sustainable Development Reserve (SDR Tupé), located on the left margin of the Negro River, west of the city of Manaus, in the state of Amazonas, Brazil. The nine sampling plots (three within each patch) are shown as nine squares in the larger image. The pink color on the smaller satellite image shows urbanized and clear-cut areas, while green shows forested habitats. This figure is in color in the electronic version.

All living woody individuals (except lianas), with diameter at breast height (DBH) ≥ 5 cm were marked with numbered aluminum tags, and had their diameter measured. Tree height was estimated with a hypsometer. Vouchers from all individuals were collected, dried, pressed, and subsequently deposited in the herbarium of the National Institute of Amazon Research (Instituto Nacional de Pesquisas da Amazônia - INPA) and in the herbarium of the Federal Institute of Amazonas (Instituto Federal do Amazonas - IFAM) (EAFM). Species were identified using analytical keys, comparison with herbarium specimens and consulting specialists (see acknowledgements). Species were classified according to APG IV (2016), and their names were standardized according to the classification of the REFLORA program.

Chemical and physical soil characterization

Soil samples at 0 to 20 cm depth were collected in the four corners and in the center of each sampling plot. The samples were homogenized in the field and joined in one composite sample per plot. The analyses were performed according to the Embrapa soil analysis protocol (Embrapa 1997). Twenty-four variables were analyzed: fine sand (0.2-0.05 mm grain diameter), coarse sand (2.0-0.2 mm), total sand (2.0-0.05 mm), silt (0.05-0.002 mm) and clay (>0.002 mm), C (carbon), OM (organic matter), pH, P, K^+, Na^+, Ca^{2+}, Mg^{2+}, Al^{3+}, H+AL (potential acidity), SB (sum of bases: $Ca^{2+} + Mg^{2+} + K^+ + Na^+$), CEC(t) (effective cation exchange capacity), CEC(T) (cation exchange capacity under neutral pH), V (saturation index for bases), m (saturation index for aluminum), Fe, Zn^+, Mn^{2+} and Cu.

Data analysis

The forest structure parameters Relative Density (RDe), Relative Dominance (RDo), Relative Frequency (RFr) and the Importance Value Index (IVI) (Curtis and McIntosh 1951) were calculated using the software Fitopac 2.1.2 (Shepperd 2010). To evaluate the local effect on species composition between the patches, two NMDS axes were generated and a MANOVA was applied to test for statistical difference in species composition among patches. Ranking was based on dissimilarity between samples (in a presence and absence matrix) calculated with the Jaccard Index (Borcard *et al.* 2011). To evaluate the effect of soil parameters in tree assemblages, we generated a new NMDS axis (k =1), based on dissimilarity between samples (in a presence and absence matrix) calculated with the Jaccard Index. The relationship between environmental variables and species composition was assessed using a Generalized Linear Mixed Model (GLMM). For the model, we used only variables that were not correlated with each other (see Supplementary Material, Table S1), as correlated variables carry the same information and could potentially mask or enhance patterns in additive multiple linear models (Magnusson and Mourão 2005). We used the patches as a random variable. Therefore, our overall multiple regression model was: NMDS = a + b (Mn^{2+}) + b (Silt %) + b (SB) + b (1 | patches).

To evaluate the effect of soil parameters on species richness and vegetation structure variation the GLMM was used separately for each parameter (species richness, relative density, average height and average basal area). Thus we used the same model (mentioned above) replacing the dependent variable for the vegetation structural parameters. To test the effects of soil variables on vegetation without the influence of the sampled patch, we included in the model the variable patches (study areas) as a random variable, so it was possible to control the effect of this variable and verify the real effect of the edaphic variables. All the multivariate analyses were performed using R vegan (R Core Team, 2014; Oksanen *et al.* 2013).

RESULTS

Vegetation structural variation

A total of 3956 trees belonging to 40 families and 140 species were recorded in the three patches (Table 1). The families with highest species richness were Fabaceae (15 species), Sapotaceae and Lauraceae (14 species each), Burseraceae, Moraceae and Myrtaceae (7 species each) and Sapindaceae (6 species).

The average DBH was 10.4 cm, with a maximum of 94.2 cm. Among the 36 individuals with DBH >45 cm, 33 were *Aldina heterophylla* Spruce ex Benth. The average height of individual trees was 7 m, with some emergent individuals, mostly *A. heterophylla*, reaching 22 m.

The highest similarity (41%) occurred between patches A and B, followed by patches A and C (27%) and B and C (22%). Many species occurred only in one patch (51.4% of all recorded species). Overall, the 10 most abundant species corresponded to 54.2% of recorded individuals. Likewise, the 10 most important species corresponded to 44.3% of the total IVI values. Only *Aldina heterophylla* was among the 10 most important (IVI) species in all three patches, and only *Aspidosperma* aff. *verruculosum* Müll.Arg., *Clusia nemorosa* G.Mey., *Simaba guianensis* Aubl., *Pradosia schomburgkiana* (A.DC.) Cronquist, and *Conceveiba terminalis* (Baill.) Müll. Arg. were among the 10 most important species in at least two of the sampled patches (Table 2). For 38 species only one individual was recorded, and for 13 species only two individuals. Together, these species corresponded to 36.4% of the total species richness. Phytosociological parameters and herbarium voucher numbers for all recorded species are available as Supplementary Material, Table S2.

Tree height and basal area differed significantly among sampling plots (ANOVA F = 0.38; P = 0.00; F = 1.92; P = 0.05 respectively) (Figure 2). However, only basal area differed significantly among patches (ANOVA F = 4.45; P = 0.01), due to a significant difference between patches A and C (Tukey test, P = 0.01). Plot ordination along the two NMDS axes captured 92.76% of the variation in species composition. Tree assemblages differed significantly among patches (MANOVA: Pillai trace = 1.5449; F = 10.182; P <0.001) (Figure 3).

Table 1. Number of individuals, families, richness (total number of species), number of rare species (only one or two recorded individuals) and number of exclusive species (present in only one patch) for nine sampling plots in three white-sand forest patches in Tupé Sustainable Development Reserve (SDR Tupé), Amazonas, Brazil.

Patch	Individuals	Families	Richness	Rare species	Exclusive species
A	1413	30	77	28	20
B	1299	35	72	22	21
C	1244	34	90	37	31
Total	3956	40	140	51	72

Table 2. Phytosociological parameters for the 10 species with highest IVI per patch of white-sand forest patches in the Tupé Sustainable Development Reserve (SDR Tupé), Amazonas (Brazil). N = number of individuals, RDe = Relative Density, RDo = Relative Dominance, RFr = Relative Frequency, IVI = Importance Value Index. Values of RDe, RDo and RFr are in percentage.

