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NÍVEL DO LENÇOL FREÁTICO É UM MELHOR PREDITOR QUE NUTRIENTES PARA ASSEMBLEIAS DE PLANTAS VASCULARES EM UMA FLORESTA DE TERRA FIRME NA AMAZÔNIA

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Manaus, Amazonas
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Manaus, Amazonas

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RESUMO

Muitas espécies podem co-ocorrer ao longo do mesmo gradiente, mas a associação espécie-habitat pode ser mais ou menos forte de acordo com o efeito que o gradiente exerce no desempenho das espécies. Essa associação comumente leva à especialização ecológica que, em plantas, envolve fatores abióticos como nutrientes e água. Nesse trabalho nós investigamos como os gradientes hídrico (Altura acima da drenagem mais próxima - HAND) e fertilidade (teor de fósforo e soma de bases K^+, $Ca2^+$ e $Mg2^+$) restringem a distribuição de espécies de seis formas de vida de comunidades vegetais em uma floresta tropical na Amazônia Central. Nossa hipótese é que as formas de vida de maior biomassa devem ser menos especializadas com base na profundidade e extensão da raiz e que os nutrientes restringem mais as espécies do que a água, uma vez que nutrientes são mais limitantes que a disponibilidade de água. Estimamos a especialização de cada espécie comparando os valores observados de ocorrência ao longo dos gradientes, com distribuição esperada pelo modelo nulo. Para comparação entre gradientes e formas de vida, calculamos o efeito padronizado (SES – Standard Effect Size) de cada espécie para cada gradiente. Usamos o SES como variável dependente em dois GLMMs. No primeiro comparamos os valores de SES para cada gradiente (variável dependente) entre as formas de vida (variável independente). No segundo GLMM comparamos os valores de SES de cada forma de vida (variável dependente) entre os 3 gradientes (variáveis independentes). Nos dois modelos a família foi declarada como variável randômica para controlar o número de espécies entre formas de vida A água restringiu mais as espécies de plantas - principalmente samambaias - do que a fertilidade. O gradiente de fósforo restringiu mais as espécies do que as bases, mas ambos restringiram mais as lianas e as palmeiras, comparado com outras formas de vida. Embora os nutrientes sempre tenham sido considerados o maior determinante para a distribuição de espécies de plantas na Amazônia, o HAND pode ser mais importante em mesoescala. Além disso, as formas de vida podem responder de forma diferente dependendo da escala dos gradientes edáficos analisados, não necessariamente seguindo o padrão baseado na profundidadedas raizes.

PALAVRAS-CHAVE: especialização ecológica; especificidade do habitat; ecologia da comunidade; tamanho de efeito padrão; Amazônia Central; formas de vida; fertilidade do solo; altura acima da drenagem mais próxima; fósforo; soma de bases.

ABSTRACT

Many species can co-occur in the same habitat, but species-habitat association can be tighter or looser depending on the gradient effect on the species performance. This association commonly leads to ecological specialization that, in plants, involves abiotic factors such as nutrients and water availability. Here we investigated how hydric (Height above the nearest drainage - HAND) and fertility (phosphorus content and the sum of K+, Ca2+ and Mg2+) gradients constrain the distribution of species from six life forms of plant communities in a tropical forest in the Central Amazon. We hypothesized greater biomass life forms would be less specialized based on root depth and span and that nutrients would constrain species more than water since the soils are poor. We estimated the specialization by comparing the observed values of occurrence along the gradients, with distribution expected by the null model for each species. To compare gradients and life forms, we calculated the standard effect (SES) of each species for each gradient. We used SES as the dependent variable in two GLMMs. In the first, we compared the SES values for each gradient (dependent variable) between life forms (independent variable). In the second GLMM we compared the SES values of each life form (dependent variable) among the 3 gradients (independent variables). In both models the family was declared as a random variable to control the number of species among life forms. Water constrained species more – mainly ferns – than fertility. The phosphorus gradient constrained more species than bases, but both constrained lianas and palms the most. Although nutrients have always been considered the greatest determinant to plant species distribution in the Amazon forests, HAND may have the same or even more important at mesoscale. Also, life forms may respond differently depending on the scales of the edaphic gradients analyzed, not necessarily following the pattern based on root depth.

KEY WORDS: ecological specialization; habitat specificity; community ecology; standard effect size; Central Amazon; life forms; soil fertility; height above the nearest drainage; phosphorus; sum of bases.

SUMÁRIO

INTRODUÇÃO GERAL

Florestas tropicais abrigam mais de 75% da diversidade de espécies de plantas e animais conhecidos (Barlow et al. 2018) e mais da metade delas constituem o Bioma Amazônico (Whitmore 1997), que é considerado um centro de biodiversidade (Barlow et al. 2018, Jenkins et al. 2013, Guénard et al. 2012, Kier et al. 2005). Entender os mecanismos e processos que geraram essa diversidade é foco constante de pesquisas (e.g. Cracraft 1985, Mayr e O'Hara. 1986, Schnitzer e Carson 2001). Frequentemente gradientes abióticos, em especial o topográfico, são usados para explicar a distribuição dos táxons em escala local em ambientes tropicais (e.g. Capaverde-Jr et al. 2018; Vasconcelos et al. 2010, Laurance et al. 2010).

O gradiente topográfico na Amazônia Central envolve os gradientes hídrico e de fertilidade, frequentemente correlacionados a altitude e elevação (Castilho et al. 2006). Uma das variáveis de fertilidade de solo é a concentração de fósforo (e.g. Quesada et al. 2010, 2012), nutriente escasso nos solos amazônicos da porção central e não correlacionado com a altitude localmente (Castilho et al. 2006). O fósforo é um elemento essencial biologicamente, pois é um dos constituintes das moléculas de DNA e ATP (Raaimakers et al. 1995). As plantas adquirem esse nutriente sobretudo pela decomposição da matéria orgânica de fonte vegetal, tal como a serrapilheira (Quesada et al. 2012), o que faz do fósforo um nutriente limitante para as plantas.

A soma de bases é outra variável comumente usada em estudos que relacionam a distribuição de plantas com a fertilidade do solo (e.g. Tuomisto et al. 1996). Essa variável é a soma de diversos cátions de macronutrientes, como cálcio, magnésio e potássio. Tais elementos conferem fertilidade ao solo através do aumento da capacidade de liberação de outros nutrientes aos quais esses cátions podem se ligar e torná-los absorvíveis pelas plantas (Ronquim 2010). Assim como o fósforo, esses nutrientes são restituídos no solo pela matéria orgânica vegetal, produzida majoritariamente por espécies maiores, tais como as árvores (Paoli and Curran 2007). A soma de bases tem relação positiva com a biomassana Amazônia (Laurance et al. 1999) e com o gradiente hídrico na Reserva Ducke (Castilho et al. 2006). Portanto, essa variável está relacionada com outras que constituem o gradiente topográfico na Amazônia, localmente ou em larga escala.

O gradiente hídrico é frequentemente relacionado à topografia na Amazônia Central e, mais recentemente, variáveis em escalas mais finas foram criadas para tornar a relação entre as espécies de plantas e a água mais acurada (veja Rennó et al. 2008). Uma dessas variáveis é a distância vertical até o corpo d'água mais próximo (HAND – Height Above the Nearest Drainage), calculada por um algorítmo desenvolvido por Rennó et al. (2008). Esse algoritmo se baseia no modelo de elevação digital e na Missão Topográfica Radar Shuttle para calcular valores de HAND a partir da distância vertical entre pontos no terreno e a drenagem mais próxima. HAND já foi correlacionado com as condições hidrológicas de terrenos e o nível do lençol freático (Nobre et al. 2011, Rennó et al. 2008), além de ter se mostrado um bom preditor para a distribuição de espécies vegetais na Reserva Ducke (Schietti et al. 2013). Apesar do HAND e de outros gradientes já possuírem relações conhecidas com a distribuição de muitos *taxa* na Amazônia Central, pouco se sabe sobre a especialização de espécies vegetais em escala local.

A restrição de ocorrência de uma espécie, frequentemente denominada especialização de habitat, pode ser caracterizada pela maior ocorrência dessa espécie em um intervalo de um dado gradiente do que seria o esperado ao acaso (e.g. Mallis e Hurd 2005). Existem diversas formas de calcular a restrição dos organismos ao longo de um gradiente (Fox e Morrow 1981, Wilson e Yoshimura 1994, Bolnick et al. 2002, Chazdon et al. 2011, Stireman et al. 2017) e a maioria usa valores de abundância (e.g. Chazdon et al. 2011, Draper et al. 2019). Mapear o grau de restrição das espécies ao longo de gradientes pode contribuir para o entendimento dos mecanismos que moldam a distribuição e ocorrência das espécies localmente (Clark et al. 1999). Medidas de restrição de ocorrência das espécies também são importantes para prever efeitos de perturbações (e.g. Tylianakis et al. 2007), além de diretamente usadas em ações de manejo e conservação.

Ecossistemas tropicais são constituídos majoritariamente por espécies infrequentes (Stevens 1989), fator que impede a investigação confiável da restrição de *taxa* pouco abundantes. Neste trabalho, propomos um método para avaliar a restrição de espécies tropicais, o qual pode ser aplicado a comunidades com muitas espécies pouco frequentes. Investigamos como os gradientes hídrico e edáfico (nutrientes do solo) afetam a restrição de ocorrência das espécies de plantas em uma floresta tropical de terra firme. Esperamos que 1. As formas de vida maiores quanto à biomassa (árvores e trepadeiras) sejam menos restritas em todos os gradientes, dado que possuem caracteres morfológicos que permitem acessar água (Nepstad et al. 2007) e nutrientes mais facilmente que as menores (i.e. ervas); 2. As demais formas de vida (i.e. palmeiras, ervas e arbustos) estejam distribuídas entre esses dois extremos, não apresentando padrões consistentes de restrição e; 3. Os gradientes de fertilidade restrinjam mais grupos que o gradiente de água, dado que os solos da Amazônia

Central são considerados pobres em nutrientes e a estação seca abrange somente um quarto do ano, diminuindo o déficit hídrico.

OBJETIVOS

Objetivo Geral

Entender como três gradientes ambientais (um hídrico e dois de fertilidade do solo) afetam a restrição das espécies de plantas de uma floresta de terra firme na Amazônia Central.

Objetivos Específicos

1. Investigar as diferenças na restrição das espécies entre formas de vida para cada um dos três gradientes (hídrico e de fertilidade do solo) e,
2. Investigar as diferenças na restrição das espécies entre os gradientes (hídrico e de fertilidade do solo) para cada forma de vida.

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CAPÍTULO ÚNICO

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Water-table level is a better predictor than nutrients of vascular plant assemblages in an Amazonian *terra-firme* forest

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ABSTRACT

Many species can co-occur in the same habitat, but species-habitat association can be tighter or looser depending on the gradient effect in species performance. This association commonly leads to ecological specialization that, in plants, involves abiotic factors such as nutrients, water availability and light. Here we investigated how hydric (Height above the nearest drainage - HAND) and fertility (phosphorus content and the sum of K+, Ca2+ and Mg2+) gradients constrain the distribution of plant species from six life forms in a tropical forest in the Central Amazon. We hypothesized that life forms with greater biomass would be less specialized based on root depth and span and nutrients would constrain more species than water since the soils are poor. We estimated the specialization by comparing the observed values of occurrence along the gradients, with distribution expected by the null model for each species. To compare gradients and life forms, we calculated the standard effect size (SES) of each species for each gradient. We used SES as the dependent variable in two GLMMs. In the first, we compared the SES values for each gradient (dependent variable) between life forms (independent variable). In the second GLMM we compared the SES values of each life form (dependent variable) among the 3 gradients (independent variables). In both models the family was declared as a random variable to control the number of species among life forms. Water constrained more species, mainly ferns,than fertility. The phosphorus gradient constrained more species than bases, but constrained both lianas and palms the most. Although nutrients have always been considered the greatest determinant of plant species distribution in the Amazon, HAND may have the same or even more important at mesoscale. Also, life forms may respond differently tothe edaphic gradients analyzed,depending on the scale and not necessarily following a pattern based on root depth.

KEY WORDS: ecological specialization; habitat specificity; community ecology; standard effect size; Central Amazon; life forms; soil fertility; height above the nearest drainage; phosphorus; sum of bases.

INTRODUCTION

Spatial structure in ecological communities can be driven by dispersal processes, mortality rates, social behavior and environmental heterogeneity (Hubbell 2000, Soininen 2016). Habitat heterogeneity encompasses the individual's needs, such as breeding and food resources, and the abiotic conditions it can thrive (Futuyma and Moreno 1988). These needs and tolerances lead their species to an environmentally induced spatial dependence (Cottenie 2005, Peres-Neto and Legendre 2010) that can result in an ecological specialization to certain levels of resources and environmental conditions (Forister et al. 2012).

Specialization, and habitat specialization, is a framework of measures and concepts constantly redefined in ecological literature (Ferry-Graham et al. 2002, Devictor et al. 2010). The niche concept of Grinnell (1917) considers a species' responses to a specific set of variables (e.g. resources). Other specialization measures make use of the niche concept (MacArthur 1972) that accounts for evolutionary trade-offs between the exploitation of various resources and the use of a limited subset (the hypothesis of the "jack-of-all-trades, master of none"). Low abundance or absence of a species at some point in the gradient may indicate that it has poor capacity to deal with those resource values (see Draper et al. 2019). Different species can co-occur in the same habitat, but the effect of each local resource on plant performance varies among species, resulting in tighter or looser associations to the habitat (Whittaker 1972).

Vagile taxa, such as most animals, use various strategies to maximize foraging andimproved dispersion, decreasing the impact of habitat heterogeneity on their survival (Brown 1999). Sessile organisms can be more constrained by resource limitation and competition, because low dispersal rates increase compositional differences among sites (Amarasekare and Nisbet 2001), leading to a stronger association with the environment (De Bie et al. 2012). Terrestrial plants disperse only reproductive material and rely mainly on abiotic factors, such as light, nutrients and water from the soil (Connell 1978), and are more likely to be constrained by the environment than other taxa because they are less affected by the homogenizing effect of dispersal (Leiboldet al. 2004). Therefore, terrestrial plants may show specialization over a variety of gradients.

Vascular plant communities are known to be associated with elevational gradients (Stevens 1992, Clark et al. 1995, Bachman et al. 2004, Brunn et al. 2006), especially in tropical systems (Lieberman et al. 1985, Tuomisto and Poulsen 2000, Vormisto et al. 2004, Costa et al. 2009). Elevational gradients are commonly used as surrogates of other important variables, such as soil fertility and water. Depending on terrain elevation, hydrological conditions segregate species distributions by their capacity to deal with drier or wetter areas (Silvertown 1999, Tuomisto and Poulsen 2000, Rodriguez-Iturbe 2000, Costa et al. 2005, 2009). Habitat heterogeneity created by seasonal droughts and floods (Arshad et al. 1996, Ferry et al. 2010) can confine species that are unable to deal with stress caused by drier soils inhigher areas (Costa et al. 2005, 2008) and species unable to withstand the waterlogging, and consequent anoxia in lower areas (Piedade et al. 2010).