Species	Family	N	RDe	RDo	RFr	IVI
Patch A						
Aspidosperma aff. *verruculosum*	Apocynaceae	607	42.96	32.76	2.34	78.04
Aldina heterophylla	Fabaceae	72	5.10	20.59	2.33	28.02
Simaba guianensis	Simaroubaceae	55	3.89	6.17	2.33	12.39
Parkia igneiflora	Fabaceae	54	3.82	3.21	2.33	9.36
Conceveiba terminalis	Euphorbiaceae	34	2.41	5	1.55	8.95
Macrolobium arenarium	Fabaceae	34	2.41	3.26	1.55	7.22
Clusia nemorosa	Clusiaceae	53	3.75	1.11	2.33	7.19
Dimorphandra vernicosa	Fabaceae	30	2.12	2.65	2.33	7.10
Byrsonima laevis	Malphiguiaceae	29	2.05	1.23	2.33	5.60
Pradosia schomburgkiana	Sapotaceae	24	1.70	0.73	2.33	4.75
Patch B						
Aldina heterophylla	Fabaceae	80	6.16	37.12	2.27	45.55
Aspidosperma aff. *verruculosum*	Apocynaceae	133	10.24	10.01	2.27	22.52
Pagamea duckei	Rubiaceae	173	13.32	2.82	2.27	18.41
Manilkara bidentata	Sapotaceae	92	7.08	8.74	2.27	18.10
Licania lata	Chrysobalanaceae	109	8.39	5.04	2.27	15.70
Clusia aff. *spathulaefolia*	Clusiaceae	99	7.62	2.24	2.27	12.13
Mauritiella armata	Arecaceae	41	3.16	4.95	1.52	9.62
Pradosia schomburgkiana	Sapotaceae	44	3.39	2.15	2.27	7.78
Clusia nemorosa	Clusiaceae	59	4.54	0.90	2.27	7.72
Humiria balsamifera	Humiriaceae	8	0.62	4.18	2.27	7.06
Patch C						
Protium paniculatum	Burseraceae	317	25.48	14.24	1.73	41.46
Aldina heterophylla	Fabaceae	18	1.45	25.66	1.73	28.85
Conceveiba terminalis	Euphorbiaceae	30	2.41	5.62	1.73	9.76
Kutchubaea sericantha	Rubiaceae	69	5.55	2.25	1.73	9.53
Swartzia tessmannii	Fabaceae	54	4.34	2.76	1.73	8.83
Pouteria aff. *elegans*	Sapotaceae	50	4.02	2.91	1.73	8.66
Vitex triflora	Verbenaceae	38	3.05	3.82	1.73	8.60
Simaba guianensis	Simaroubaceae	36	2.89	3.77	1.73	8.40
Simarouba amara	Simaroubaceae	21	1.69	3.56	1.73	6.98
Aniba santalodora	Lauraceae	24	1.93	2.74	1.73	6.40

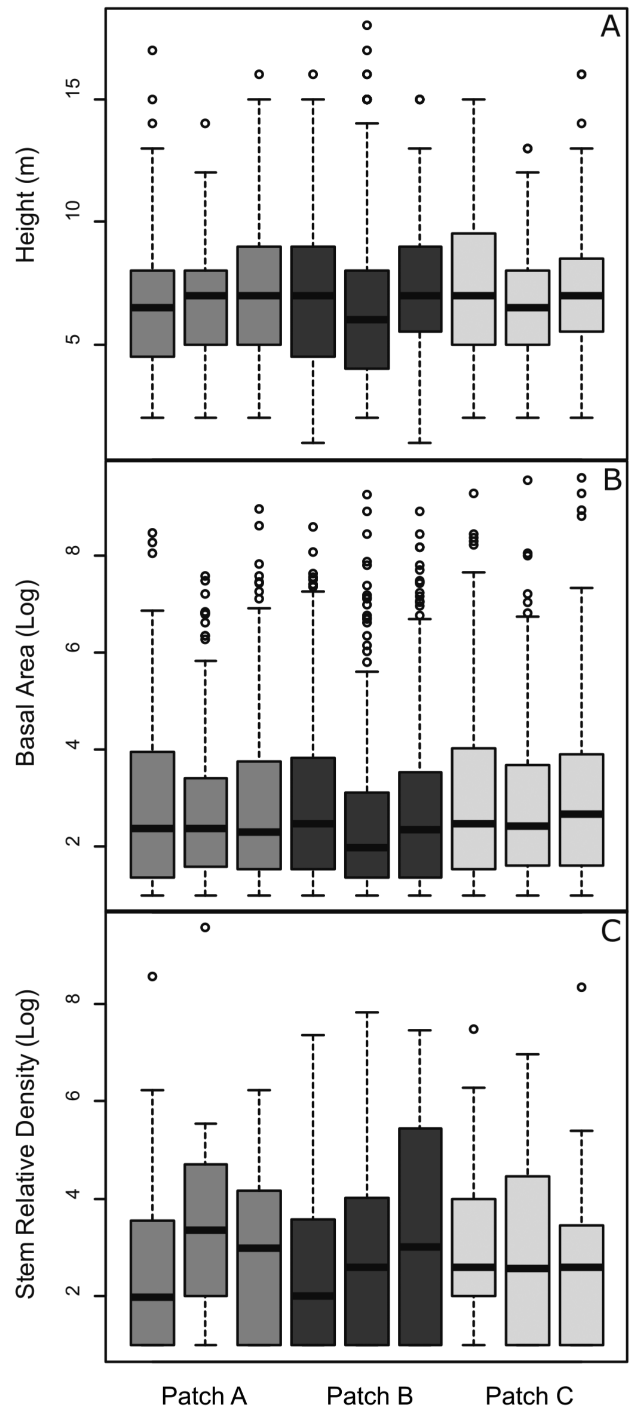

Figure 2. Comparison of forest structure parameters (tree height, A; basal area, B; and relative density, C) among nine sampling plots in three white-sand vegetation patches in the Tupé Sustainable Development Reserve (SDR Tupé), Amazonas, Brazil. The box indicates the 25th and 75th percentiles, the line inside the box represents the median, the capped bars indicate the 10th and 90th percentiles, and the circles represent the extreme values. Different grey tones group plots belonging to each of the three forest patches. This figure is in color in the electronic version.

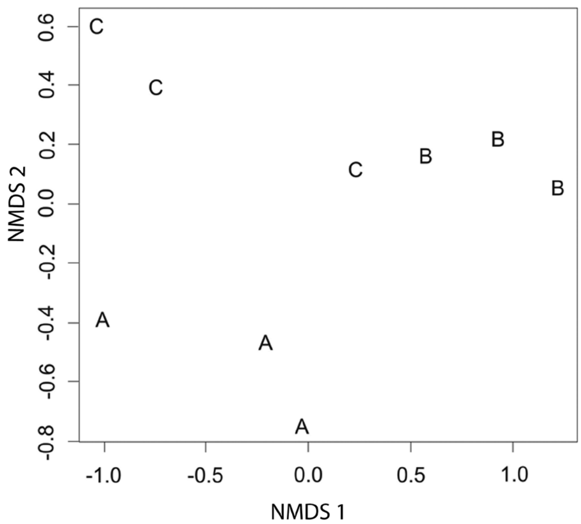

Figure 3. NMDS ordination diagram of the nine sampling plots in three white-sand forest patches in the Tupé Sustainable Development Reserve (SDR Tupé), Amazonas (Brazil) based on species occurrence of trees with DBH ≥ 5 cm.