In the Amazon, the elevational gradient is highly related to edaphic variation (Quesada et al. 2012). In the Peruvian Amazon (Western portion) soils in lower areas have high clay and nutrient content, and sandy soils in higher areas are poor in nutrients (Vormisto et al. 2000). This pattern is reversed in Central Amazonia, where clayey soils on plateaus are richer in nutrients and poorer sandy soils are confined to the valleys (Castilho et al. 2006). Soils in central Amazonia are relatively old (Fittkau 1971, Quesada et al. 2012) and weathering has resulted in the loss of many nutrients, such as phosphorus and base cations (Walker and Syers, 1976). Phosphorous is generally thought to be the most limiting nutrient for primary production, as it is essential in photosynthesis, and in structuring ATP and DNA molecules (see Raaimakers et al. 1995). While phosphorus is not correlated with some altitudinal gradients, the sum of base cations is highly correlated with altitude, soil pH and water, being locally more abundant in clay soils of higher areas in the Central Amazon (Castilho et al. 2006). Valleys normally have more available water than higher areas, where the water table is deeper (Daws et al. 2002, Brown et al. 2004). Nevertheless, because of local geomorphological arrangements, even high-altitude areas far from streams in cartographic distance can be close to the water table in the Central Amazon (Rennó et al. 2008, Schietti et al. 2013). Although many associations between plant communities and abiotic gradients have been documented in the Amazon, it remains unclear to what extent fertility and water availability constrain plant-species distributions.

Different plant life forms may differ in sensitivity to resource gradients due to their different dispersal modes (Costa et al. 2005, Zuquim et al. 2019). Also, functional or taxonomic groups are frequently used as environmental indicators or predictor of other plant groups (see Landeiro et al. 2012 and Zuquim et al. 2014, 2019) though differences in specialization between life forms are rarely compared. Here, we investigated how hydric and fertility gradients constrain the distribution of vascular plant communities in a lowland tropical forest at a mesoscale (1-100 km^2). We also identified the most specialized life form in each of the gradients, as well as the most constraining gradient for each life form, as these indices can be used to explore different facets of species specialization (Forister et al. 2012). We hypothesized that trees and lianas would be more generalists than other taxa because they have greater root depth and span (Nepstad et al. 2007, Saleska et al. 2007, Metcalfe et al. 2008). A greater distribution of roots (Lynch 1995) may allow trees to access deeper soil horizons than shallow-rooted plants, giving them greater access to available water (Nepstad et al. 2007) and soil nutrients. Because herbs are generally shallow-rooted and have short life spans, we hypothesized that they would be proportionally more specialist species. We expected the other groups to be spread in the interval between these extremes because they are generally considered to be intermediate in root depth and span. Additionally, we expected that fertility gradients would constrain more groups than water availability, because soils in the Central Amazon are poor in nutrients and precipitation seasonality is less marked than other tropical regions.

METHODS

Study Area

Ducke Reserve is located north the city of Manaus (2º55’ 47.80’’S; 59º58’ 30.34’’W at the reserve headquarters), in the Brazilian Amazon (Fig. 1). The Reserve covers 100 km² of lowland evergreen tropical forest with a 30-37 m closed canopy and emergent trees reaching more than 40 m (Ribeiro et al. 1999). A survey system in a grid format covering 64 km² with 72 permanent plots at least 1 km distant from each other and from the Reserve border was installed in the area in 2000. Surveys were made along the entire length of the 250-m long plot center line in each plot (Costa and Magnusson 2010). The plots are regularly spaced and the center lines follow topographic contour lines in order to minimize within-plot edaphic variation, which varies with altitude (Chauvel and Boulet., 1987, Costa et al. 2005).

The topography is representative of that found in Central-Amazonian lowland forests (30-120 m a.s.l.) and three zones have been distinguished: plateaus, valleys and slopes (Fig. 1). The plateaus are mostly composed by Oxisols (allic yellow latosols in the Brazilian classification system), which are richer in nutrients and clay content. The valleys have spodosols (Chauvel and Boulet 1987, Bravard and Righi 1989) that are sandy, poorer in nutrients and strongly leached in the surface layer. The slopes are generally intermediate between plateaus and valleys, with ultisols (podzol in the Brazilian classification system). In general, all the soils are acidic and poor in essential nutrients, such as phosphorus and potassium (Chauvel and Boulet 1987, Bravard and Righi 1989).

The Reserve has a dense network of streams; eastern streams flow to the Amazon River and those in the western drainage to the Negro River. The streams are of first to third order, some up to 10 m wide. The vertical distance to the nearest drainage in the 72 plots ranges from 1-53 m (Schietti et al. 2013). The Reserve is not under direct influence of large rivers overflow , but the valleys may be waterlogged for a few hours in the rainy season due to their proximity to the water table.

The annual means of temperature and rainfall at the Reserve, both measured between the years of 1965 and 1980, were 26ºC and ca. 2400 mm, respectively. Mean monthly rainfall reach a minimum in August with less than 100 mm and a maximum in March with about 350 mm (Marques-Filho et al. 1981). The dry season occurs from July to September when monthly rainfall is lower than 100 mm (Marques-Filho et al. 1981).

Floristic data

Many studies investigating floristic inventories have been done at Ducke Reserve, each focusing on one life form. We compiled six datasets from trees, shrubs, lianas, palms, non-fern herbs and ferns (Kinupp and Magnusson 2005, Costa et al. 2005, 2009, Castilho et al. 2006, Nogueira et al. 2006). Some samples were taken in all 72 uniformly-distibuted plots inthe Reserve, but only 22 plots were sampled for all life forms (Appendix S1: Figure S1). The sampling period differed among these studies, ranging from 2001 for herbs and ferns to 2006 for lianas. Details on the sampling protocols can be found in Schietti et al. (2013).

Environmental data

We used soil fertility and soil-water availability to calculate habitat specialization. We used phosphorus and sum of bases (the sum of K^+, Ca^{2+} and Mg^{2+}) as fertility measures, since P is the most critical nutrient determining plant growth (Quesada et al. 2012) and the sum of bases is strongly related to both regional and local plant diversity (Clark et al. 1995, Vormisto et al. 2004, Castilho et al. 2006, John et al. 2007, Costa et al. 2009). The soil was sampled 5 cm deep in six points along the plot axis every 50 m. These samples were bulked into a single composite sample per plot and cleaned of roots and detritus, air-dried and sieved through a 2 mm mesh. After that, the soil samples were chemically analyzed for the nutrients at the Soil Laboratory of EMBRAPA-Manaus (see EMBRAPA, 1997 and Castilho et al. 2006).

Height above the nearest Drainage (HAND) is defined here as the vertical relative draining potential, which may reflect the amount of water available to plant roots (Schietti et al. 2013). The HAND algorithm used was developed by Rennó et al. (2008), which uses the vertical distance between points on the terrain and the closest drainage, based on a digital elevation model. Under the gravitational potential, water can infiltrate the soil or moves downhill on the surface when soil is waterlogged, flowing to a stream. The algorithm measures the water net capacity to drain from an elevated position to the nearest drainage channel (Nobre et al. 2011). High HAND values mean greater draining potential and low HAND values mean proximity to the water table, frequently causing short-term waterlogging, especially after heavy rains. More details on the HAND calculation can be found in Nobre et al. (2011) and Rennó et al. (2008) for the Amazon and Schietti et al. (2013) for its validation at Ducke Reserve.

Data analysis

We calculated habitat specialization separately for three different abiotic gradients in the Ducke Reserve. Concentration ($mg. kg^{-1}$) of phosphorus and sum of bases were used as fertility gradients and HAND (meters above ground) as a proxy of soil-water availability.

The concept of habitat specialization is frequently related to the range of some resource or environmental variable, such as soil fertility, water availability or hosts for parasites, in which the species occur (e.g. Prudic et al. 2005, Costa et al. 2005). As the number of occupied sites increases, the range of the environmental variables where a given species occurs also increases (Brown 1984). Therefore, independent of habitat specificity, more occurrences in different sites would mean greater habitat occupation (Clark et al. 1999). To account for this relationship, we defined habitat specialization as the occurrence of a species in a narrower range in a given gradient than expected by chance. We used a resampling procedure to determine the variation in habitat variables expected to be found in occupied sites when the null hypothesis (no habitat specificity) was true (Kinupp and Magnusson 2005). For each species, we randomly sampled the survey sites and determined the weighted standard deviations of phosphorus (WSD_P), sum of bases (WSD_B) and HAND (WSD_H).The standard deviation was weighted by the number of individuals sampled in plots. We only considered species that occured in three or more plots. Even though all Ducke Reserve sites could potentially harbor all life forms of our dataset, life forms were collected at different numbers of sites. Therefore, we opted for a more conservative view, randomly sampling the abundances of species only in the sites that the given life form was surveyed. This process was repeated 999 times for each species.

We used the Standard Effect Size (SES) (Gotelli and McCabe 2002) as a measure of the Ecological Specialization for each species in each gradient. The Ecological Specialization (SES) measures the weighted standard deviations of the observed values that are above or below the weighted standard deviations of the null model (i.e. simulated community data):

$$ES\ (SES) = \frac{Wsd_{obs} - \overline{Wsd}_{null}}{\sigma_{Wsd\ null}},$$

where Wsd_{obs} corresponds to the weighted standard deviation calculated from the observed data, $\overline{\mathrm{Wsd}}_{null}$ corresponds to the mean of the weighted standard deviations calculated by the randomization and $\sigma_{\mathrm{Wsd}_{null}}$ corresponds to the standard deviation of the null weighted standard deviations. Values of zero indicate no differences between observed distribution of plant species and null models, while positive and negative values mean indicate that species are less or more specialized than expected by chance, respectively. Species with positive and zero SES values were considered generalists and negative SES values indicate specialist species. Three Ecological Specialization (SES) values were obtained per species: one for each of abiotic gradients investigated.

We fitted a generalized linear mixed model (GLMM) using the ES (SES) per species for each gradient as dependent variable and life forms (trees, shrubs, lianas, palms, non-fern herbs and ferns) as independent variable, since these groups are consistent in life history, phylogeny and biology. We also compared the SES values of each life form among the 3 gradients. In both models the family was declared as a random variable to control the number of species among life forms, since the number of taxa differs greatly among life forms (e.g. trees correspond to 81% of all species). We also conducted *post-hoc* tests to compare the Ecological Specialization (SES) between life forms using “single step” adjustment for P-values (Bretz et al. 2010). We calculated P-values for each species using Wsd_{obs} and Wsd_{null} to assess the proportion of each life form was more different than expected by chance. GLMM models were created with the *lme4* package (Bates *et al.*, 2015), and graphed using *ggplot2* (Wickham 2016) package in R (R core team 2018).

RESULTS

The Ecological Specialization (SES) was calculated for 723 trees, 32 shrubs, 28 lianas, 32 palms, 47 non-fern herbs and 16 ferns, totaling 875 species or morphospecies of vascular plants. These species were distributed in plots where the gradients of HAND varied from 1.44 to 52.4m, the sum of bases from 0.021 to 1.04 cmol/kg and phosphorus from 1 to 12 cmol/kg.

Considering plant species of all life forms, 65.71 % of species were more specialized than expected by chance ($p<0.05$) in at least one abiotic gradient. HAND gradient, followed by sum of bases and phosphorus, had a higher number of specialist species with 23.2 % of specialist plant species. The sum of bases gradient had 21.48 % and phosphorus gradient 21.03 % of more specialized species.

There was a difference in the degree of specialization of plant species between plant life forms (Fig. 2). For the HAND gradient, ferns and lianas species had on average the lowest negative values of SES, while herbs and trees had the highest values (Fig. 2A). Ferns were the most constrained life form by HAND gradient, differing from less constrained life forms like herbs and trees (Fig. 2A). For the sum of bases gradient, lianas and palms had the lowest values of SES, differing only from ferns that had the highest values of SES (Fig. 2B). Similar to HAND gradient, differences among life forms in SES values were subtle in the sum of bases gradient (Fig. 2B). For the phosphorus gradient, fern and shrub species had smaller values of SES than herbs and trees, but there were no clear groups among life forms (Fig. 2C). Ferns and herbs had higher values along the phosphorus gradient, with herbs differing from all other groups except ferns. On average, lianas and palms seem to be the most specialized life forms along this gradient (Fig. 2C).

There was a difference in the degree of specialization of plant species in each plant life form among gradients (Fig. 3). For ferns, all species were specialized in the HAND gradient (SES<0), with less specialized species in the sum of bases, and almost none species specialized in the phosphorus gradient (Fig. 3A). The degree of specialization of fern species differed substantially among the three gradients (F = 12.1, N = 10 , p<0.001). To all other life forms, HAND had proportionally more specialist species, followed by phosphorus and bases. Sum of bases had SES values centered at zero for most life form species with on average few specialized species (Fig. 3B-F). For herbs, HAND gradient had a higher number of species with low values of SES, differing from the other two gradients (F = 7.7, N = 20, p=0.001) (Fig. 3B). Lianas (F = 2.3, N = 20, p=0.10) and palms (F = 3.25, N = 22, p=0.04) had no differences among gradients (Fig. 3C-D). For shrubs, only sum of bases differed from HAND and phosphorus (F = 9.7, N = 24, p<0.001) (Fig. 3E). For trees, the degree of specialization of species differed among the three gradients (F = 57.0, N = 489, p<0.001).

DISCUSSION

Nutrients availability have been considered the most important factor determining the distribution of Amazonian plant species (e.g. Young and Leon 1989, Nasto et al. 2017). However, more recently, new ways to measure soil-water availability in larger scales (Rennó et al. 2008) allowed a better investigation of its relation with plant diversity patterns (e.g. Moulatlet et al. 2014, Schietti et al. 2013). We found that water (HAND) and fertility gradients constrain species in similar ways but, on average, water gradient seems to be more important to determine the ecological specialization of species. Water availability constrained ferns and lianas the most, while sum of bases and phosphorus constrained on average more species of lianas and palms. The ecological specificity was higher than expected by chance in more than half of all life forms' species, but for ferns, all species were specialists in the water gradient. In summary, liana and palm species formed a group specialized in the fertility gradients, while water was more important to ferns, and also to a certain point to lianas. Lianas had a greater proportion of species specialized in both water and nutrient gradients, reinforcing their role as good predictors of other-taxa diversity (Landeiro et al. 2012).

Contrary to our hypothesis, that in general vascular plants would be strongly constrained by nutrients, the hydrological gradient generated more specialism than fertility. Species of all life forms tended to have narrow tolerances (WSD_H) along hydrological gradient than expected by chance. Schietti et al. (2013) found that each life-form assemblage composition had different HAND thresholds mainly associated with slopes, which are transitional areas between plateaus and valleys. Our data suggest that water may be the most limiting factor for most of life forms, but we are unable to discern if this pattern emerges from low tolerance to drought or to waterlogging.

High biomass life forms as trees, that corresponds to 82.6% of all species analyzed, were relatively more specialized in the fertility gradient as we hypothesized, while in general other life forms were more specialized in the hidrological gradient. Plant species fill very similar niches (Gentry 1988) and generally acquire the resources by similar ways (Aarssen and Epp 1990, Goldberg and Barton 1992, Gurevitch et al. 1992), therefore, interspecific competition should be an important mechanism to promote coexistence in most plant communities (Silvertown 2004), specially trees and lianas in the Amazon. Since plants niche are related mainly to local resource availability promoting plant growth like light, nutrients and water gradients, two of the most important axes of a species' niche are accounted for by the habitat specialization we measured. Coexistence of trees may be more dependent more on how the use of those resources mediates competition (MacArthur and Levins 1967) and how the competition leads to a predictable non-random co-occurence pattern in trees (Diamond 1975, Silvertown 2004, Nasto et al. 2017), instead of the pure increased access to soil nutrients by root span (Nepstad et al. 2007).

At a mesoscale, shallow-rooted life forms as ferns had more restricted distributions along the HAND gradient. Since life forms differ in root span (Becker and Castillo 1990, Nepstad et al. 1994, Lynch 1995, Restom and Nepstad 2004, Ramos et al. 2009) and drought tolerance (Engelbrecht et al. 2007, Nepstad et al. 2007), the depletion of water availability in superficial soil layers may induce mortality of shallow-rooted plants (Nepsted et al. 2007) and prevent the sexual reproduction of ferns that depend on free water to complete their life cycle (Page 2002). On the other hand, species with roots that do not tolerate anoxic conditions may not occupy areas under seasonal flooding or frequently water-logged soils (Piedade et al. 2010).