Vegetation variation and soil fertility

The three patches were characterized by sand predominance and nutrient-poor soils (Table 3). The single NMDS axis (k=1) explained 58.8% of the variation in species composition. The GLMM using this NMDS axis as dependent variable and soil parameters as independent variables explained 60.50% of the variation in species composition (NMDS = $-1.165^{-17} + 1.286^{-1}$ QM $- 2.489^{-2}$ PS $- 4.083^{-1}$ SB; $\chi^2 = 9.7086$; $R^2 = 0.6050$; $P = 0.02$), yet only the variable sum of bases (SB) contributed significantly to the model ($t = -3.094$; $P = 0.03$) (Table 4). However, there was no significant effect of soil parameters on species richness and structural variation.

Some species were widely distributed along the fertility gradient, while others were restricted to parts of it. Species such as *Ocotea amazonica* (Meisn.) Mez and *Pouteria oblanceolata* Pires were strongly associated with localities with the lowest fertility, while *Mauritiella armata* (Mart.) Burret and *Protium heptaphyllum* (Aubl.) Marchand were more frequently found in plots with the greatest fertility (Figure 4).

Table 3. Soil parameter values for three white-sand forest patches (A, B and C) in the Tupé Sustainable Development Reserve (SDR Tupé), Amazonas (Brazil) and for other WSV areas in other studies. Values are the mean ± standard deviation [except * = variation coefficient (%)].

Soil variables	Patch A	Patch B	Patch C	Damasco *et al*. 2013	Targhetta *et al*. 2015
Granulometric variables					
Coarse Sand (%)	69.40 ± 9.20	69.31 ± 9.20	75.46 ± 3.42	-	-
Fine Sand (%)	25.91 ± 8.47	25.87 ± 8.70	21.41 ± 3.28	-	-
Total Sand (%)	95.31 ± 0.72	95.20 ± 0.94	96.87 ± 0.20	70.30 ± 20*	93.40 ± 1.50
Silt (%)	1.99 ± 1.09	3.03 ± 0.77	1.67 ± 0.46	17.90 ± 30*	4.80 ± 0.80
Clay (%)	2.68 ± 0.37	1.76 ± 0.34	1.45 ± 0.26	11.80 ± 96*	1.80 ± 1
Edaphic variables					
pH (H_2O)	4.29 ± 0.04	4.21 ± 0.07	4.27 ± 0.11	4.50 ± 4*	4.27 ± 0.32
C (g/kg)	8.64 ± 1.47	10.05 ± 2.58	6.59 ± 0.94	-	1.20 ± 0.20
OM (g/kg)	14.87 ± 2.54	17.29 ± 4.44	11.34 ± 1.61	-	-
P (mg/dm^3)	2.33 ± 0.57	2.66 ± 0.57	2 ± 0	10.90 ± 94*	4.70 ± 1.80
K (mg/dm^3)	16.33 ± 2.88	16.66 ± 3.21	10 ± 1	26.70 ± 72*	13.30 ± 3.50
Na (mg/dm^3)	3.66 ± 2.08	7.33 ± 1.15	4.66 ± 1.52	-	-
Ca ($cmolc/dm^3$)	0.06 ± 0.02	0.04 ± 0.02	0.04 ± 0	0.14 ± 79*	0.03 ± 0.01
Mg ($cmolc/dm^3$)	0.13 ± 0.05	0.11 ± 0.02	0.07 ± 0	0.10 ± 50*	0.06 ± 0.01
Al ($cmolc/dm^3$)	0.68 ± 0.13	0.81 ± 0.20	0.61 ± 0.10	0.58 ± 76*	0.80 ± 0.20
H+Al ($cmolc/dm^3$)	4.21 ± 0.29	4.44 ± 1.21	3.20 ± 0.33	-	-
SB ($cmolc/dm^3$)	0.25 ± 0.07	0.23 ± 0.04	0.15 ± 0	-	0.15 ± 0.02
CTC (t) ($cmolc/dm^3$)	0.93 ± 0.12	1.04 ± 0.25	0.77 ± 0.10	-	-
CTC (T) ($cmolc/dm^3$)	4.46 ± 0.34	4.68 ± 1.26	3.35 ± 0.32	-	-
V (%)	5.59 ± 1.39	5.06 ± 0.41	4.67 ± 0.54	-	-
m (%)	72.86 ± 8.36	77.52 ± 1.12	79.55 ± 3.01	-	-
Fe (mg/dm^3)	3.66 ± 0.57	5.33 ± 1.52	3 ± 0	78.20 ± 98*	13.50 ± 9.50
Zn (mg/dm^3)	0.41 ± 0.12	0.35 ± 0.07	0.33 ± 0.04	0.29 ± 116*	0.20 ± 0.10
Mn (mg/dm^3)	0.92 ± 0.67	0.89 ± 0.75	1.27 ± 0.49	1.50 ± 186*	0.50 ± 0.10
Cu (mg/dm^3)	0.11 ± 0	0.09 ± 0.01	0.08 ± 0.01	-	0.07 ± 0.01

C (organic carbon), OM (organic matter), pH in water (proportion 1:2,5), H+AL (potential acidity), SB (sum of bases), CTC(t) (effective cation exchange capacity), CTC(T) (cation exchange capacity under neutral pH), V (saturation index for bases), m (saturation index for aluminum).

Table 4. Effects of edaphic variables on tree species composition in three white-sand forest patches in the Tupé Sustainable Development Reserve (SDR Tupé), Amazonas (Brazil). Estimate = β value of analyzed fixed variables; Std. Error = standard error; t value = t-test value; P value: probability value.

Fixed Effects	Estimate	Std. Error	t value	P value
Intercept	-1.165^{-17}	1.059^{-1}	-	-
Mn^{2+}	1.286^{-1}	1.255^{-1}	1.025	0.36
Silt	-2.489^{-2}	1.247^{-1}	– 0.200	0.82
Sum of Bases (SB)	-4.083^{-1}	1.320^{-1}	– 3.094	0.03*