At fine-scales, the composition of herb and fern assemblages changes according to the horizontal distance from streams (Drucker et al., 2008). Therefore, areas with low HAND values near stream edges may harbor more herbaceous species than most plateaus at higher elevation, and ferns be constrained to this portion of the water gradient. Competition between herbaceous plants could be higher at lower areas intensifying ecological specialization (Costa et al. 2005) since soil-water availability may enhance niche partitioning in tropical forests (Engelbrecht et al. 2007 for tree species). Morphological and physiological traits related to rooting systems probably enable the largest or the smallest life forms to colonize only one of the HAND gradient extremes.

Liana was the second most specialized life form in the water gradient, even though lianas have deep roots as trees (Nepstad et al. 2004) and high dispersal capacity (Macía et al. 2007). Several lianas species grow mainly during the dry season (Schnitzer and Heijden 2019), at larger scales, are more specious and abundant where droughts are pronounced (Schnitzer, 2005). About three fourth of all individuals of the five most specialized species are distributed in plots where HAND values are under five meters (maximum HAND value in lianas plots = 45 m - data not shown). Therefore, specialization of lianas may be caused by their growth requirements of greater amounts of water from the soil during dry seasons.

Most palms constituted the second most specialized life form in fertility gradients. Lianas and palms were the most environmental and spatial congruent groups at the Ducke Reserve (Landeiro et al. 2012). Costa et al. (2009), also working at Ducke, showed that palm composition is associated with clay content and distance to the nearest water course, evidencing soil texture as an important environmental factor to those populations. On the other hand, bases content explained seven per cent of the variance in palm composition, while distance from streams at lower areas explained 43%, at the same study. These results are in accordance with ours: Palms and lianas are more restricted by soil nutrients, making fertility a stronger generator of specialism than water.

Several lianas, palms and shrubs were more specialized than expected by chance along the phosphorus gradient. This nutrient is an important axis in most plant niches due to its major role in vegetative growth – wood density, litter production and forest growth rates

(Paoli and Curran 2007, Quesada et al. 2010) – and to the limitation of primary production at community level caused by its deficiency (Quesada et al. 2009). Lianas and shrubs may be the most important groups to contribute to primary production after trees, estimated to be about 10% of the tree biomass increment for tropical forests (Clark et al. 2001). Most of high biomass species may have evolved narrower niches by competition to optimize phosphorus absorption in each part of the edaphic range. However, future investigations on plant specialism would shed light on the width of the edaphic gradients each species occupies in tropical forests.

Ferns and Angiosperm herbs were similarly associated to soil gradients in studies comparing different functional groups (Tuomisto and Ruokolainen 1994, Vormisto et al. 2000, Costa et al. 2005). These life forms showed different degrees of specialization to the fertility gradient in our study: Ferns were more specialized in HAND; while herbs were more specialized in the sum of bases, but not on phosphorus. However, when gradients are compared within each life form, water was more constraining than phosphorus and bases for both life forms, and bases was more constraining in herbs than in ferns.

The generalism of ferns and herbs in sum of bases may be associated with the gradient range, since large scale patterns of specialization may not be detected in mesoscale. Sum of bases were considered a strong predictor of fern distribution at the Brazilian Amazon scale (Zuquim et al 2014). Most fern species have small range of tolerance in the bases gradient (0.1 – 1 cmol/kg from a total range of 0,1 – 50 cmol/kg) (Moulatlet et al. 2017). Except of one plot analyzed in this study, the range of sum of bases varies from 0,02 to ~0.6 cmol/kg, indicating the edaphic gradient at Ducke is not wide enough to evaluate broad-scale specialization in ferns and, also may underestimate the tolerances of other life forms.

Nutrient and water gradients are known for creating opposite patterns on fern distribution and specialization regarding to scales (see Costa et al. 2005, Schietti et al. 2013 and Zuquim et al. 2014). Therefore, based on other studies and on our own results, we suggest that the adequacy of scale size may increase linearly with life form biomass to test the influence of water gradients and decrease linearly to test the influence of fertility gradients in the Amazon basin.

Even though mesoscales are very useful for ecological studies (e.g. ter Steege et al. 1993, Tuomisto and Ruokolainen 1994, Clark et al. 1999, Vormisto et al. 2000, Svenning et al. 2004, Vormisto, Tuomisto and Oksanen 2004) and of utmost importance to define land management (Costa et al. 2009), we still know relatively little about processes operating at this scale. For instance, processes affecting species distribution may change in importance when we scale down from region/landscape to mesoscale (Jones et al. 2006, Costa et al. 2009), as gradients depend on the scale to have distinguishable patterns. At larger scales, nutrients may be strong predictor of plant species diversity, but our results suggests that at mesoscale, the water availability may be more important for species distribution (see Bruun et al. 2006 for altitude and topography in alpine assemblages and Drucker et al. 2008 for stream's distance in tropical herb assemblages).

Specialization, as we measured, seems to be a good approach to understand the environmentally induced tolerance of plants at mesoscale. Even though small ranges of edaphic gradients may not account for the differences in specialization of widespread species, we found consistent habitat specificity combining predicted to observed data in a unique measure for both gradient types – hydrological and nutritional resources to vascular plants. Soil fertility, mainly phosphorus, have always been thought of as the most important predictor for plant distribution in tropical forests (Jordan and Herrera 1981). However, water-table level may better distinguish patterns of specialism among species with lower biomass, as ferns and herbs. In a similar way, phosphorus may be a better predictor for higher biomass life forms, as trees and lianas, and water may be a general predictor for habitat specificity in the Amazon – even at regional scales (Moulatlet et al. 2014). We believe that the investigation of habitat specifity in other scales, using this same approach, would enrich the knowledge about how the environment limit the distribution of rare and widespread species in the Amazon Basin.

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FIGURE LEGENDS

Fig. 1 Location of Ducke Reserve in Central Amazonia, Brazil. Brownish colors represent higher areas (*plateaus* and *vertentes*) and blueishcolors represent lower areas (*baixios*). The black lines show the Reserve limits and yellow dots indicate the locations of the 250 m-longpermanent plots on a 1 km equidistant sampling grid.

Fig. 2 Differences of Ecological Specialization (SES) among life formsin each abiotic gradient. A: HAND gradient; B: Sum of bases gradient; and C: Phosphorus gradient. Different letters mean statistical difference after corrections for multiple tests. Species are represented by gray points. Dashed red lines represent the point where there is no difference between observed and expected specialization values. Positive values of SES indicate more generalization in each gradient, while negative values more specialization than the expected by the null model.

Fig. 3 Differences of Ecological Specialization (SES) among the three gradients in each life form. A: Ferns; B: Herbs; C: Lianas; D: Palms; E: Shrubs; and F: Trees.Different letters mean statistical difference after corrections for multiple tests. Species are represented by gray points. Dashed red lines represent the point where there is no difference between observed and expected specialization values. Positive values of SES indicate more generalization in each gradient, while negative values more specialization than the expected by the null model.

FIGURES

Fig. 1

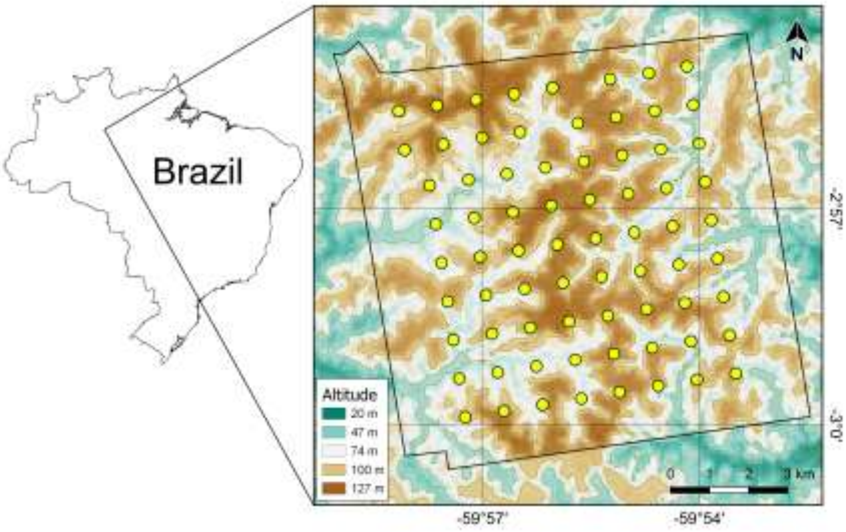


Fig. 2

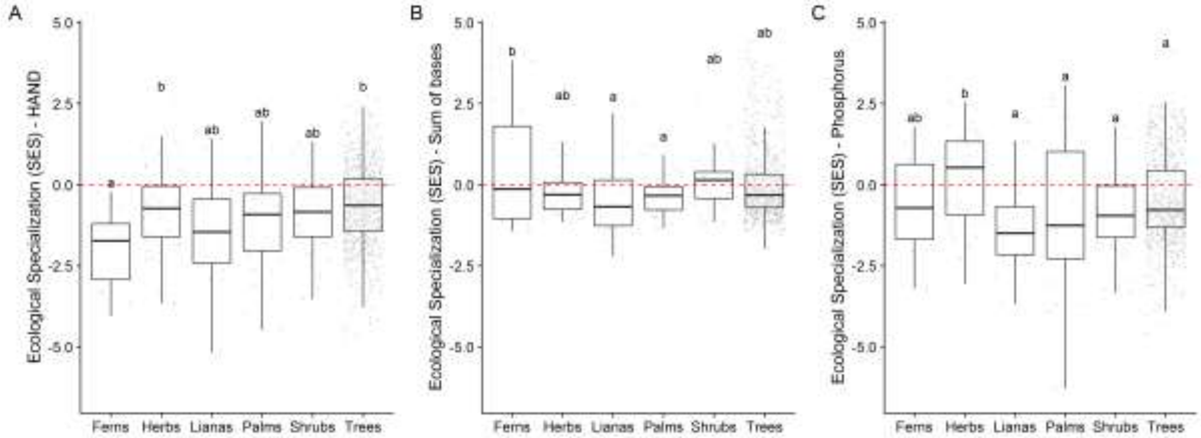
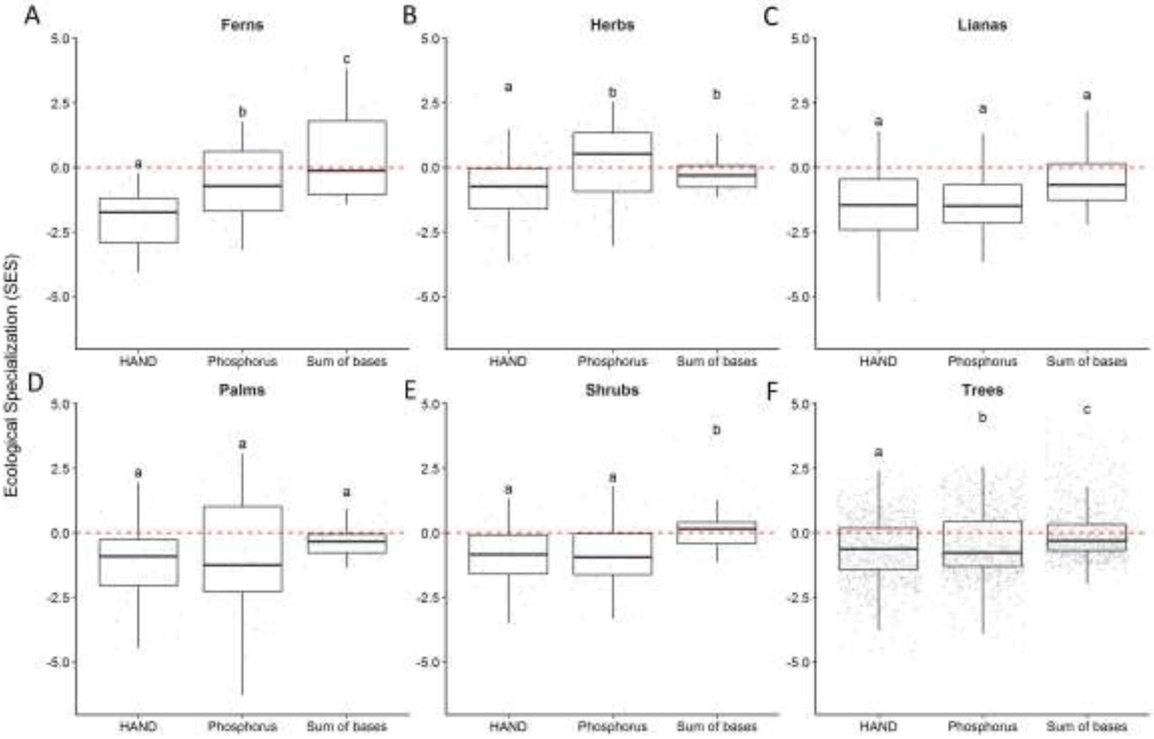

A
Ecological Specialization (SES) - HAND
5.0
2.5
0.0
-2.5
-5.0
a
b
ab
ab
ab
b
Ferns
Herbs
Lianas
Palms
Shrubs
Trees
B
Ecological Specialization (SES) - Sum of bases
5.0
2.5
0.0
-2.5
-5.0
b
ab
a
a
ab
ab
Ferns
Herbs
Lianas
Palms
Shrubs
Trees
C
Ecological Specialization (SES) - Phosphorus
5.0
2.5
0.0
-2.5
-5.0
ab
b
a
a
a
a
Ferns
Herbs
Lianas
Palms
Shrubs
Trees

Fig. 3


A
Ferns
B
Herbs
C
Lianas
D
Palms
E
Shrubs
F
Trees
Ecological Specialization (SES)
5.0
2.5
0.0
-2.5
-5.0
HAND
Phosphorus
Sum of bases
a
b
c

APPENDIX S1

Table S1. Values of SES to the three gradients analyzed, including lifeform and family.