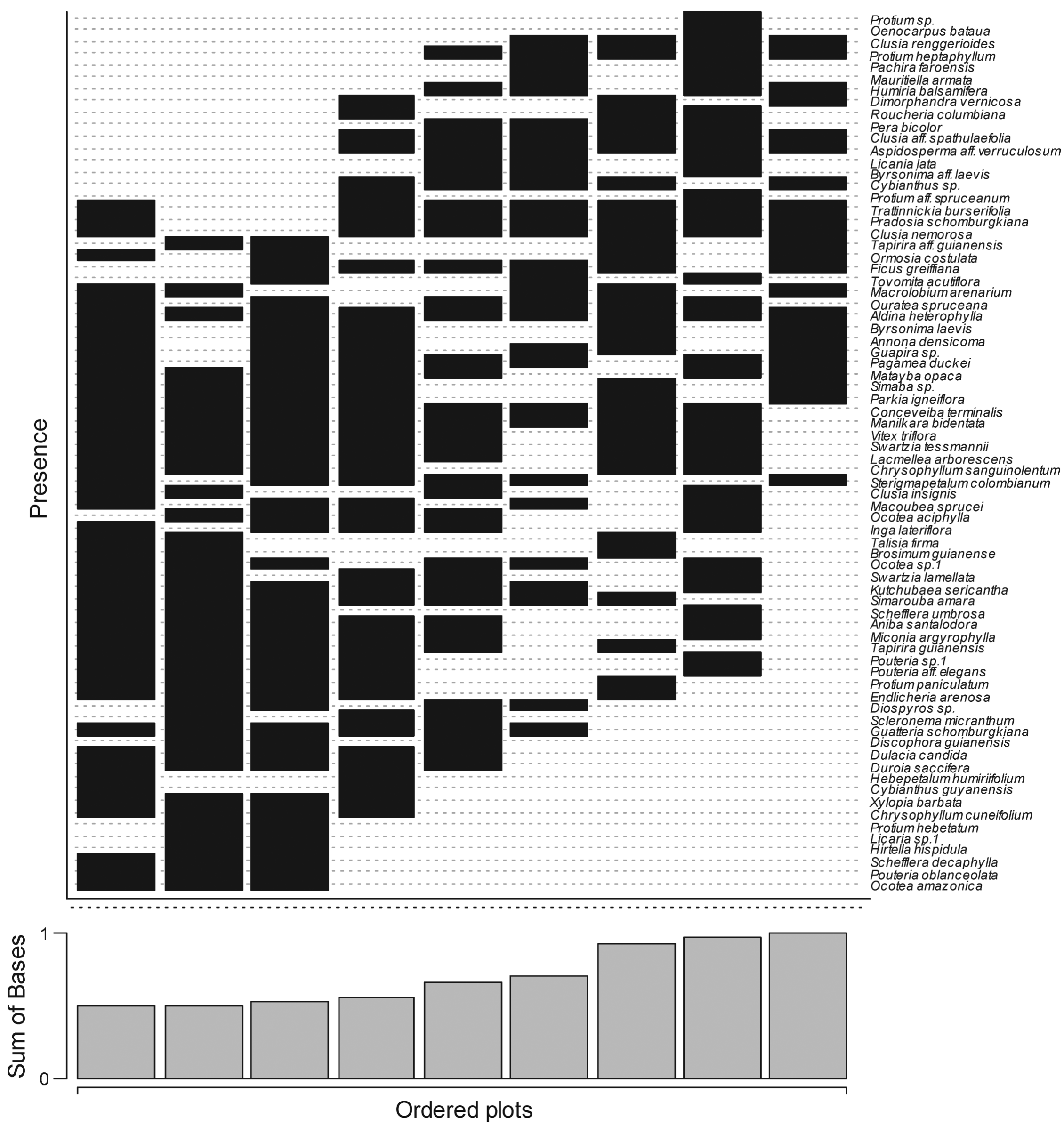

Figure 4. Species ordination along the soil fertility gradient represented by the sum of bases SB content of the nine sampling plots in three white-sand forest patches in the Tupé Sustainable Development Reserve (SDR Tupé), Amazonas, Brazil. Only species that had five or more recorded individuals with DBH ≥ 5 cm were included.

DISCUSSION

Our results show that, although the floristic composition and basal area differed significantly between patches and the height differed significantly among plots, only the variation in species composition was related to soil parameters. This soil effect on species composition may explain why the most important species (IVI) varied among relatively nearby patches.

Fabaceae, followed by Sapotaceae, were the families with the highest species richness, which agrees with previous studies in other WSV areas in the Amazon (Anderson 1981; Coomes and Grubb 1996; Ferreira 2009; Fine *et al.* 2010; Stropp *et al.* 2011; Damasco *et al.* 2013; Targhetta *et al.* 2015; Guevara *et al.* 2016). Apocynaceae and Burseraceae are also important, mainly due to the high abundance of *Aspidosperma* aff. *verruculosum* and *Protium paniculatum* var. *modestum* Daly, respectively. Lauraceae, Moraceae and Myrtaceae had high richness, but low abundance in the study patches. Common families in other Amazonian forests, such as Lecythidaceae and Myristicaceae (Gentry 1988), were poorly represented in the white-sand forest patches in SDR Tupé.

The greatest height and DBH values achieved by *Aldina heterophylla* exemplify the important ecological role of this species in WSV, as was also found in other studies (Anderson *et al.* 1975; Stropp *et al.* 2011; Targhetta *et al.* 2015). The smaller size of the majority of species when compared to other dominant forest formations in Amazonia, such as *terra-firme* and seasonal flooded forests, justifies the adoption of the individual inclusion criteria of DBH ≥ 5 cm. If the inclusion criteria commonly used in Amazon forests of DBH ≥ 10 cm had been adopted, 60% of the individuals in our sampling plots, including abundant species such as *Pagamea duckei* Standl., would not have been sampled.

Patches had significantly different floristic composition, but plots in the same patch tended to have similar species composition. Previous studies have related differences in floristic composition to factors such as the insular characteristics of WSV (Anderson 1981; Prance 1996), the dispersion capacity limited to anemochory and ornithochory (Macedo and Prance 1978), the effect of fire (Vicentini 2004; Adeney *et al.* 2016), past anthropogenic actions (Prance and Schubart 1978) and differences in abiotic characteristics among patches (Tiessen *et al.* 1994; Damasco *et al.* 2013; Adeney *et al.* 2016).

The dominance of just a few species, as found in this study, is common in WSV; the sum of the 10 most abundant species often exceeds 50% of all individuals (Boubli 2002; Fine *et al.* 2010; Stropp *et al.* 2011). This pattern also occurs in other Amazonian forest formations (Pitman *et al.* 2001; ter Steege *et al.* 2013). Only one species was among the 10 most dominant species in all patches, and only three were among the 10 most dominant species in at least two of the sampled patches. This disagrees with Fine *et al.* (2010) who, on a regional scale, proposed that dominant species in an area of WSV tend also to be dominant in other nearby WSV areas. However, the reduced spatial scale and the limited number of sampling units in our study preclude any further extrapolations.

Variations in edaphic characteristics change significantly the distribution and abundance of woody species in local environments (Comes and Grubb 1996; Clark *et al.* 1998; Tuomisto *et al.* 2003; John *et al.* 2007), and our results showed that this effect occurs even among nearby white-sand forest patches, and should be investigated in more detail.

The sum of bases SB was the only parameter strongly linked to floristic composition. SB is a good indicator of soil fertility and was closely related to floristic composition in oligotrophic ecosystems (Assis *et al.* 2011). In other vegetation types on less oligotrophic soils, SB was also the best predictor of species composition (Ruggiero *et al.* 2002; Zuquim *et al.* 2014). SB is composed of macronutrients that influence directly the basic processes of plants, such as hydration regulation, stomatal movement and photosynthesis, having an essential role in all stages of plant development (Larcher 2000). The presence and quantity of the elements that compose the SB are directly related to other soil parameters such as soil texture and variation in groundwater level. Although soil texture is not a physiologically important edaphic factor, elements such as silt and clay may increase water-holding and nutrient retention capacity (Mendonça *et al.* 2015). The continuous variation in groundwater level, intrinsically related to soil properties, leaches the soil components to lower layers (Franco and Dezzeo 1994). Thus, the interaction between texture and groundwater level is essential to predict soil fertility and species composition (Targhetta *et al.* 2015).