Lifeform	Family	Species	SES Phosphorus	SES Sum of bases	SES HAND
Trees	Fabaceae	*Abarema adenophora*	0.782103592	-0.822118472	-4.863283225
Trees	Fabaceae	*Abarema jupunba*	1.75596379	-0.378568636	-0.591544637
Trees	Fabaceae	*Abarema piresii*	1.046118971	0.05806014	0.826365879
Lianas	Bignoniaceae	*Adenocalymma adenophorum*	-2.865444168	0.052070692	-2.964837151
Lianas	Bignoniaceae	*Adenocalymma bracteosum*	-1.340548835	-0.33845815	-1.89046171
Lianas	Bignoniaceae	*Adenocalymma flaviflorum*	-2.140323955	-1.470303945	-1.84729098
Lianas	Bignoniaceae	*Adenocalymma longilineum*	-3.66929314	-1.721710839	-2.215411402
Lianas	Bignoniaceae	*Adenocalymma moringifolium*	-2.21721586	-0.552656816	-1.081456603
Lianas	Bignoniaceae	*Adenocalymma neoflavidum*	-2.198060104	-2.216670376	-2.473337694
Lianas	Bignoniaceae	*Adenocalymma subincanum*	-1.696996053	0.12062586	-0.465003722
Lianas	Bignoniaceae	*Adenocalymma tanaeciicarpum*	-2.096778763	0.207376587	-2.919084789
Ferns	Pteridaceae	*Adiantum tomentosum*	-0.93798704	-1.428902606	-1.300967669
Trees	Opiliaceae	*Agonandra sylvatica*	-0.507740801	-0.292313689	0.209722224
Trees	Lauraceae	*Aiouea* cf. *grandifolia*	-0.69939523	0.052427544	0.525935096
Trees	Lauraceae	*Aiouea grandifolia*	2.01417706	0.288896059	0.43642527
Trees	Lauraceae	*Aiouea myristicoides*	0.799994138	2.653868589	1.450085782
Trees	Euphorbiaceae	*Alchornea* sp.	0.359406067	0.550442275	2.08288243
Trees	Euphorbiaceae	*Alchornea discolor*	0.604360441	0.650046083	0.779092682
Trees	Cariodendreae	*Alchorneopsis floribunda*	1.874838752	-0.604229294	-1.944797623
Trees	Lecythidaceae	*Allantoma lineata*	1.27994629	-0.503166442	0.289590116
Trees	Apocynaceae	*Ambelania acida*	-0.787373577	0.148064133	0.173033456
Trees	Apocynaceae	*Ambelania duckei*	-1.064698281	2.606977712	-2.190229962

Trees	Ulmaceae	*Ampelocera edentula*	-1.463788872	1.160203484	-1.237900221
Lianas	Bignoniaceae	*Amphilophium magnoliifolium*	1.304843835	-0.811068305	-2.633840751
Lianas	Bignoniaceae	*Amphilophium parkeri*	-1.337123396	-0.77495616	-0.53089842
Lianas	Bignoniaceae	*Amphilophium pulverulentum*	-1.187956032	0.281521854	-0.554077076
Trees	Violaceae	*Amphirrhox longifolia*	-1.03295469	-0.093633028	-1.232671655
Trees	Anacardiaceae	*Anacardium parvifolium*	-1.235442888	-0.097978104	-0.856593694
Trees	Anacardiaceae	*Anacardium spruceanum*	-1.533252771	-0.633775611	0.082164164
Trees	Fabaceae	*Andira* sp.	0.136655498	-0.529474859	1.814786704
Trees	Fabaceae	*Andira micrantha*	2.087702105	-1.170965701	0.615822241
Trees	Fabaceae	*Andira parviflora*	-0.34541277	-1.119627163	-0.948404601
Trees	Fabaceae	*Andira unifoliolata*	-2.061334282	-0.329217794	1.436645728
Lianas	Bignoniaceae	*Anemopaegma robustum*	1.346704549	-0.23059763	-5.172108694
Trees	Lauraceae	*Aniba* sp.	0.311197322	-0.428541466	0.29034937
Trees	Lauraceae	*Aniba* aff. *williamsii*	2.132320743	-0.273975238	-1.020223915
Trees	Lauraceae	*Aniba canelilla*	-1.484913465	-1.132374434	-0.080132031
Trees	Lauraceae	*Aniba ferrea*	-1.108262174	0.37400302	0.338559139
Trees	Lauraceae	*Aniba panurensis*	-0.867805199	-1.114458607	-0.906081059
Trees	Lauraceae	*Aniba panurensis* s.l.	1.695386055	-0.394247482	1.529889296
Trees	Lauraceae	*Aniba parviflora*	-1.289689363	-0.012151999	0.582487646
Trees	Lauraceae	*Aniba williamsii*	-1.514347599	-0.1920504	-0.569532104
Trees	Anisophylleaceae	*Anisophyllea manausensis*	-1.859969155	0.425322943	-0.218592363
Trees	Annonaceae	*Annona amazonica*	-0.807351902	-0.350357658	0.350227244
Trees	Euphorbiaceae	*Anomalocalyx uleanus*	1.341222851	-0.07563778	2.147912504
Trees	Euphorbiaceae	*Aparisthmium cordatum*	-0.719033698	-0.146725071	-1.413632493
Trees	Malvaceae	*Apeiba echinata*	0.085391799	1.140209144	-1.683895499
Trees	Olacaceae	*Aptandra tubicina*	1.99304075	0.334701435	0.124934079
Trees	Apocynaceae	*Aspidosperma* sp.	-0.509932403	-0.503712349	0.709971768
Trees	Apocynaceae	*Aspidosperma desmanthum*	-0.893763935	-0.525341753	-0.500254581
Trees	Apocynaceae	*Aspidosperma marcgravianum*	-0.211592512	2.738008386	-0.35050975
Trees	Apocynaceae	*Aspidosperma nitidum*	-0.207588222	-0.558865036	-1.283232385

Trees	Apocynaceae	*Aspidosperma sandwithianum*	1.605819406	0.094175105	-0.397413516
Trees	Apocynaceae	*Aspidosperma* sp.	0.095544745	-0.541970898	-0.410091371
Palms	Arecaceae	*Aspidosperma spruceanum*	-1.482795037	-0.997705237	-1.125291883
Palms	Arecaceae	*Astrocaryum acaule*	-3.906068782	1.198899079	0.092488863
Palms	Arecaceae	*Astrocaryum social*	-6.281977335	-0.075978153	-3.444427532
Trees	Anacardiaceae˜	*Astronium le.cointei*	-1.428947948	-1.234248463	0.255443491
Palms	Arecaceae	*Attalea attaleoides*	-4.791075306	0.397233352	-2.690499717
Palms	Arecaceae	*Attalea microcarpa*	1.581195047	-0.813230234	-3.122983364
Palms	Arecaceae	*Bactris acanthocarpa*	-3.716249282	-0.727191883	-0.503383787
Palms	Arecaceae	*Bactris acanthocarpa* var. *intermedia*	-1.244380157	-0.77439258	-0.723285183
Palms	Arecaceae	*Bactris acanthocarpa* var. *trailiana*	-1.273483072	-0.284587076	1.957626068
Palms	Arecaceae	*Bactris acanthocarpoides*	2.055034546	-0.1619849	-3.993599695
Palms	Arecaceae	*Bactris concinna*	-0.74716457	-0.94640192	-1.566294598
Palms	Arecaceae	*Bactris elegan*	-3.018290779	-1.20056335	-2.169139257
Palms	Arecaceae	*Bactris gastoniana*	-2.414244926	-0.143765871	-2.305382189
Palms	Arecaceae	*Bactris hirta*	3.066312649	-0.510258218	-1.991379703
Palms	Arecaceae	*Bactris simplicifron*	-1.110850314	-0.155786674	-0.6329005
Palms	Arecaceae	*Bactris syagroides*	-1.430188129	-0.288201604	0.837335292
Palms	Arecaceae	*Bactris tomentosa* var. *sphaerocarpa*	-2.215882199	-1.015970397	-0.630566664
Trees	Fabaceae	*Balizia pedicellaris*	-0.974945252	0.476581644	0.41081309
Lianas	Bignoniaceae	*Bignonia aequinoctialis*	1.9176184	-1.298558589	1.412862918
Lianas	Bignoniaceae	*Bignonia prieurei*	-1.810658966	-1.251369217	-0.727685685
Trees	Annonaceae	*Bocageopsis multiflora*	-1.162822691	-1.143683894	-0.819652223
Trees	Annonaceae	*Bocageopsis pleiosperma*	-1.237286189	-0.723252572	-1.5043215
Trees	Fabaceae	*Bocoa viridiflora*	-3.678028926	-1.078754315	-2.680930298
Trees	Malvaceae	*Bombacopsis macrocalyx*	-0.593562614	-1.091196697	-1.303776306
Trees	Malvaceae	*Bombacopsis nervosa*	1.135404001	2.082662178	-0.964696684
Trees	Rubiaceae	*Botryarrhena pendula*	-1.121522366	0.176384333	1.611347602
Herbs	Bromeliaceae	*Bromelia tubulosa*	-1.626912088	-0.7891837	-1.431444722
Trees	Moraceae	*Brosimum* sp.	1.469955498	-1.083091881	0.492250521

Trees	Moraceae	*Brosimum acutifolium*	-1.114154886	-0.085953386	-0.280299665
Trees	Moraceae	*Brosimum guianense*	-1.921241549	0.555426517	-1.316450869
Trees	Moraceae	*Brosimum lactescens*	-2.065361926	2.138908495	-2.539013735
Trees	Moraceae	*Brosimum longifolium*	0.905963949	-0.239828124	1.595636389
Trees	Moraceae	*Brosimum parinarioides*	-3.098586169	0.350740372	-1.174371688
Trees	Moraceae	*Brosimum potabile*	0.903365898	-0.636447288	-0.618719952
Trees	Moraceae	*Brosimum rubescens*	-1.631119549	-1.962221604	-0.566115655
Trees	Moraceae	*Brosimum utile*	-0.026076974	0.368990219	-1.127189954
Trees	Combretaceae	*Buchenavia* sp.	-0.188744313	1.567811564	0.962767133
Trees	Combretaceae	*Buchenavia congesta*	0.44963403	-0.531356175	0.209923769
Trees	Combretaceae	*Buchenavia grandis*	-1.238120066	-0.389116508	0.845870261
Trees	Combretaceae	*Buchenavia guianensis*	0.918273061	-0.014569512	-0.11156197
Trees	Combretaceae	*Buchenavia macrophylla*	-0.748036587	-0.340020304	-0.856730602
Trees	Combretaceae	*Buchenavia parvifolia*	-0.78209629	-0.224920382	-0.931537344
Trees	Combretaceae	*Buchenavia tomentosa*	-1.545181149	-0.468073953	-0.49246086
Trees	Malpighiaceae	*Byrsonima* sp.	0.707418146	-0.094994852	0.199619475
Trees	Malpighiaceae	*Byrsonima crispa*	-0.99961376	-0.004661909	-0.524134825
Trees	Malpighiaceae	*Byrsonima duckeana*	-1.552101112	-0.604318497	-0.392252071
Trees	Malpighiaceae	*Byrsonima incarnata*	1.76073013	2.249585194	0.213644819
Herbs	Marantaceae	*Calathea altissima*	-1.903469568	-0.81322349	-2.048987608
Herbs	Marantaceae	*Calathea cannoides*	-0.685131484	1.026596099	-0.7969976
Herbs	Marantaceae	*Calathea mansonis* var.1	-0.012837144	-0.917562532	-0.973483876
Herbs	Marantaceae	*Calathea panamensis*	1.920477482	-1.046310167	-1.579445056
Herbs	Marantaceae	*Calathea* sp.1	2.328000253	-0.62640931	-1.475152103
Herbs	Marantaceae	*Calathea* sp.2	0.491541779	1.253842269	-1.697882488
Trees	Fabaceae	*Calliandra tenuiflora*	-0.781407386	-0.116013427	-1.553890989
Lianas	Bignoniaceae	*Callichlamys latifolia*	1.087629082	1.324349149	1.403260486
Trees	Myrtaceae	*Calophyllum brasiliense*	-0.034350012	-0.930392984	-1.03844291
Herbs	Cyperaceae	*Calyptranthes cuspidata*	-0.928703812	0.11537663	-0.515363787
Herbs	Cyperaceae	*Calyptrocarya* aff. *glomerulata*	1.270110746	-0.649107839	1.367255643

Herbs	Cyperaceae	*Calyptrocarya* aff. *poeppigiana*	0.125085615	-1.034823062	-1.557723006
Trees	Callophyllaceae	*Caraipa* sp.	2.501278337	-0.580302909	-1.142104877
Trees	Callophyllaceae	*Caraipa heterocarpa*	0.576383236	4.414444946	-1.30209269
Trees	Lecythidaceae	*Caraipa punctulata*	2.211097308	-0.71672581	-3.036330714
Trees	Lecythidaceae	*Cariniana decandra*	1.015493153	3.201365441	0.019502128
Trees	Lecythidaceae	*Cariniana integrifolia*	1.628908722	-1.03302749	-3.785741725
Trees	Lecythidaceae	*Cariniana micrantha*	-1.367880127	0.469356632	-1.625048932
Trees	Achariaceae	*Carpotroche crispidentata*	-1.415457702	0.018585648	-0.981566284
Trees	Caryocaraceae	*Caryocar* sp.	-0.656619404	0.318518429	-0.776723458
Trees	Caryocaraceae	*Caryocar glabrum*	0.93398908	0.801640186	1.458632251
Trees	Caryocaraceae	*Caryocar pallidum*	1.39451416	0.318908838	0.08573935
Trees	Salicaceae	*Caryocar villosum*	-0.757764735	-0.316615089	-1.747587026
Trees	Salicaceae	*Casearia* sp.	2.257979215	0.293208522	0.916959005
Trees	Salicaceae	*Casearia duckeana*	-1.137192734	-0.43456209	0.010984191
Trees	Salicaceae	*Casearia javitensis*	-0.796130363	0.77103889	-2.194909481
Trees	Salicaceae	*Casearia pitumba*	-0.745296606	2.136841304	1.346305881
Trees	Fabaceae	*Cassia* sp.	-0.36842479	-0.171020477	1.587902423
Trees	Fabaceae	*Cassia rubriflora*	1.032079589	-0.3784459	0.397516895
Trees	Malvaceae	*Catostemma milanezii*	1.717558273	-1.087472235	-2.16226313
Trees	Urticaceae	*Cecropia* sp.	1.082680079	-0.323507892	-0.862339891
Trees	Urticaceae	*Cecropia distachya*	0.219588555	0.3888526	-1.064215577
Trees	Urticaceae	*Cecropia sciadophylla*	-0.479202698	-0.443320785	0.078939759
Trees	Fabaceae	*Cedrelinga cateniformis*	-0.824320494	-0.735221558	-1.483310361
Trees	Fabaceae	*Chamaecrista adiantifolia*	1.605223506	3.905090798	-1.254031911
Trees	Olacaceae˜	*Chaunochiton kappleri*	-0.993504303	1.671531508	-0.593891411
Trees	Rubiaceae	*Chimarrhis barbata*	-1.652995036	0.394849347	-0.03719597
Trees	Rubiaceae	*Chimarrhis duckeana*	-0.957717343	-0.408025612	-0.525736594
Trees	Sapotaceae	*Chromolucuma rubriflora*	0.298567274	-0.388407117	-3.118532136
Trees	Sapotaceae	*Chrysophyllum* sp.	-0.280446416	0.081437289	0.170769804
Trees	Sapotaceae	*Chrysophyllum amazonicum*	-0.134671351	0.207541115	-0.420953444

Trees	Sapotaceae	*Chrysophyllum manaosense*	-0.512175701	-1.074497358	-1.146295844
Trees	Sapotaceae	*Chrysophyllum pomiferum*	-0.517737522	3.258173353	-0.745612681
Trees	Sapotaceae	*Chrysophyllum prieurii*	-1.890053575	-1.01023853	0.590923041
Trees	Sapotaceae	*Chrysophyllum sanguinolentum*	1.952974486	-0.518552915	-2.814730138
Trees	Sapotaceae	*Chrysophyllum sparsiflorum*	0.516775534	-0.118635334	0.814203637
Trees	Sapotaceae	*Chrysophyllum ucuquirana.branca*	-1.247534034	-0.68055729	-0.316787642
Trees	Moraceae	*Clarisia* sp.	2.194246662	-0.356734462	1.152807819
Trees	Moraceae	*Clarisia racemosa*	-1.588953381	0.513710866	-1.738605494
Trees	Clusiaceae	*Clusia insignis*	2.06694478	-0.379661939	2.66077922
Trees	Euphorbiaceae	*Conceveiba guianensis*	-0.835615705	1.159670616	0.597785195
Trees	Euphorbiaceae	*Conceveiba martiana*	2.032490204	-0.093724234	-2.405281007
Trees	Connaraceae	*Connarus perrottetii*	-0.761597379	-0.881597751	-3.065434269
Trees	Fabaceae	*Copaifera multijuga*	-2.012008571	-1.237802187	-1.623939396
Trees	Boraginaceae	*Cordia* sp.	-0.1200023	-0.067044763	-0.901569848
Trees	Boraginaceae	*Cordia exaltata*	-0.819492674	-0.369230579	-0.739510928
Trees	Lecythidaceae	*Corythophora alta*	-2.503331567	-0.721062028	-3.403671323
Trees	Lecythidaceae	*Corythophora rimosa*	-1.486772133	-0.538013008	-1.80286222
Trees	Chrysobalanaceae	*Couepia* sp.	0.407461435	-0.810303538	0.339196293
Trees	Chrysobalanaceae	*Couepia bracteosa*	-1.250967119	1.260361773	-0.081285181
Trees	Chrysobalanaceae	*Couepia canomensis*	0.453396333	-0.765363516	1.054413986
Trees	Chrysobalanaceae	*Couepia elata*	-1.017769898	1.914332278	-2.157694754
Trees	Chrysobalanaceae	*Couepia guianensis*	-2.316005856	0.114833997	-1.380854137
Trees	Chrysobalanaceae	*Couepia longipendula*	-0.822305178	-0.026124377	-1.176221826
Trees	Chrysobalanaceae	*Couepia magnoliifolia*	-1.489154241	-0.815816321	0.192111738
Trees	Chrysobalanaceae	*Couepia obovata*	-0.323257848	-0.900625572	-1.335412354
Trees	Chrysobalanaceae	*Couepia ulei*	-0.93707872	-1.107116559	-1.65055667
Trees	Apocynaceae	*Couma guianensis*	0.829905495	-0.949542246	-0.884051658
Trees	Lecythidaceae	*Couratari guianensis*	0.540170824	1.636775919	-0.422584523
Trees	Lecythidaceae	*Couratari longipedicellata*	0.799906241	-0.094477256	-0.295018567
Trees	Lecythidaceae	*Couratari stellata*	-1.217554548	1.150357108	-1.202945675

Trees	Lecythidaceae	*Couratari tauari*	0.009865747	-0.720905544	-0.664398204
Trees	Urticaceae	*Coussapoa trinervia*	1.920873445	0.264949509	-1.224261482
Trees	Rubiaceae	*Coussarea revoluta*	-0.485205897	0.903055187	-1.084278529
Trees	Burseraceae	*Crepidospermum rhoifolium*	-0.817734066	0.318740052	-1.177961353
Trees	Euphorbiaceae	*Croton lanjouwensis*	-1.91032272	-1.142006947	-2.015106257
Trees	Burseraceae	*Dacryodes* sp.	-0.803512564	0.317952648	0.412650139
Ferns	Maratticeae	*Danaea trifoliata*	-1.567321118	2.619551469	-2.178326978
Trees	Metteniusaceae	*Dendrobangia boliviana*	1.087643527	4.124109305	0.33001513
Palms	Arecaceae	*Desmoncus polyacanthos*	-0.223934984	-0.723226321	0.257532598
Trees	Fabaceae	*Dialium guianense*	-1.53940091	-0.813443887	-0.406253434
Trees	Fabaceae	*Dicorynia paraensis*	2.143094258	-0.01045079	0.497979772
Herbs	Araceae	*Dieffenbachia elegans*	1.606284375	-0.233220268	1.490759406
Herbs	Araceae	*Dieffenbachia* sp.1	1.219519193	-0.148966272	-0.510184163
Herbs	Araceae	*Dieffenbachia* sp.3	1.366862567	-0.140256659	-3.250591564
Herbs	Araceae	*Dieffenbachia* sp.4	0.274950463	2.4723734	0.972695808
Trees	Fabaceae	*Dimorphandra* sp.	-0.330587834	0.093326922	0.718248856
Trees	Fabaceae	*Dimorphandra parviflora*	-1.187231697	-0.523052382	-0.383122965
Trees	Fabaceae	*Dimorphandra pennigera*	0.135117001	-0.569193056	-2.596500576
Trees	Fabaceae	*Dimorphandra* sp.1	0.58895758	3.334512366	-1.719306237
Trees	Fabaceae	*Dinizia excelsa*	-0.910560417	-0.550829743	-1.723702446
Trees	Ebenaceae	*Diospyros cavalcantei*	-0.843127059	3.204613833	-1.739442624
Trees	Ebenaceae	*Diospyros guianensis*	-1.183847594	-0.848527325	-0.78618935
Trees	Ebenaceae	*Diospyros vestita*	-0.512995006	0.367201003	0.528215896
Herbs	Cyperaceae	*Diplasia karataefolia*	-0.955869405	-0.891380608	0.439414752
Trees	Fabaceae	*Diplotropis triloba*	-0.899049899	-0.469042246	-0.647493812
Trees	Fabaceae	*Dipteryx magnifica*	-1.712497814	1.324164726	-0.044083783
Trees	Fabaceae	*Dipteryx odorata*	-1.097748738	0.624008763	-0.375142395
Trees	Fabaceae	*Dipteryx polyphylla*	-0.945051667	-0.084550555	-0.506741963
Trees	Fabaceae	*Dipteryx punctata*	-1.072011627	-0.649483554	0.349244288
Herbs	Araceae	*Dracontium longipes*	0.26537267	-1.095244717	-0.240239562

Trees	Putranjivaceae	*Drypetes* sp.	-1.09654226	-0.713031143	-1.350504914
Trees	Putranjivaceae	*Drypetes variabilis*	-0.731047373	-0.55650988	-2.195436843
Trees	Solanaceae	*Duckeodendron cestroides*	-1.676761712	-0.465347448	-0.514296337
Trees	Humiriaceae	*Duckesia verrucosa*	-1.390772374	-0.762774033	-1.845983631
Trees	Annonaceae	*Duguetia* sp.	1.368081321	-0.589760864	0.477272509
Trees	Annonaceae	*Duguetia megalocarpa*	-0.889190666	-0.301612428	-2.126622817
Trees	Annonaceae	*Duguetia pycnastera*	-0.264239709	2.512121606	-2.277018179
Trees	Annonaceae	*Duguetia stelechantha*	-1.905150206	0.799412186	-0.634404007
Trees	Annonaceae	*Duguetia surinamensis*	-1.469848747	-0.838815487	0.150835399
Trees	Chrysobalanaceae	*Dulacia* sp.	-1.3343669	-0.533748802	0.828968736
Trees	Chrysobalanaceae	*Dulacia candida*	-1.023093208	0.70210341	0.199772499
Trees	Chrysobalanaceae	*Dulacia guianensis*	-1.719261871	-0.271412483	-0.478829104
Trees	Rubiaceae	*Duroia longiflora*	1.521922593	-0.681361991	-0.895683913
Trees	Rubiaceae	*Duroia macrophylla*	-1.113708939	1.137042688	-0.625823397
Trees	Rubiaceae	*Duroia saccifera*	0.670494893	-0.398268428	-0.826442705
Trees	Clusiaceae	*Dystovomita brasiliensis*	-0.45103814	-0.335811449	0.095834552
Trees	Sapotaceae	*Ecclinusa guianensis*	4.096531462	-1.552617881	1.815192022
Trees	Sapotaceae	*Elaeoluma nuda*	1.310917325	-0.778018162	0.946501585
Trees	Fabaceae	*Elizabetha speciosa*	-0.975307148	1.881296136	0.180718504
Trees	Metteniusaceae	*Emmotum* aff. *nitens*	-1.595458028	-0.589119086	-0.318716357
Trees	Metteniusaceae	*Emmotum nitens*	-0.62160672	-0.595102976	-0.075227568
Trees	Lecythidaceae	*Endlicheria bracteata*	-0.550543859	-0.16816109	-0.259887666
Trees	Lecythidaceae	*Endlicheria sericea*	1.454849451	0.010524619	0.721488273
Trees	Humiriaceae	*Endopleura uchi*	-2.086030614	-0.248690261	-1.930106654
Trees	Fabaceae	*Enterolobium schomburgkii*	-1.577896747	-0.460012001	-1.029984413
Trees	Fabaceae	*Eperua duckeana*	1.358755413	-1.353952591	-4.605786655
Trees	Fabaceae	*Eperua glabriflora*	2.471159079	0.267550643	-0.481745875
Trees	Annonaceae	*Ephedranthus amazonicus*	-1.627953348	0.456277433	-1.958486655
Trees	Malvaceae	*Eriotheca globosa*	1.76527383	0.073118234	2.413561131
Trees	Vochysiaceae	*Erisma* sp.	1.851912541	0.222818647	0.01707088

Trees	Vochysiaceae	*Erisma bicolor*	-1.803333697	3.656143936	-1.10162212
Trees	Vochysiaceae	*Erisma* sp.3	-1.044941902	-0.185974307	0.168049342
Trees	Erythroxylaceae	*Erythroxylum citrifolium*	-0.498764698	-0.191865264	-0.094796209
Trees	Lecythidaceae	*Eschweilera amazoniciformis*	-0.748610143	-0.869257874	-0.506730313
Trees	Lecythidaceae	*Eschweilera atropetiolata*	-4.034210435	-1.374303694	-2.344677786
Trees	Lecythidaceae	*Eschweilera bracteosa*	-2.450028673	-0.581095675	-0.656304674
Trees	Lecythidaceae	*Eschweilera carinata*	-1.503143981	-0.276660845	-0.746208275
Trees	Lecythidaceae	*Eschweilera collina*	-1.542609875	-0.339987242	-0.596076095
Trees	Lecythidaceae	*Eschweilera coriacea*	-1.345910454	0.706603483	-3.595977188
Trees	Lecythidaceae	*Eschweilera cyathiformis*	-1.000559958	-0.291906273	-0.927462797
Trees	Lecythidaceae	*Eschweilera grandiflora*	-3.324145365	0.786668945	-2.82022022
Trees	Lecythidaceae	*Eschweilera laevicarpa*	1.980845049	-0.608501584	0.221225065
Trees	Lecythidaceae	*Eschweilera micrantha*	2.05128952	-0.624971785	1.004458339
Trees	Lecythidaceae	*Eschweilera pedicellata*	-2.975303883	0.688265411	-3.266575987
Trees	Lecythidaceae	*Eschweilera pseudodecolorans*	-3.151701284	-1.47135891	-2.374396101
Trees	Lecythidaceae	*Eschweilera rankiniae*	-1.355869823	0.145534893	-0.214130214
Trees	Lecythidaceae	*Eschweilera rhododendrifolia*	-3.193160886	-1.141974506	-1.305703658
Trees	Lecythidaceae	*Eschweilera romeu.cardosoi*	-1.547300397	-0.190269247	-2.725334678
Trees	Lecythidaceae	*Eschweilera sp.*	2.361671623	-0.684452186	2.26104083
Trees	Lecythidaceae	*Eschweilera tessmannii*	-3.115093012	-0.412932712	-2.209829466
Trees	Lecythidaceae	*Eschweilera truncata*	-3.531711096	-1.389652268	-2.38483226
Trees	Lecythidaceae	*Eschweilera wachenheimii*	-3.373358134	2.714546318	-1.466776633
Trees	Myrtaceae	*Eugenia* sp.	-1.71012124	0.975469308	-1.085088088
Trees	Myrtaceae	*Eugenia* aff. *citrifolia*	-0.781609789	-0.417534163	0.417575029
Trees	Myrtaceae	*Eugenia citrifolia*	-0.585994937	-0.124417105	1.709747992
Trees	Myrtaceae	*Eugenia cuspidifolia*	-0.088013961	-0.739431015	-1.976568052
Trees	Myrtaceae	*Eugenia diplocampta*	-1.020280474	0.224819823	0.849229482
Trees	Myrtaceae	*Eugenia florida*	-0.859184952	-0.002531367	0.911533388
Trees	Myrtaceae	*Eugenia patrisii*	-0.537795832	-0.280664282	-0.519301081
Trees	Myrtaceae	*Eugenia pseudopsidium*	-0.81729977	1.492578005	-1.31259267

Trees	Myrtaceae	*Eugenia* sp.1	-0.787901551	-0.180766309	1.246113265
Trees	Myrtaceae	*Eugenia* sp.3	-0.706262212	-0.461381564	-1.008696396
Palms	Arecaceae	*Euterpe precatoria*	0.598878286	-0.232716332	0.098578755
Trees	Rubiaceae	*Faramea* sp.	-0.887212873	-0.006762091	0.492344718
Trees	Rubiaceae	*Faramea corymbosa*	-0.600439629	-0.507743125	-0.023129045
Trees	Rubiaceae	*Faramea platyneura*	-0.568729358	0.220456611	-0.564535321
Trees	Rubiaceae	*Ferdinandusa*	-1.702858645	-0.351863426	-1.203850449
Lianas	Bignoniaceae	*Fridericia chica*	-0.576013293	0.850308592	-0.411152395
Lianas	Bignoniaceae	*Fridericia cinnamomea*	-1.77768974	-0.641719551	-0.629100079
Lianas	Bignoniaceae	*Fridericia nigrescens*	-1.472114103	2.428847149	-0.164302651
Lianas	Bignoniaceae	*Fridericia prancei*	-0.260416665	2.192795094	1.128971493
Lianas	Bignoniaceae	*Fridericia triplinervia*	-2.410461302	-0.754773395	-2.39594062
Trees	Annonaceae	*Fusaea longifolia*	-1.705423389	-0.58208266	-1.140402776
Trees	Apocynaceae	*Geissospermum argenteum*	-2.016682935	1.02618945	-3.029573428
Trees	Apocynaceae	*Geissospermum urceolatum*	-1.75199819	-1.124694706	-2.970636848
Palms	Arecaceae	*Geonoma aspidiifolia*	-1.353407684	0.00949315	-1.114530358
Palms	Arecaceae	*Geonoma maxima* var. *chelinodura*	2.118439484	-0.762104122	1.085655121
Palms	Arecaceae	*Geonoma maxima* var. *maxim*	-1.533108348	0.119861225	-0.697967478
Palms	Arecaceae	*Geonoma maxima* var. *spixiana*	-2.239104695	0.919774795	-1.649173011
Palms	Arecaceae	*Geonoma* sp.1	-0.803202512	0.702353297	-0.629246979
Palms	Arecaceae	*Geonoma stricta*	1.685348182	0.470759163	0.037557848
Herbs	Rubiaceae	*Geophila cordifolia*	-0.802098173	-0.399612953	-0.877515043
Trees	Malpighiaceae	*Glandonia macrocarpa*	0.516497042	-0.448614375	-2.851510722
Trees	Euphorbiaceae	*Glycydendron amazonicum*	-1.779369611	1.615677073	-1.392073701
Trees	Goupiaceae	*Goupia glabra*	-1.764333827	-0.033323172	-1.156994227
Trees	Nyctaginaceae	*Guapira* sp.1	-0.956595397	-0.45504455	-1.356432003
Trees	Meliaceae	*Guarea* sp.	0.127378087	0.178994538	1.613418211
Trees	Meliaceae	*Guarea* cf. *cinnamomea*	-0.56750415	-1.046326921	-1.058026461
Trees	Meliaceae	*Guarea convergens*	-0.750480296	-0.275059331	0.144193273
Trees	Meliaceae	*Guarea humaitensis*	-0.050284549	0.175761251	-0.994706295