The variation in SB was significantly related to species composition, but it was not related to species richness nor vegetation structure. In the WSV of Viruá National Park, soil fertility directly influenced the vegetation structure in different phytophysiognomies and may counterbalance the negative effects of flooding (Damasco *et al.* 2013). In our study soil fertility in white-sand forest patches was less variable than in Viruá NP, but was nevertheless enough to influence floristic composition.

This lack of relation between soil fertility and vegetation structure may reflect the need for plants growing in oligotrophic environments to allocate much of their energy to form secondary compounds for defending themselves against herbivory, in detriment of both growth in height and diameter (Jansen 1974; Fine *et al.* 2006). It also suggests that other factors rather than soil may be involved in structuring the vegetation.

A significant change in species composition related to small changes in soil parameters is compatible with the extreme condition experienced by WSV. In addition to the extreme nutrient poverty of the soil, seasonal hydric saturation can act as an additional filter, selecting species capable of surviving periods of soil anoxia (Parolin and Wittmann 2010; Piedade *et al.* 2013). In contrast, periods of moisture loss accentuated by high light penetration, high porosity and low water retention capacity of sandy soils, can subject WSV to physiological constraints during the dry season, when effective drought conditions prevail (Franco and Dezzeo 1994; Vicentini 2004).

Our results highlight the role of edaphic variations in promoting species composition heterogeneity in white-sand forest patches. In this extremely nutrient-poor ecosystem, any nutrient addition may change the habitat partitioning of component species, and therefore may cause changes in species distribution and assemblage composition (Grubb 1977; Oliveira *et al.* 2014). The differentiation of species composition based on minor resource variations may be an important mechanism for niche differentiation in plant communities.

CONCLUSIONS

We detected significant differences among white-sand forest patches located at about 4 km from each other in an area in the central Brazilian Amazon. Sampling plots within patches tended to have similar species composition. We also found that small differences in soil parameters explained species composition heterogeneity in the white-sand forest patches, reflected in the large number of species (51.4%) that were exclusive to only one patch. Changes in the sum of bases were likely to be linked to species composition variation. Although these changes do not necessarily influence species richness and other structural parameters, they may be related to differential responses of a species abundance, or whether it is present or absent from a white-sand area.

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SUPPLEMENTARY MATERIAL

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DEMARCHI *et al*. Floristic composition, structure and soil-vegetation relations in three white-sand soil patches in central Amazonia.

Table S1. Correlation matrix of soil parameters collected in three white-sand vegetation patches in Tupé Sustainable Development Reserve, in the central Brazilian Amazon. (This table is available in electronic edition only).

Table S2. Phytosociological parameters of species found in the three areas of white-sand vegetation sampled in Tupé Sustainable Development Reserve, central Brazilian Amazon. N. = number of individuals, N Par = number of parcels in wich species occurred, RDe = Relative Density, RDo = Relative Dominance, RFr = Relative Frequency, IVI = Importance Value Index. Voucher number refers to material deposited in the herbaria of Instituto Nacional de Pesquisas da Amazônia (INPA) and Instituto Federal do Amazonas (EAFM). (This table is available in electronic edition only).

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	co.sand	fi.sand	to.sand	silt	clay	pH	C	O.M	P	K	Na	Ca	Mg	Al	H+Al	SB	CTC(t)	CTC(T)	V	m	Fe	Zn	Mn	Cu
co.sand		**	*	**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
fi.sand	-0.99		*	**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
to.sand	0.74	-0.66		**	NS	NS	NS	NS	NS	**	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS
silt	-0.81	0.77	-0.80		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
clay	0.03	-0.09	-0.42	-0.22		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	**
pH	-0.24	0.28	0.10	-0.22	0.17		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
C	-0.01	-0.08	-0.63	0.36	0.46	-0.33		**	NS	**	NS	NS	*	**	**	*	**	**	NS	NS	**	NS	NS	NS
OM	-0.01	-0.08	-0.62	0.36	0.47	-0.32	1.00		NS	**	NS	NS	*	**	**	*	**	**	NS	NS	**	NS	NS	NS
P	-0.19	0.14	-0.46	0.49	0.00	-0.49	0.36	0.35		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
K^+	-0.46	0.38	-0.87	0.57	0.54	-0.09	0.84	0.84	0.44		NS	*	**	NS	*	**	*	*	NS	NS	*	NS	NS	NS
Na^+	-0.01	-0.01	-0.16	0.42	-0.37	-0.43	0.16	0.16	0.38	-0.05		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Ca^{2+}	-0.06	-0.01	-0.46	0.07	0.64	0.14	0.63	0.63	0.28	0.72	-0.45		**	NS	*	**	NS	*	NS	*	NS	NS	NS	NS
Mg^{2+}	-0.18	0.12	-0.56	0.23	0.56	0.08	0.68	0.68	0.49	0.85	-0.29	0.90		NS	*	**	NS	*	*	*	NS	NS	NS	NS
Al^{3+}	0.36	-0.45	-0.31	0.09	0.36	-0.61	0.84	0.84	0.28	0.46	0.40	0.30	0.28		**	NS	**	**	NS	NS	**	NS	NS	NS
H+Al	0.12	-0.22	-0.58	0.24	0.57	-0.44	0.92	0.92	0.54	0.74	0.21	0.67	0.68	0.87		*	**	**	NS	NS	**	NS	NS	NS
SB	-0.22	0.14	-0.67	0.34	0.57	-0.01	0.77	0.77	0.54	0.90	-0.16	0.89	0.98	0.40	0.77		*	**	*	*	NS	NS	NS	*
CTC(t)	0.23	-0.33	-0.47	0.19	0.48	-0.51	0.94	0.94	0.40	0.67	0.28	0.54	0.55	0.96	0.97	0.65		**	NS	NS	**	NS	NS	NS
CTC(T)	0.09	-0.19	-0.59	0.25	0.58	-0.42	0.92	0.92	0.55	0.77	0.19	0.69	0.71	0.85	1.00	0.80	0.96		NS	NS	**	NS	NS	NS
V	-0.51	0.50	-0.42	0.31	0.21	0.50	0.18	0.18	0.24	0.58	-0.44	0.65	0.77	-0.35	0.08	0.70	-0.07	0.13		**	NS	NS	NS	NS
m	0.54	-0.53	0.48	-0.32	-0.29	-0.43	-0.14	-0.14	-0.38	-0.57	0.44	-0.68	-0.77	0.36	-0.13	-0.71	0.07	-0.18	-0.96		NS	NS	NS	NS
Fe	-0.04	-0.05	-0.60	0.49	0.23	-0.39	0.89	0.89	0.38	0.65	0.57	0.31	0.38	0.86	0.82	0.52	0.88	0.81	-0.07	0.11		NS	NS	NS
Zn	0.40	-0.44	0.03	-0.37	0.51	-0.35	0.06	0.06	0.00	-0.10	0.23	-0.07	-0.14	0.43	0.33	-0.07	0.34	0.30	-0.52	0.42	0.12		NS	NS
Mn^{2+}	0.35	-0.35	0.19	-0.14	-0.10	0.14	0.18	0.19	0.13	0.02	-0.09	0.54	0.36	0.09	0.23	0.35	0.18	0.25	0.32	-0.29	0.11	-0.25		NS
Cu	-0.14	0.08	-0.49	-0.03	0.83	0.27	0.32	0.32	0.33	0.51	-0.14	0.65	0.63	0.16	0.52	0.65	0.34	0.54	0.41	-0.54	0.19	0.41	0.11	