Trees	Meliaceae	*Guarea pubescens*	-0.731861428	-1.062601043	-2.06582774
Trees	Meliaceae	*Guarea scabra*	2.404797138	1.127192009	-0.825033907
Trees	Meliaceae	*Guarea silvatica*	-1.26954585	-0.100163091	-1.009972496
Trees	Meliaceae	*Guarea* sp.	-0.618308214	-0.413629525	-0.139424193
Trees	Meliaceae	*Guarea trunciflora*	-1.31726688	-0.135156486	-1.668068694
Trees	Annonaceae	*Guatteria* sp.	1.46552317	-0.761410566	-1.611001039
Trees	Annonaceae	*Guatteria citriodora*	-1.104037821	-0.464450576	-0.080423158
Trees	Annonaceae	*Guatteria discolor*	-1.886857823	0.194146566	-0.173729655
Trees	Annonaceae	*Guatteria foliosa*	-0.586108381	-0.568320083	0.43210168
Trees	Annonaceae	*Guatteria guianensis*	1.320847051	-0.75160379	-0.35669943
Trees	Annonaceae	*Guatteria meliodora*	0.212763029	0.622145657	-1.983582595
Trees	Annonaceae	*Guatteria olivacea*	-1.582124804	-1.176153419	-0.926175543
Trees	Lecythidaceae	*Gustavia elliptica*	-1.524773519	-1.166077425	-1.316576378
Trees	Lecythidaceae	*Gustavia hexapetala*	-0.850944951	-1.047239288	-1.499259414
Trees	Linaceae	*Hebepetalum humiriifolium*	1.917376734	-1.093246189	0.247215421
Trees	Olacaceae	*Heisteria* sp.	-0.052030252	-1.014048412	1.543879613
Trees	Olacaceae	*Heisteria barbata*	-0.96657273	-0.082707222	-0.104426757
Trees	Olacaceae	*Heisteria densifrons*	0.570837789	-0.767313971	1.172761473
Trees	Moraceae	*Helianthostylis sprucei*	-3.902229758	-0.83776843	-2.333797107
Herbs	Heliconiaceae	*Heliconia acuminata*	1.486295633	0.148117872	0.561423246
Herbs	Heliconiaceae	*Heliconia psittacorum*	-1.237371733	-0.520587079	-0.60200959
Trees	Moraceae	*Helicostylis scabra*	0.359547021	-0.629780612	-1.783498785
Trees	Moraceae	*Helicostylis tomentosa*	-2.837472692	0.178078687	-0.632656666
Trees	Melastomataceae	*Henriettella caudata*	-0.521529134	-0.903910142	0.444030222
Trees	Euphorbiaceae	*Hevea guianensis*	0.773265344	1.26490723	-1.285594399
Trees	Apocynaceae	*Himatanthus stenophyllus*	-1.250557099	-0.219542589	-3.224496926
Trees	Apocynaceae	*Himatanthus sucuuba*	-0.647036667	-0.72622522	-1.887767658
Trees	Chrysobalanaceae	*Hirtella bicornis*	-1.1652774	-1.199916965	-2.349007529
Trees	Chrysobalanaceae	*Hirtella fasciculata*	2.038821263	-1.20975036	0.272731993
Trees	Chrysobalanaceae	*Hirtella rodriguesii*	-1.250863821	2.891098178	-3.769004964

Trees	Fabaceae	*Humiria balsamifera*	-0.676830974	0.580388297	0.719044499
Trees	Fabaceae	*Hymenaea* sp.	2.059119553	-0.666654225	0.816076813
Trees	Fabaceae	*Hymenaea intermedia*	1.727303585	2.323843919	-0.250165186
Trees	Fabaceae	*Hymenaea parvifolia*	0.71781028	-0.408344282	-1.171865666
Trees	Fabaceae	*Hymenaea* sp.2	-0.403283701	-0.392676159	0.607297794
Trees	Fabaceae	*Hymenolobium* sp.	0.579843154	-0.602808685	-0.757028204
Trees	Fabaceae	*Hymenolobium modestum*	-0.511160295	-0.331845498	0.279318558
Trees	Fabaceae	*Hymenolobium sericeum*	-1.788711445	-0.482729543	-0.379809465
Palms	Arecaceae	*Hyospathe elegans*	1.462773906	0.15609939	-0.432700469
Herbs	Cyperaceae	*Hypolytrum schraderianum*	0.807339248	1.318979609	-1.84232057
Herbs	Poaceae	*Ichnanthus panicoides*	-2.299778805	-0.200459388	0.58359746
Trees	Fabaceae	*Inga* sp.	-2.55004383	-0.868500228	-1.761531789
Trees	Fabaceae	*Inga alba*	-1.049030692	-0.299958551	-0.64145449
Trees	Fabaceae	*Inga bicoloriflora*	0.062383134	-0.415317699	-0.294328391
Trees	Fabaceae	*Inga chrysantha*	-0.537333207	-1.009766603	-1.528736714
Trees	Fabaceae	*Inga gracilifolia*	-2.178008681	-0.906949274	-0.421125683
Trees	Fabaceae	*Inga grandiflora*	0.903804941	-0.053967186	1.067546638
Trees	Fabaceae	*Inga huberi*	-0.880458378	-0.275260291	-0.540464177
Trees	Fabaceae	*Inga lateriflora*	1.160407169	-0.618842934	1.238279931
Trees	Fabaceae	*Inga laurina*	-0.948865198	0.347319045	-0.980522058
Trees	Fabaceae	*Inga leiocalycina*	-0.593273686	-0.283630058	-2.013090148
Trees	Fabaceae	*Inga marginata*	-0.600628917	0.20141304	-0.2128008
Trees	Fabaceae	*Inga obidensis*	1.399770334	-1.219785835	-0.283246946
Trees	Fabaceae	*Inga paraensis*	-1.045142481	1.060289781	-0.213809544
Trees	Fabaceae	*Inga pezizifera*	-0.959047428	0.116907007	-0.075099643
Trees	Fabaceae	*Inga rhynchocalyx*	0.309611076	0.165061078	-0.024286898
Trees	Fabaceae	*Inga stipularis*	-0.924893013	-0.391907149	-0.105186841
Trees	Fabaceae	*Inga thibaudiana*	1.146751009	0.233405869	-1.233353839
Trees	Fabaceae	*Inga umbratica*	-1.265565482	0.367955574	0.091962634
Palms	Arecaceae	*Iriartella setigera*	0.867683725	-0.979257626	-1.835959632

Trees	Myristicaceae	*Iryanthera* sp.	1.756437107	-0.920050049	-1.011207841
Trees	Myristicaceae	*Iryanthera coriacea*	-0.881531385	0.287183995	-0.477811836
Trees	Myristicaceae	*Iryanthera elliptica*	-0.702838272	-0.754820318	-0.648055205
Trees	Myristicaceae	*Iryanthera juruensis*	2.39606684	-0.666870145	-0.989911384
Trees	Myristicaceae	*Iryanthera laevis*	-1.522578964	1.365998477	0.871141002
Trees	Myristicaceae	*Iryanthera lancifolia*	0.32310375	-0.101413323	-0.292935811
Trees	Myristicaceae	*Iryanthera paradoxa*	2.104043705	-0.506573969	-1.149192613
Trees	Myristicaceae	*Iryanthera* sp.	0.847203731	-0.598184028	0.026456709
Trees	Myristicaceae	*Iryanthera ulei*	0.989114995	0.556327859	-1.347230604
Herbs	Marantaceae	*Ischnosiphon arouma*	1.826817507	0.911092256	-0.529885104
Herbs	Marantaceae	*Ischnosiphon gracilis*	-1.634062482	-1.145437095	-2.053059606
Herbs	Marantaceae	*Ischnosiphon hirsutus*	-1.160554336	-0.173257339	0.973549071
Herbs	Marantaceae	*Ischnosiphon killipii*	0.934280838	-0.034625894	-0.088470853
Herbs	Marantaceae	*Ischnosiphon martianus*	-1.775292622	0.290187135	-0.534324204
Herbs	Marantaceae	*Ischnosiphon puberulus*	1.202419732	-0.593268955	0.797276299
Trees	Bignoniaceae	*Jacaranda* sp.	1.100036018	-0.201946538	0.805610172
Trees	Bignoniaceae	*Jacaranda copaia*	-0.625269859	1.390867065	-0.865731679
Trees	Lauraceae	*Kubitzkia mezii*	-1.068484951	-0.386335809	-0.381813976
Trees	Lacistemataceae	*Lacistema aggregatum*	1.550608366	-0.209758964	0.743472709
Trees	Lacistemataceae	*Lacistema polystachyum*	-0.410063079	-0.02683436	-1.115525175
Trees	Apocynaceae	*Lacmellea gracilis*	0.548503819	-0.907448155	-1.786606079
Trees	Quiinaceae	*Lacunaria* sp.	-0.78794601	0.010555436	-0.352045818
Trees	Quiinaceae	*Lacunaria jenmanii*	0.675058977	2.107618785	-0.98724691
Trees	Salicaceae	*Laetia procera*	-1.309405521	-0.695653117	-2.468543526
Trees	Lecythidaceae	*Lecythis chartacea*	-0.846117064	-0.094378306	-1.00621853
Trees	Lecythidaceae	*Lecythis gracieana*	-2.58200518	-0.984374124	-3.003276838
Trees	Lecythidaceae	*Lecythis parvifructa*	-1.22291514	-0.166918027	-1.405934841
Trees	Lecythidaceae	*Lecythis pisonis*	1.903329749	-0.156994038	-0.709464245
Trees	Lecythidaceae	*Lecythis poiteaui*	-2.10513834	-0.606684163	0.540089039
Trees	Lecythidaceae	*Lecythis prancei*	-2.933949528	-0.777580147	-4.541976315

Trees	Lecythidaceae	*Lecythis retusa*	-1.429185352	2.094686	-1.377355663
Trees	Lecythidaceae	*Lecythis* sp.	-1.100729008	-0.566838966	0.147436924
Trees	Lecythidaceae	*Lecythis zabucajo*	-0.036037875	-0.777579069	1.347182679
Trees	Chrysobalanaceae	*Licania* sp.	-0.295994493	0.565621031	-0.885134085
Trees	Chrysobalanaceae	*Licania adolphoduckei*	1.416422456	-0.454209853	0.766484916
Trees	Chrysobalanaceae	*Licania apelata*	-2.0246082	-1.044749662	-2.101157015
Trees	Chrysobalanaceae	*Licania bracteata*	-2.530786478	0.225802715	-1.443376415
Trees	Chrysobalanaceae	*Licania canescens*	-0.888737119	1.563827289	-0.399028553
Trees	Chrysobalanaceae	*Licania caudata*	-0.733516679	1.588476594	-0.3190957
Trees	Chrysobalanaceae	*Licania coriacea*	-1.635455652	0.191571282	0.05809669
Trees	Chrysobalanaceae	*Licania egleri*	-0.724828207	-0.825906056	-1.967488371
Trees	Chrysobalanaceae	*Licania gracilipes*	-0.874029448	-0.68516277	0.35501179
Trees	Chrysobalanaceae	*Licania heteromorpha*	-2.836766205	-0.307593978	-0.764307106
Trees	Chrysobalanaceae	*Licania impressa*	-1.292379559	-1.101740014	-1.969798153
Trees	Chrysobalanaceae	*Licania laevigata*	1.916367342	-0.622281168	-0.112523948
Trees	Chrysobalanaceae	*Licania lata*	1.499314554	-0.576919619	-2.593643926
Trees	Chrysobalanaceae	*Licania latifolia*	1.594138061	-0.130050065	-0.547389831
Trees	Chrysobalanaceae	*Licania laxiflora*	-0.470541327	0.115797715	0.167876424
Trees	Chrysobalanaceae	*Licania longistyla*	-0.700559955	-0.69929706	0.231541869
Trees	Chrysobalanaceae	*Licania macrophylla*	0.941297399	1.742273065	-1.288124186
Trees	Chrysobalanaceae	*Licania micrantha*	-1.675423449	1.063086961	-2.031400843
Trees	Chrysobalanaceae	*Licania niloi*	-1.054015033	-0.707925575	-0.162718318
Trees	Chrysobalanaceae	*Licania oblongifolia*	0.48543854	0.847465278	-4.095375572
Trees	Chrysobalanaceae	*Licania octandra*	-1.839593285	0.432307898	-1.927049523
Trees	Chrysobalanaceae	*Licania pallida*	-1.374531315	0.172016517	0.355611174
Trees	Chrysobalanaceae	*Licania prismatocarpa*	-0.732101014	1.591298114	-1.042104281
Trees	Chrysobalanaceae	*Licania reticulata*	-0.156946843	2.85268713	-2.137141235
Trees	Chrysobalanaceae	*Licania rodriguesii*	-0.663013307	-0.124940625	-1.265260258
Trees	Chrysobalanaceae	*Licania sandwithii*	-1.71315654	-0.522754677	-0.739135938
Trees	Chrysobalanaceae	*Licania sothersiae*	-0.959100221	-0.794841878	0.131002534

Trees	Chrysobalanaceae	*Licania sprucei*	-2.248074964	-0.07357289	-1.584184966
Trees	Chrysobalanaceae	*Licania unguiculata*	-0.428425518	1.735962285	0.157210163
Trees	Lauraceae	*Licaria* sp.	1.788565509	-0.232724463	-0.235130339
Trees	Lauraceae	*Licaria cannella*	0.045005048	-1.57572672	1.002260074
Trees	Lauraceae	*Licaria chrysophylla*	-0.987704611	0.269316586	-0.068980196
Trees	Lauraceae	*Licaria guianensis*	-2.52810988	-0.335214866	-1.069124021
Trees	Lauraceae	*Licaria martiniana*	-0.963403064	-0.422134495	1.118956807
Trees	Lauraceae	*Licaria pachycarpa*	-1.346390844	-0.644498777	-0.870149489
Trees	Lauraceae	*Licaria rodriguesii*	-1.086503702	-0.216005978	0.779612885
Ferns	Dennstaedtiaceae	*Lindsaea guianensis*	0.273221985	-0.455896464	-3.621270264
Ferns	Dennstaedtiaceae	*Lindsaea lancea var falcata*	1.782327174	-0.342286633	-4.057808216
Ferns	Dennstaedtiaceae	*Lindsaea lancea var lancea*	-2.045574475	-1.006419601	-1.531123503
Trees	Clusiaceae	*Lorostemon coelhoi*	-0.859843375	-0.356575342	-1.38240474
Trees	Malvaceae	*Lueheopsis rosea*	-2.620493821	-0.851901964	-1.736389276
Trees	Euphorbiaceae	*Mabea* sp.	-1.06780776	-0.772434353	0.252892131
Trees	Euphorbiaceae	*Mabea angularis*	-0.269934187	-0.829342166	-1.745276599
Trees	Euphorbiaceae	*Mabea piriri*	1.555773612	-0.184903474	0.309938708
Trees	Euphorbiaceae	*Mabea speciosa*	-1.256936964	1.631003564	-1.84083491
Trees	Euphorbiaceae	*Mabea subsessilis*	1.783350663	-0.631658522	-0.464951512
Trees	Fabaceae	*Macrolobium limbatum*	2.143697345	1.297655071	-2.902186702
Trees	Fabaceae	*Macrolobium microcalyx*	0.915228021	-0.360919318	0.85338654
Trees	Fabaceae	*Macrolobium* sp.2	0.150043991	-0.788769397	-3.953646342
Trees	Fabaceae	*Macrolobium suaveolens*	1.563585907	-0.98755902	-1.052235177
Trees	Sapotaceae	*Manilkara* sp.	-1.062117988	-1.194435381	0.191383117
Trees	Sapotaceae	*Manilkara bidentata*	-2.413991366	-0.916069265	0.023059667
Trees	Sapotaceae	*Manilkara cavalcantei*	-1.180293747	-0.899080588	-2.285223152
Herbs	Cyperaceae	*Mapania sylvatica*	-0.797082314	0.546288384	-1.033102026
Trees	Moraceae	*Maquira calophylla*	-1.814739807	-0.981002492	-1.786043397
Trees	Moraceae	*Maquira sclerophylla*	-1.482888193	2.202461465	-2.294708735
Trees	Myrtaceae	*Marlierea umbraticola*	-0.641942858	-1.017366012	-0.101778844

Trees	Arecaceae	*Mauritia flexuosa*	0.521736913	0.884238889	-2.361601696
Palms	Arecaceae	*Maximiliana maripa*	-0.471605602	-0.788784819	-0.320587653
Trees	Celastraceae	*Maytenus guianensis*	-0.317747517	-0.02003782	1.144981563
Ferns	Metaxyaceae	*Metaxya rostrata*	0.579308895	0.08146669	-0.442642994
Trees	Lauraceae	*Mezilaurus* sp.	-1.299859697	0.370613286	0.960513371
Trees	Lauraceae	*Mezilaurus duckei*	-1.545463708	-0.643242599	-2.701194211
Trees	Lauraceae	*Mezilaurus itauba*	-2.424417255	-1.239471907	-1.11029022
Trees	Lauraceae	*Mezilaurus itauba* s.l.	0.10326395	-0.329625079	0.533975975
Trees	Melastomataceae	*Miconia* sp.	-1.698143456	-0.202231444	-0.372997218
Trees	Melastomataceae	*Miconia argyrophylla*	-1.761132352	-0.317504632	-0.78134556
Trees	Melastomataceae	*Miconia dispar*	-1.255583744	0.413635334	-1.737128759
Trees	Melastomataceae	*Miconia lepidota*	-0.403808167	2.101482532	-0.741041777
Trees	Melastomataceae	*Miconia minutiflora*	-0.931502978	-0.327805151	0.047268707
Trees	Melastomataceae	*Miconia phanerostila*	-1.067598469	2.064786102	-1.131818177
Trees	Melastomataceae	*Miconia pyrifolia*	-0.485480166	0.344442173	-1.104495431
Trees	Euphorbiaceae	*Micrandra siphonioides*	1.709327639	1.514855972	-4.47654225
Trees	Euphorbiaceae	*Micrandra spruceana*	0.677629793	-0.068674964	-2.65875892
Trees	Sapotaceae	*Micropholis* sp.	0.638789976	0.779787491	0.937420953
Trees	Sapotaceae	*Micropholis casiquiarensis*	-0.690634771	-1.121841086	-0.472557511
Trees	Sapotaceae	*Micropholis cylindrocarpa*	-1.354080503	1.49819866	-1.424021975
Trees	Sapotaceae	*Micropholis guyanensis*	0.840227561	0.190235451	-1.462565919
Trees	Sapotaceae	*Micropholis mensalis*	0.144795604	0.13714238	-0.791142183
Trees	Sapotaceae	*Micropholis* sp.	0.544201378	0.338259671	-1.942904055
Trees	Sapotaceae	*Micropholis splendens*	1.696759428	-0.84950214	-1.313242722
Trees	Sapotaceae	*Micropholis trunciflora*	-0.43565352	-0.861195392	-1.542836787
Trees	Sapotaceae	*Micropholis venulosa*	0.932780517	1.246628719	-0.370216056
Trees	Sapotaceae	*Micropholis williamii*	-2.326372364	-0.670965535	-0.446640556
Trees	Olacaceae˜	*Minquartia* sp.	0.697054125	2.246341416	-0.518237426
Trees	Olacaceae˜	*Minquartia guianensis*	-3.486831397	0.727180335	-1.789286691
Trees	Fabaceae	*Monopteryx inpae*	0.740030319	3.585027305	-2.379768057

Herbs	Marantaceae	*Monotagma densiflorum*	-0.533996876	-0.754597121	-0.524141165
Herbs	Marantaceae	*Monotagma spicatum*	2.541048475	0.206979677	-0.673454547
Herbs	Marantaceae	*Monotagma tomentosum*	0.611698656	-0.277854534	-2.084902371
Herbs	Marantaceae	*Monotagma vaginatum*	0.716805103	-1.000895548	-2.304358732
Trees	Clusiaceae	*Moronobea coccinea*	-0.782634658	-0.080736504	0.992474294
Trees	Melastomataceae	*Mouriri* sp.	-1.918635822	-0.650330771	-0.851343228
Trees	Melastomataceae	*Mouriri angulicosta*	-1.770049728	1.932921142	-0.845095675
Trees	Melastomataceae	*Mouriri collocarpa*	-1.240462135	-0.36450096	-1.965338362
Trees	Melastomataceae	*Mouriri dimorphandra*	-0.937536817	0.381557521	-1.23342068
Trees	Melastomataceae	*Mouriri duckeana*	-1.760385005	-0.325226379	-1.127021722
Trees	Melastomataceae	*Mouriri duckeanoides*	-0.096190697	0.536438124	1.289927714
Trees	Melastomataceae	*Mouriri huberi*	-0.993965112	0.027785957	0.527927898
Trees	Melastomataceae	*Mouriri lunatanthera*	-1.05987095	-0.875926349	-0.291568981
Trees	Melastomataceae	*Mouriri nigra*	2.224671756	1.268642803	-1.285700889
Trees	Melastomataceae	*Mouriri torquata*	-0.291149175	-0.196315327	-0.610168362
Trees	Myrtaceae	*Myrcia* sp.	-1.347834617	-0.497814754	-1.812395252
Trees	Myrtaceae	*Myrcia fallax*	1.454847604	-0.885530137	-0.199899528
Trees	Myrtaceae	*Myrcia magnoliifolia*	-0.787483458	-0.315329429	0.825698141
Trees	Moraceae	*Naucleopsis* sp.	-0.961911711	0.255599222	-1.171123579
Trees	Moraceae	*Naucleopsis caloneura*	-2.773090351	-0.696423645	-2.337442407
Trees	Moraceae	*Naucleopsis ulei*	-1.162570278	1.985881727	-2.250254533
Herbs	Gesneriaceae˜	*Nautilocalyx pictus*	1.325946793	-0.132525971	0.096985805
Trees	Euphorbiaceae	*Nealchornea yapurensis*	-0.516492736	-0.357561399	-1.134179818
Trees	Nyctaginaceae	*Neea* sp.	-2.185253681	1.275042278	-0.850325634
Trees	Nyctaginaceae	*Neea floribunda*	-0.365339846	-0.907320812	-0.845534037
Trees	Nyctaginaceae	*Neea madeirana*	-1.355586094	-0.812151741	-1.096402661
Trees	Nyctaginaceae	*Neea oppositifolia*	-0.809624393	-0.869623817	-2.10359887
Trees	Nyctaginaceae	*Neea ovalifolia*	-0.860844847	-1.196050839	-0.892711016
Trees	Lauraceae	*Ocotea* sp.	-1.782233776	0.922821174	-1.012334242
Trees	Lauraceae	*Ocotea ceanothifolia*	0.332007461	-0.908353293	0.028914561

Trees	Lauraceae	*Ocotea cinerea*	-1.893633064	-1.066329304	-1.649716177
Trees	Lauraceae	*Ocotea cujumari*	-0.807918865	0.127506223	0.779140003
Trees	Lauraceae	*Ocotea immersa*	1.234863683	-0.735299182	-2.729910467
Trees	Lauraceae	*Ocotea matogrossensis*	-1.609894676	-0.526188452	-0.433686996
Trees	Lauraceae	*Ocotea myriantha*	1.39308161	0.132096364	0.564520254
Trees	Lauraceae	*Ocotea nigrescens*	-1.738582417	-0.225273104	0.969389868
Trees	Lauraceae	*Ocotea nitida*	-0.23938503	0.355965118	0.986637859
Trees	Lauraceae	*Ocotea percurrens*	-1.750704679	-0.783361143	-1.126435676
Trees	Lauraceae	*Ocotea puberula*	0.104406765	-0.686367179	-1.486795689
Trees	Lauraceae	*Ocotea rhodophylla*	-0.146908689	2.721315044	-0.586031416
Trees	Lauraceae	*Ocotea rhynchophylla*	1.098750365	-0.751639807	-2.186218324
Trees	Lauraceae	*Ocotea* sp.1	-1.020006189	-0.46642997	-0.525094408
Trees	Lauraceae	*Ocotea* sp.2	-1.213898867	-0.67559217	-1.042101168
Trees	Lauraceae	*Ocotea* sp.3	-0.997095365	-0.487009636	0.153373819
Trees	Lauraceae	*Ocotea splendens*	-1.109692904	-0.288869602	-0.706888636
Trees	Lauraceae	*Ocotea subterminalis*	-1.004524405	-0.109273809	0.394997114
Palms	Arecaceae	*Oenocarpus bacab*	-3.714869826	-1.35585282	-2.610150249
Palms	Arecaceae	*Oenocarpus bataua*	2.416614768	-0.425499409	-4.471637013
Palms	Arecaceae	*Oenocarpus minor*	-3.15402829	-0.732895835	-1.629202119
Trees	Fabaceae	*Ormosia* sp.	-0.297739195	2.305170108	-1.206662278
Trees	Fabaceae	*Ormosia grandiflora*	0.675193035	-0.587790168	-0.783194177
Trees	Fabaceae	*Ormosia grossa*	1.924762498	-0.508524619	-1.875877462
Trees	Fabaceae	*Ormosia paraensis*	-1.100385404	-0.139165306	-2.885095026
Trees	Myristicaceae	*Osteophloeum platyspermum*	-0.054474601	1.299916727	-2.006186628
Trees	Ochnaceae	*Ouratea* sp.	1.737458742	-0.052442524	0.015781323
Trees	Ochnaceae	*Ouratea discophora*	0.427667546	-0.363040036	0.113775284
Lianas	Bignoniaceae	*Pachyptera aromatica*	-2.73840867	-1.363047355	-2.162001065
Herbs	Orchidaceae	*Palmorchis sobralioides*	-1.319613096	-0.386136165	0.591651817
Herbs	Poaceae	*Pariana campestris*	0.563786998	-0.673127141	-1.426845193
Herbs	Poaceae	*Pariana graciles*	-2.243681544	1.102727595	-1.363239037

Herbs	Poaceae	*Pariana radiciflora*	1.05744876	-0.905629431	2.750625582
Herbs	Poaceae	*Pariana* sp.2	1.499992028	-0.319110786	-3.383592019
Trees	Chrysobalanaceae	*Parinari excelsa*	-1.393682867	-1.115789309	-1.107640306
Trees	Chrysobalanaceae	*Parinari parvifolia*	-0.903695338	-0.917999182	0.055981932
Trees	Fabaceae	*Parkia* sp.	-0.982033523	-0.396438343	0.064284078
Trees	Fabaceae	*Parkia igneiflora*	-0.466866358	-0.789284879	0.867860927
Trees	Fabaceae	*Parkia multijuga*	-0.920993067	0.490266472	-1.107908595
Trees	Fabaceae	*Parkia nitida*	-0.86207083	-0.014270488	-0.886769463
Trees	Fabaceae	*Parkia panurensis*	0.947191636	0.378220848	-2.637608233
Trees	Fabaceae	*Parkia pendula*	-1.245880855	-0.342648832	-0.035648269
Trees	Fabaceae	*Parkia velutina*	1.481454878	2.421028894	-2.446614199
Trees	Violaceae	*Paypayrola grandiflora*	0.074092396	1.607449026	0.322671245
Trees	Fabaceae	*Peltogyne* sp.	0.636313837	2.452776162	-0.947758862
Trees	Fabaceae	*Peltogyne catingae*	-0.559183951	0.319444397	-0.31804455
Trees	Fabaceae	*Peltogyne excelsa*	-1.463581083	-0.922331551	-2.161213149
Trees	Fabaceae	*Peltogyne paniculata*	-1.278330245	1.85221624	-0.159402391
Herbs	Bromeliaceae	*Pepinia sprucei*	1.327848787	-0.802988902	-2.395084671
Trees	Peraceae	*Pera* sp.	-0.447381726	3.627850025	-0.442841658
Trees	Peraceae	*Pera glabrata*	-0.847683935	0.288407519	0.378944828
Trees	Peraceae	*Pera schomburgkiana*	-0.496541196	-0.117903275	-0.6372959
Trees	Moraceae	*Perebea mollis*	-1.126353242	0.525969925	-1.476327133
Trees	Peridiscaceae	*Peridiscus lucidus*	1.229679135	3.040030554	-4.402673048
Herbs	Strelitziaceae	*Phenakospermum guyanense*	1.69069411	0.062142697	-1.052708135
Shrubs	Piperaceae	*Piper alatabaccum*	-1.719386878	0.234882189	-1.0859352
Shrubs	Piperaceae	*Piper baccans*	1.36639314	-0.930820905	1.007998883
Shrubs	Piperaceae	*Piper bartlingianum*	-3.229965695	0.139600555	-2.327089696
Shrubs	Piperaceae	*Piper capitarianum*	-1.274676863	0.147654668	-0.367410566
Shrubs	Piperaceae	*Piper curtistilum*	-1.011665338	-1.147036709	-0.004920112
Shrubs	Piperaceae	*Piper cyrtopodon*	0.262939813	-0.247262734	0.110644784
Shrubs	Piperaceae	*Piper duckei*	-1.271727524	0.262323061	-1.541068976

Shrubs	Piperaceae	*Piper durilignum*	-0.074028949	0.262925382	0.474823918
Shrubs	Piperaceae	*Piper erectipilum*	-1.594751332	-0.403027561	-2.117777066
Shrubs	Piperaceae	*Piper gurupanum*	-1.336686496	1.269629618	-0.935493756
Shrubs	Piperaceae	*Piper humaytanum*	1.114545218	-0.714211279	-0.836393183
Shrubs	Piperaceae	*Piper humillimum*	-1.077077547	0.701573625	-1.466852686
Shrubs	Piperaceae	*Piper liesneri*	1.410759017	0.758936694	-0.619490776
Shrubs	Piperaceae	*Piper mastersianum*	-0.820603841	0.149808053	-0.788717856
Shrubs	Piperaceae	*Piper mourai*	-0.888961969	-0.670167007	-0.751849364
Shrubs	Piperaceae	*Piper* sp.1	0.240717124	0.491320058	0.036366864
Trees	Fabaceae	*Platymiscium duckei*	-0.592670864	2.607701093	-0.909950239
Lianas	Bignoniaceae	*Pleonotoma albiflora*	-1.279827094	-1.92440022	-2.489990896
Lianas	Bignoniaceae	*Pleonotoma dendrotricha*	-0.702780411	-0.991146885	-0.411027518
Herbs	Cyperaceae	*Pleurostachys sparsiflora*	-3.054431464	-0.738223153	-1.005923438
Trees	Peraceae	*Pogonophora schomburgkiana*	-2.113417094	2.610792524	-0.105409854
Ferns	Dryopteridaceae	*Polybotrya osmundaceae*	0.760334798	3.646907108	-0.221818783
Trees	Metteniusaceae	*Poraqueiba*	-0.821083024	-0.011994146	-0.557787965
Trees	Metteniusaceae	*Poraqueiba guianensis*	-2.469461897	0.471560075	-0.843040387
Trees	Urticaceae	*Pourouma*	0.19759586	0.92886628	-1.304686959
Trees	Urticaceae	*Pourouma bicolor*	-0.773057479	0.926580701	-1.348598503
Trees	Urticaceae	*Pourouma guianensis*	-0.240258411	-0.940332576	-1.696487362
Trees	Urticaceae	*Pourouma minor*	0.112796583	-1.139770693	-2.140797116
Trees	Urticaceae	*Pourouma ovata*	0.009458947	-1.484332177	-4.207821344
Trees	Urticaceae	*Pourouma tomentosa*	0.032723219	-1.192539968	-2.36607788
Trees	Sapotaceae	*Pouteria* sp.	-1.430115677	0.238871117	-0.169287577
Trees	Sapotaceae	*Pouteria* aff. *cuspidata*	-1.355867437	-0.100928101	0.29082076
Trees	Sapotaceae	*Pouteria* aff. *gardneri*	-0.756221536	3.811258645	0.426186059
Trees	Sapotaceae	*Pouteria ambelaniifolia*	-0.467024774	-0.71177309	-0.177170561
Trees	Sapotaceae	*Pouteria anomala*	-1.537427031	-1.361547008	-0.103083062
Trees	Sapotaceae	*Pouteria caimito*	-1.984977507	-0.491846358	-0.700537669
Trees	Sapotaceae	*Pouteria campanulata*	-1.785217321	0.710133419	-1.192211222