co. sand (coarse sand); fi. sand (fine sand); to. sand (total sand); pH in water (proportion 1:2;5); V (Saturation Index for Bases); m (Saturation Index for Aluminum) Measured in %. C (carbon); OM (organic matter) measured in g/kg; P (phosphorus); K^+ (potassium); Na^+ (sodium) measured in mg/dm^3; Ca^{2+} (calcium); Mg^{2+} (magnesium); Al^{3+} (aluminum); H+AL (potential acidity); SB (sum of bases); CTC(t) (effective cation exchange capacity); CTC(T) (cation exchange capacity under neutral pH) measured in $cmolc/dm^3$; Fe (iron); Zn^+ (zinc); Mn^{2+} (manganese) and Cu (copper) measured in mg/dm^3; NS: non significant; *: $p \leq 0.05$; **: $p \leq 0.01$.

Table S2. Phytosociological parameters of species found in the three areas of white-sand vegetation sampled in Tupé Sustainable Development Reserve, central Brazilian Amazon. N. = number of individuals, N Par = number of parcels in wich species occurred, RDe = Relative Density, RDo = Relative Dominance, RFr = Relative Frequency, IVI = Importance Value Index. Voucher number refers to material deposited in the herbaria of Instituto Nacional de Pesquisas da Amazônia (INPA) and Instituto Federal do Amazonas (EAFM).

Family/Species	N	N Par	RDe	RDo	RFr	IVI	Voucher Number
ANACARDIACEAE							
Spondias sp.	3	2	0.08	0.06	0.46	0.60	EAFM: 11194 / 11195
Tapirira guianensis Aubl.	24	6	0.61	1.19	1.38	3.18	EAFM: 11192
Tapirira aff. *guianensis* Aubl.	12	4	0.30	0.16	0.92	1.39	EAFM: 11193
ANNONACEAE							
Annona densicoma Mart.	22	5	0.56	0.18	1.15	1.89	INPA: 262118 / 262119 / 262120 EAFM: 11207
Guatteria schomburgkiana Mart.	28	6	0.71	0.53	1.38	2.62	INPA: 262116 / 262117 EAFM: 11205 / 11206
Xylopia barbata Hoffmanns. ex Mart.	14	5	0.35	0.26	1.15	1.77	EAFM: 11204
APOCYNACEAE							
Aspidosperma excelsum Benth.	1	1	0.03	0.23	0.23	0.49	Not Collected
Aspidosperma aff. *verruculosum* Müll.Arg.	740	6	18.71	13.12	1.38	33.21	EAFM: 11073
Lacmellea arborescens (Müll.Arg.) Markgr.	32	7	0.81	0.50	1.61	2.92	INPA: 262072 / 262073 / 262074 EAFM: 11074
Macoubea sprucei (Müll.Arg.) Markgr.	28	5	0.71	0.24	1.15	2.10	INPA: 262070 / 262071 EAFM: 11069 / 11070
Malouetia cf. *flavescens* (Willd. ex Roem. & Schult.) Müll.Arg.	1	1	0.03	0	0.23	0.26	EAFM: 11072
ARALIACEAE							
Schefflera decaphylla (Seem.) Harms	20	3	0.51	0.39	0.69	1.59	INPA: 262113 / 262114 EAFM: 11201 / 11202
Schefflera umbrosa Frodin & Fiaschi	6	4	0.15	0.06	0.92	1.14	INPA: 262115 – EAFM: 11203
ARECACEAE							
Leopoldinia pulchra Mart.	2	1	0.05	0.02	0.23	0.30	Not Collected
Mauritiella armata (Mart.) Burret	41	2	1.04	1.67	0.46	3.17	Not Collected
Oenocarpus bataua Martius.	5	1	0.13	0.23	0.23	0.59	Not Collected
BURSERACEAE							
Protium hebetatum Daly	5	2	0.13	0.07	0.46	0.66	EAFM: 11141
Protium heptaphyllum (Aubl.) Marchand	50	5	1.26	0.24	1.15	2.66	INPA: 262094 / 262095 EAFM: 11139 / 11139
Protium paniculatum var. modestum Daly	336	5	8.49	5.63	1.15	15.27	INPA: 262091 / 262092 EAFM: 11135 / 11136
Protium aff. *spruceanum* (Benth.) Engl.	8	2	0.20	0.09	0.46	0.75	INPA: 262093 - EAFM: 11137
Protium sp.	6	1	0.15	0.05	0.23	0.44	EAFM: 11140
Trattinnickia burserifolia Mart.	16	7	0.40	0.25	1.61	2.27	INPA: 262090 - EAFM: 11133 / 11134
Trattinnickia sp.	1	1	0.03	0	0.23	0.26	EAFM:11132
CHRYSOBALANACEAE							
Hirtella hispidula Miq.	8	2	0.20	0.25	0.46	0.91	EAFM: 11131
Licania gracilipes Taub.	1	1	0.03	0.05	0.23	0.31	EAFM: 11130
Licania lata J.F.Macbr.	109	3	2.76	1.70	0.69	5.15	EAFM: 11128 / 11129
Licania sp.1	4	2	0.10	0.16	0.46	0.72	EAFM: 11126
Licania sp.2	1	1	0.03	0	0.23	0.26	EAFM: 11127
CLUSIACEAE							
Clusia insignis Mart.	7	4	0.18	0.29	0.92	1.39	EAFM: 10926
Clusia nemorosa G.Mey.	116	7	2.93	0.66	1.61	5.20	INPA: 262057 / 262058 - EAFM: 10927 / 10928
Clusia renggerioides Planch. & Triana	8	4	0.20	0.26	0.92	1.38	INPA: 262056 - EAFM: 10924 / 10925
Clusia aff. *spathulaefolia* Engl.	116	6	2.93	0.86	1.38	5.17	INPA: 262059 - EAFM: 10929
Tovomita acutiflora M.S. de Barros & G. Mariz	21	3	0.53	0.16	0.69	1.38	INPA: 262060 / 262061 / 262062 EAFM: 10930
COMBRETACEAE							
Buchenavia macrophylla Eichler	4	4	0.10	0.15	0.92	1.17	EAFM: 10952
Buchenavia sp.	2	1	0.05	0.04	0.23	0.32	EAFM: 10953

Table S2. Continued.

Family/Species	N	N Par	RDe	RDo	RFr	IVI	Voucher Number
DICHAPETALACEAE							
Tapura lanceolata (Ducke) Rizzini	4	2	0.10	0.11	0.46	0.67	EAFM: 10950
EBENACEAE							
Diospyros sp.	9	4	0.23	0.12	0.92	1.27	EAFM: 10933 / 10934
ELAEOCARPACEAE							
Sloanea sp.	1	1	0.03	0.04	0.23	0.30	EAFM: 11078
EUPHORBIACEAE							
Alchornea discolor Poepp.	4	2	0.10	0.02	0.46	0.58	EAFM: 11179
Aparisthmium cordatum (A.Juss.) Baill.	3	1	0.08	0.02	0.23	0.33	EAFM: 11178
Conceveiba terminalis (Baill.) Müll.Arg.	85	8	2.15	3.93	1.84	7.92	INPA: 262105 - EAFM: 11181 / 11182
Mabea subsessilis Pax & K.Hoffm.	1	1	0.03	0.01	0.23	0.27	EAFM: 11180
FABACEAE							
Abarema adenophora (Ducke) Barneby & J.W.Grimes	4	1	0.10	0.07	0.23	0.40	EAFM: 11095
Aldina heterophylla Spruce ex Benth.	170	9	4.30	28.04	2.07	34.41	EAFM: 11103 / 11104
Andira micrantha Ducke	3	2	0.08	0.07	0.46	0.61	EAFM: 11101 / 11102
Dimorphandra vernicosa Spreng. ex Benth.	30	3	0.76	0.79	0.69	2.24	INPA: 262081 / 262082 - EAFM: 11099 / 11100
Diplotropis aff. *purpurea* (Rich.) Amshoff	2	1	0.05	0.01	0.23	0.29	EAFM: 11096
Hymenolobium modestum Ducke	1	1	0.03	0.01	0.23	0.26	EAFM: 11094
Inga lateriflora Miq.	19	5	0.48	0.34	1.15	1.97	INPA: 262083 - EAFM: 11105
Macrolobium arenarium Ducke	77	5	1.95	2.23	1.15	5.33	EAFM: 11087
Macrolobium campestre Huber	1	1	0.03	0.02	0.23	0.28	EAFM: 11085
Macrolobium limbatum Spruce ex Benth.	1	1	0.03	0.01	0.23	0.26	EAFM: 11086
Ormosia costulata (Miq.) Kleinh.	5	4	0.13	0.03	0.92	1.08	EAFM: 11097 / 11098
Parkia igneiflora Ducke	64	6	1.62	1.23	1.38	4.23	EAFM: 11092
Swartzia lamellata Ducke	23	5	0.58	0.50	1.15	2.23	EAFM: 11088 / 11089
Swartzia tessmannii Harms	105	7	2.65	1.85	1.61	6.11	INPA: 262080 - EAFM: 11090 / 11091
Tachigali glauca Tul.	1	1	0.03	0	0.23	0.26	EAFM: 11093
HUMIRIACEAE							
Humiria balsamifera (Aubl.) J.St.-Hil.	20	4	0.51	1.71	0.92	3.14	EAFM: 11184
Sacoglottis sp.	3	2	0.08	0.08	0.46	0.62	EAFM: 11185
ICACINACEAE							
Discophora guianensis Miers	10	3	0.25	0.09	0.69	1.03	INPA: 262077 / 262078 / 262079 EAFM: 11082
LAMIACEAE							
Vitex triflora Vahl	57	7	1.44	1.6	1.61	4.66	EAFM: 10946
LAURACEAE							
Aniba hostmanniana (Nees) Mez	1	1	0.03	0.01	0.23	0.27	EAFM: 11159
Aniba santalodora Ducke	32	6	0.81	1.20	1.38	3.39	INPA: 262099 - EAFM: 11160 / 11161
Endlicheria arenosa Chanderb.	43	5	1.09	0.28	1.15	2.52	INPA: 262100 - EAFM: 11162
Licaria aff. *chrysophylla* (Meisn.) Kosterm.	1	1	0.03	0.03	0.23	0.28	EAFM: 11174
Licaria sp.1	8	2	0.20	0.20	0.46	0.86	INPA: 262104 - EAFM: 11177
Licaria sp.2	1	1	0.03	0.02	0.23	0.27	EAFM: 11175
Licaria sp.3	1	1	0.03	0.01	0.23	0.26	EAFM: 11176
Ocotea aciphylla (Nees & Mart.) Mez	25	5	0.63	0.92	1.15	2.70	EAFM: 11165 / 11166
Ocotea amazonica (Meisn.) Mez	19	3	0.48	0.15	0.69	1.32	EAFM: 11169 / 11170
Ocotea oblonga (Meisn.) Mez	2	1	0.05	0.02	0.23	0.30	EAFM: 11168
Ocotea olivaceae A.C.Sm.	1	1	0.03	0.01	0.23	0.26	EAFM: 11167
Ocotea sp.1	16	6	0.40	0.08	1.38	1.87	INPA: 262101 / 262102 / 262103 EAFM: 11171
Ocotea sp.2	1	1	0.03	0.01	0.23	0.27	EAFM: 11163
Ocotea sp.3	3	1	0.08	0.02	0.23	0.32	EAFM: 11164

Table S2. Continued.

Family/Species	N	N Par	RDe	RDo	RFr	IVI	Voucher Number
LECYTHIDACEAE							
Allantoma decandra (Ducke) S.A.Mori et al.	3	1	0.08	0.14	0.23	0.45	EAFM: 10951
LINACEAE							
Hebepetalum humiriifolium (G.Planch.) Benth.	8	2	0.20	0.15	0.46	0.81	EAFM: 11066 / 11067
Roucheria columbiana Hallier	10	3	0.25	0.10	0.69	1.04	INPA: 262069 - EAFM: 11068
MALPHIGUIACEAE							
Byrsonima laevis Nied.	34	5	0.86	0.47	1.15	2.48	INPA: 262064 - EAFM: 10937 / 10938 / 10940
Byrsonima aff. *laevis* Nied.	32	3	0.81	0.49	0.69	1.99	INPA: 262065 - EAFM: 10939 / 10941
MALVACEAE							
Pachira faroensis (Ducke) W.S.Alverson	6	2	0.15	0.43	0.46	1.04	INPA: 262068 - EAFM: 10947 / 10948
Scleronema micranthum (Ducke) Ducke	6	3	0.15	0.20	0.69	1.04	EAFM: 10949
MELASTOMATACEAE							
Henriettea maroniensis Sagot	2	1	0.05	0.01	0.23	0.29	INPA: 262112 - EAFM: 11199
Melastomatacea sp.	1	1	0.03	0.02	0.23	0.28	EAFM: 11200
Miconia argyrophylla DC.	58	6	1.47	0.30	1.38	3.15	INPA: 262109 / 262110 / 262111 EAFM: 11196
MELIACEAE							
Trichilia sp.	1	1	0.03	0	0.23	0.26	EAFM: 11125
MORACEAE							
Brosimum guianense (Aubl.) Huber	6	3	0.15	0.06	0.69	0.91	INPA: 262084 / 262085 EAFM: 11107 / 11108
Brosimum sp.	1	1	0.03	0	0.23	0.26	EAFM: 11106
Ficus greiffiana Dugand	6	5	0.15	0.25	1.15	1.55	INPA: 262087 - EAFM: 11112
Ficus mathewsii (Miq.) Miq.	1	1	0.03	1.03	0.23	1.29	EAFM: 11111
Ficus paraensis (Miq.) Miq.	1	1	0.03	0	0.23	0.26	EAFM: 11110
Ficus sp.	1	1	0.03	0.83	0.23	1.08	INPA: 262086 - EAFM: 11109
Helicostylis scabra (J.F.Macbr.) C.C.Berg	1	1	0.03	0.01	0.23	0.26	EAFM: 11113
MYRISTICACEAE							
Iryanthera sp.	1	1	0.03	0.01	0.23	0.26	EAFM: 11114
Virola calophylla Warb.	1	1	0.03	0.01	0.23	0.26	EAFM: 11115
Virola pavonis (A.DC.) A.C.Sm.	2	1	0.05	0.16	0.23	0.45	EAFM: 11116
MYRTACEAE							
Eugenia moschata (Aubl.) Nied. ex T.Durand & B.D.Jacks.	2	2	0.05	0.01	0.46	0.52	EAFM: 11214
Eugenia sp.1	1	1	0.03	0	0.23	0.26	EAFM: 11215
Eugenia sp.2	1	1	0.03	0.01	0.23	0.26	EAFM: 11216
Marlierea caudata McVaugh	2	1	0.05	0.02	0.23	0.30	EAFM: 11217
Myrcia aff. *amazonica* DC.	2	2	0.05	0.11	0.46	0.62	INPA: 262121 - EAFM: 11210
Myrcia sp.1	2	2	0.05	0.01	0.46	0.53	EAFM: 11212
Myrcia sp.2	1	1	0.03	0.01	0.23	0.27	EAFM: 11213
NYCTAGINACEAE							
Guapira sp.	17	6	0.43	0.34	1.38	2.15	INPA: 262107 - EAFM: 11187 / 11188
OCHNACEAE							
Ouratea spruceana Engl.	17	6	0.43	0.11	1.38	1.92	INPA: 262108 - EAFM: 11190 / 11191
OLACACEAE							
Dulacia candida (Poepp.) Kuntze	29	5	0.73	0.20	1.15	2.08	INPA: 262063 - EAFM: 10935 / 10936
OPILIACEAE							
Agonandra aff. *silvatica* Ducke	1	1	0.03	0.03	0.23	0.28	EAFM: 11065
PERACEAE							
Pera bicolor (Klotzsch) Müll.Arg.	8	4	0.20	0.22	0.92	1.34	INPA: 262106 - EAFM: 11183

Table S2. Continued.

Family/Species	N	N Par	RDe	RDo	RFr	IVI	Voucher Number
PRIMULACEAE							
Cybianthus guyanensis (A.DC.) Miq.	7	2	0.18	0.04	0.46	0.68	INPA: 262075 / 262076 EAFM: 11080 / 11081
Cybianthus sp.	21	5	0.53	0.34	1.15	2.02	EAFM: 11079
Rhizophoraceae							
Sterigmapetalum colombianum Monach.	27	6	0.68	0.54	1.38	2.61	EAFM: 11186
RUBIACEAE							
Duroia saccifera (Schult. & Schult.f.) K.Schum.	37	5	0.94	0.24	1.15	2.33	INPA: 262125 / 262126 / 262127 / 262128
Kutchubaea oocarpa (Spruce ex Standl.) C.H.Perss.	4	2	0.10	0.02	0.46	0.58	INPA: 262131 / 262132 EAFM: 11228 / 11229
Kutchubaea sericantha Standl.	110	7	2.78	1.17	1.61	5.56	INPA: 262129 / 262130 EAFM: 11226 / 11227
Pagamea duckei Standl.	217	7	5.49	1.19	1.61	8.29	INPA: 262123 / 262124 EAFM: 11220 / 11221
Pagamea guianensis Aubl.	3	2	0.08	0.04	0.46	0.57	INPA: 262122 - EAFM: 11218
SAPINDACEAE							
Matayba inelegans Spruce ex Radlk.	4	2	0.10	0.02	0.46	0.58	INPA: 262088 / 262089 EAFM: 11118 / 11119
Matayba opaca Radlk.	59	7	1.49	0.61	1.61	3.72	EAFM: 11120
Matayba sp.	2	1	0.05	0.01	0.23	0.29	EAFM: 11117
Talisia firma Radlk.	8	3	0.20	0.08	0.69	0.97	EAFM: 11121 / 11122
Talisia ghilleana Acev.-Rodr.	4	2	0.10	0.02	0.46	0.58	EAFM: 11123
Vouarana guianensis Aubl.	2	2	0.05	0.01	0.46	0.52	EAFM: 11124
SAPOTACEAE							
Chrysophyllum cuneifolium (Rudge) A.DC.	30	4	0.76	0.31	0.92	1.99	INPA: 262098 - EAFM: 11154
Chrysophyllum sanguinolentum (Pierre) Baehni	24	6	0.61	0.62	1.38	2.61	EAFM: 11153
Chrysophyllum sp.	1	1	0.03	0.04	0.23	0.30	EAFM: 11152
Manilkara bidentata (A.DC.) A.Chev.	129	8	3.26	4.02	1.84	9.13	EAFM: 11157 / 11158
Micropholis aff. *guyanensis* (A.DC.) Pierre	1	1	0.03	0	0.23	0.26	EAFM: 11155
Pouteria cuspidata (A.DC.) Baehni	1	1	0.03	0.02	0.23	0.27	EAFM: 11149
Pouteria aff. *cuspidata* (A.DC.) Baehni	2	1	0.05	0.11	0.23	0.40	EAFM: 11148
Pouteria aff. *elegans* (A.DC.) Baehni	80	5	2.02	1.64	1.15	4.82	INPA: 262096 - EAFM: 11142 / 11143
Pouteria oblanceolata Pires	23	3	0.58	0.63	0.69	1.90	INPA: 262097 / EAFM: 11150
Pouteria sp.1	20	5	0.51	0.35	1.15	2.01	EAFM: 11144 / 11145
Pouteria sp.2	1	1	0.03	0.03	0.23	0.28	EAFM: 11146
Pouteria sp.3	1	1	0.03	0.01	0.23	0.27	EAFM: 11147
Pradosia schomburgkiana (A.DC.) Cronquist	70	7	1.77	0.98	1.61	4.36	EAFM: 11156
Sapotaceae sp.	1	1	0.03	0.20	0.23	0.46	Not Collected
SIMAROUBACEAE							
Simaba guianensis Aubl.	91	6	2.30	3.21	1.38	6.89	EAFM: 10942
Simarouba amara Aubl.	48	7	1.21	1.66	1.61	4.49	INPA: 262066 - EAFM: 10943 / 10944
URTICACEAE							
Coussapoa asperifolia Trécul	1	1	0.03	0.01	0.23	0.26	EAFM: 11077
VOCHYSIACEAE							
Vochysia sp.	1	1	0.03	0.01	0.23	0.26	EAFM: 11189