Trees	Sapotaceae	*Pouteria cladantha*	-1.372876136	-0.329826226	1.699235302
Trees	Sapotaceae	*Pouteria cuspidata*	-1.774558232	-0.533374117	0.905368707
Trees	Sapotaceae	*Pouteria durlandii*	-2.148982123	-0.640119319	-2.200960225
Trees	Sapotaceae	*Pouteria engleri*	-0.621049341	-0.334057797	-0.677123176
Trees	Sapotaceae	*Pouteria erythrochrysa*	-1.550924209	-0.259846037	0.975386
Trees	Sapotaceae	*Pouteria eugeniifolia*	-1.747782149	-0.067952299	-0.836023036
Trees	Sapotaceae	*Pouteria filipes*	-2.38010374	-0.869113171	-1.594297081
Trees	Sapotaceae	*Pouteria fimbriata*	-1.279575312	1.688247508	-1.697240622
Trees	Sapotaceae	*Pouteria flavilatex*	-1.7717557	0.878858401	-1.420371465
Trees	Sapotaceae	*Pouteria freitasii*	-1.897555634	-0.409555725	0.145245479
Trees	Sapotaceae	*Pouteria guianensis*	-2.161212034	1.26385647	-1.397531937
Trees	Sapotaceae	*Pouteria hispida*	-1.232726145	-0.233784591	-0.280722816
Trees	Sapotaceae	*Pouteria laevigata*	-0.151014272	2.211878376	1.274712607
Trees	Sapotaceae	*Pouteria macrophylla*	-1.160702399	0.008455206	-1.142348841
Trees	Sapotaceae	*Pouteria manaosensis*	-1.379502408	-0.646695566	-0.914569784
Trees	Sapotaceae	*Pouteria maxima*	2.090690774	-1.386294177	-1.490440438
Trees	Sapotaceae	*Pouteria minima*	-0.916547785	-1.125882224	-0.272981271
Trees	Sapotaceae	*Pouteria oblanceolata*	-1.068881615	-0.937399149	-0.190333502
Trees	Sapotaceae	*Pouteria opposita*	-1.242063925	-1.232916861	-3.223401634
Trees	Sapotaceae	*Pouteria pallens*	-0.671284837	0.912118488	-0.29352091
Trees	Sapotaceae	*Pouteria peruviensis*	-0.7562903	-0.271399509	0.620031592
Trees	Sapotaceae	*Pouteria petiolata*	0.028170847	-0.83610806	0.426730217
Trees	Sapotaceae	*Pouteria platyphylla*	-1.217714416	0.118585266	-0.269007367
Trees	Sapotaceae	*Pouteria reticulata*	-2.331466311	-1.093473109	-0.997006941
Trees	Sapotaceae	*Pouteria retinervis*	-1.184316685	-0.597798103	-0.540285253
Trees	Sapotaceae	*Pouteria stipulifera*	-0.891977212	-0.36820901	-0.032683159
Trees	Sapotaceae	*Pouteria torta*	-0.814837139	-0.398178759	-2.800567858
Trees	Sapotaceae	*Pouteria venosa*	-0.01457139	0.930662723	-1.687417739
Trees	Sapotaceae	*Pouteria vernicosa*	-1.385157142	-0.796286391	-0.026227156
Trees	Sapotaceae	*Pouteria virescens*	-2.07299455	-0.809694533	-0.719670242

Trees	Sapotaceae	*Pouteria williamii*	2.143296457	-0.689058309	-1.213731492
Trees	Sapotaceae	*Pradosia cochlearia*	1.355978949	0.400217342	1.442652054
Trees	Sapotaceae	*Pradosia decipiens*	1.631312891	-0.925741651	-1.923593974
Trees	Sapotaceae	*Pradosia verticillata*	-0.962343902	-0.698043769	-0.634449328
Trees	Burseraceae	*Protium* sp.	2.546496263	-0.354104512	1.784727188
Trees	Burseraceae	*Protium altsonii*	-1.660140558	1.060771109	-1.407503231
Trees	Burseraceae	*Protium amazonicum*	-0.371676679	-1.098155178	-1.753939915
Trees	Burseraceae	*Protium apiculatum*	-3.335232066	-1.07376102	-1.111851505
Trees	Burseraceae	*Protium aracouchini*	1.215559965	-0.336321046	-1.61001945
Trees	Burseraceae	*Protium crassipetalum*	-0.087330071	-1.09253939	1.081252882
Trees	Burseraceae	*Protium decandrum*	-1.289572927	1.458660812	-2.238528491
Trees	Burseraceae	*Protium divaricatum*	2.278639058	-0.399142848	-2.578781627
Trees	Burseraceae	*Protium ferrugineum*	0.962073086	-0.34159872	0.028718961
Trees	Burseraceae	*Protium gallosum*	-0.896141671	-0.007279925	0.060764797
Trees	Burseraceae	*Protium grandifolium*	2.328427087	-0.420363478	-1.727115353
Trees	Burseraceae	*Protium hebetatum*	-4.568234639	-0.870524325	-2.945689979
Trees	Burseraceae	*Protium heptaphyllum*	2.357196869	-1.077237811	0.124477454
Trees	Burseraceae	*Protium klugii*	1.079722391	-0.309481231	-0.47151273
Trees	Burseraceae	*Protium nitidifolium*	-1.90813816	-1.187020009	-1.529292723
Trees	Burseraceae	*Protium opacum*	1.10098297	-0.266040496	-0.838951572
Trees	Burseraceae	*Protium pallidum*	-0.685586476	2.962825749	-0.719300523
Trees	Burseraceae	*Protium paniculatum*	-2.027354177	-0.544712325	-1.065518478
Trees	Burseraceae	*Protium pilosissimum*	-0.594326679	3.560959211	-0.126344685
Trees	Burseraceae	*Protium polybotryum*	0.234228548	-0.853656248	0.233264458
Trees	Burseraceae	*Protium rubrum*	1.450228323	-1.086626897	0.207295055
Trees	Burseraceae	*Protium* sp.	-0.147936732	-0.610868856	-0.657518619
Trees	Burseraceae	*Protium spruceanum*	-1.526962332	1.176796739	-0.500770979
Trees	Burseraceae	*Protium strumosum*	-2.102814651	0.479901295	-0.20496053
Trees	Burseraceae	*Protium subserratum*	0.598612283	-1.170253531	-0.136363777
Trees	Burseraceae	*Protium trifoliolatum*	-2.233600378	1.410902581	-0.550351562

Trees	Sapindaceae	*Pseudima* sp.1	-1.657229203	-0.704941402	-0.475683938
Trees	Sapindaceae	*Pseudolmedia* sp.	-0.8868003	-0.039375274	0.705853758
Trees	Moraceae	*Pseudolmedia laevigata*	-1.486957386	-0.166883937	-1.835061671
Trees	Moraceae	*Pseudolmedia laevis*	-1.889431377	1.770893494	-1.93344087
Trees	Fabaceae	*Pseudopiptadenia psilostachya*	-2.003464945	-0.539554465	0.596092935
Trees	Annonaceae	*Pseudoxandra coriacea*	-0.768672986	-0.541393863	0.900032441
Shrubs	Rubiaceae	*Psychotria astrellantha*	-2.972425558	-0.665648192	-0.637982886
Shrubs	Rubiaceae	*Psychotria bahiensis*	1.783669185	0.095686933	-3.518319597
Shrubs	Rubiaceae	*Psychotria brachybotrya*	-2.189376089	0.953359804	-1.467307874
Shrubs	Rubiaceae	*Psychotria cincta*	-1.876072792	0.192618506	-0.115822058
Shrubs	Rubiaceae	*Psychotria deinocalyx*	-0.755365216	-0.481579206	-1.797611485
Shrubs	Rubiaceae	*Psychotria iodotricha*	-1.412597786	0.371175624	-0.64898057
Shrubs	Rubiaceae	*Psychotria manauensis*	-1.075026061	0.245609048	-0.835513771
Shrubs	Rubiaceae	*Psychotria mapourioides*	-0.366432588	-0.260787415	1.318051635
Shrubs	Rubiaceae	*Psychotria medusula*	0.094969408	1.804034348	0.672501604
Shrubs	Rubiaceae	*Psychotria pacimonica*	0.730669954	3.60866115	0.166323371
Shrubs	Rubiaceae	*Psychotria podocephala*	-1.957660898	-0.564288022	-1.246402505
Shrubs	Rubiaceae	*Psychotria polycephala*	-0.322637614	-0.353590862	-2.143148439
Shrubs	Rubiaceae	*Psychotria prancei*	-2.163860166	0.097121024	-1.242163223
Shrubs	Rubiaceae	*Psychotria rhombibractea*	-3.333970586	-0.383615955	-3.227846244
Shrubs	Rubiaceae	*Psychotria sciaphila*	-0.842482938	2.562868695	-2.810250151
Shrubs	Rubiaceae	*Psychotria sphaerocephala*	-0.843854669	-1.148245443	-2.08777969
Trees	Malpighiaceae	*Pterandra arborea*	-0.75713884	3.362984235	0.254887657
Trees	Fabaceae	*Pterocarpus officinalis*	1.027677961	0.87193532	-0.684290744
Trees	Fabaceae	*Pterocarpus rohrii*	0.517088647	0.447215245	-0.886844415
Trees	Olacaceae˜	*Ptychopetalum olacoides*	-1.061031587	-0.528913177	0.170302189
Trees	Vochysiaceae	*Qualea* sp.	-1.059062696	2.537891607	1.263176649
Trees	Vochysiaceae	*Qualea paraensis*	-1.885367598	1.262974775	-1.662058732
Trees	Vochysiaceae	*Qualea* sp.1	0.594296094	-0.496270134	1.105767701
Trees	Malvaceae	*Quararibea* sp.	-0.46290798	3.781456521	-1.427683551

Trees	Malvaceae	*Quararibea ochrocalyx*	-1.485819709	-0.822705035	-0.403143373
Trees	Quiinaceae	*Quiina* cf. *negrensis*	-0.94618209	0.079623429	0.486803559
Trees	Quiinaceae	*Quiina negrensis*	-1.328941537	-0.550642786	-0.418402128
Herbs	Rapateaceae	*Rapatea paludosa*	1.706329789	0.056069564	-2.273340649
Herbs	Zingiberaceae	*Renealmia floribunda*	0.874441905	-0.302099192	-0.115502236
Trees	Rhabdodendraceae	*Rhabdodendron amazonicum*	-0.589480576	-0.094353295	-1.030748325
Trees	Rhabdodendraceae	*Rhigospira quadrangularis*	0.266743015	-0.127529868	-2.452798858
Trees	Rhabdodendraceae	*Rhodognaphalopsis duckei*	0.188732933	-0.662010102	-0.256558903
Trees	Lauraceae	*Rhodostemonodaphne grandis*	1.502456932	-0.479055962	-0.788829741
Trees	Lauraceae	*Rhodostemonodaphne negrensis*	-0.795311922	-0.699424127	-0.517199378
Trees	Lauraceae	*Rhodostemonodaphne peneia*	-0.962011649	-0.38234707	-2.050278058
Trees	Lauraceae	*Rhodostemonodaphne recurva*	-0.354976543	-0.744040608	0.104011573
Trees	Violaceae	*Rinorea* sp.	-1.126798223	3.455529272	-1.064106467
Trees	Violaceae	*Rinorea amapensis*	-0.710737026	2.651112494	1.911508089
Trees	Violaceae	*Rinorea guianensis*	-1.175426754	-0.149583904	-1.785046673
Trees	Violaceae	*Rinorea racemosa*	-2.752658592	-1.931689773	-3.115574439
Trees	Annonaceae	*Rollinia insignis*	-0.867918778	-0.790026293	0.609007939
Trees	Linaceae	*Roucheria punctata*	1.231207177	-1.251625293	-2.238474298
Trees	Vochysiaceae	*Ruizterania albiflora*	1.452255023	-0.663930963	2.75193315
Trees	Vochysiaceae	*Ruizterania cassiquiarensis*	1.747776722	-0.146866813	1.458329546
Trees	Humiriaceae	*Sacoglottis* sp.	1.432913802	-1.088931431	0.247577765
Trees	Humiriaceae	*Sacoglottis ceratocarpa*	1.531052803	0.855071455	-2.945713941
Trees	Humiriaceae	*Sacoglottis guianensis*	-2.24758877	-0.954472153	-2.2250968
Trees	Humiriaceae	*Sacoglottis mattogrossensis*	-1.601429947	-0.154045524	0.011425894
Trees	Celastraceae	*Salacia* sp.	-1.499622257	-0.713201761	-0.252390818
Trees	Sapotaceae	*Sarcaulus brasiliensis*	-0.922270183	2.155897052	-2.093711594
Herbs	Rapateaceae	*Saxofredericia cordata*	1.6368569	-0.400009753	-3.634421
Herbs	Rapateaceae	*Saxofridericia* sp.	-1.495251829	-0.861743414	-0.298690664
Ferns	Schizaeaceae	*Schizaea elegans*	-1.106386382	2.299692527	-1.030049843
Herbs	Cyperaceae	*Scleria secans*	-0.527526052	0.942469873	1.132790779

Trees	Fabaceae	*Sclerolobium*	-1.756121946	-0.980373188	-0.361542315
Trees	Fabaceae	*Sclerolobium chrysophyllum*	-1.356945043	-0.232788374	1.120104723
Trees	Fabaceae	*Sclerolobium guianense*	-0.335882216	1.466000788	-0.882885302
Trees	Fabaceae	*Sclerolobium melanocarpum*	-0.785137954	-1.248040533	-1.773983672
Trees	Fabaceae	*Sclerolobium micropetalum*	-1.459826572	-0.259092922	-1.782344805
Trees	Fabaceae	*Sclerolobium setiferum*	-0.83990914	-0.016265606	-1.96150076
Trees	Fabaceae	*Sclerolobium* sp.1	0.609385677	-0.747938864	-0.613924797
Trees	Fabaceae	*Sclerolobium* sp.6	-0.27014441	-0.05446243	-0.156703942
Trees	Malvaceae	*Scleronema micranthum*	0.539126357	0.250180929	1.874418649
Ferns	Selaginellaceae	*Selaginella palmiformis*	-0.641338782	-1.137826513	-0.663910273
Ferns	Selaginellaceae	*Selaginella parkeri*	1.293225085	1.634807893	-1.618017637
Trees	Euphorbiaceae	*Senefeldera macrophylla*	0.421340583	-0.928651904	-1.227184688
Trees	Lauraceae	*Sextonia rubra*	-0.593791375	1.341174814	0.063253977
Trees	Simaroubaceae	*Simaba* sp.	-0.153087301	0.13926986	0.595864018
Trees	Simaroubaceae	*Simaba cedron*	-0.778186502	0.045114908	0.697932793
Trees	Simaroubaceae	*Simaba polyphylla*	-0.973909155	-0.787180046	-0.963493595
Trees	Simaroubaceae	*Simaba* sp. nova	-0.558633781	-1.172315894	0.405089318
Trees	Simaroubaceae	*Simarouba amara*	0.728272649	0.755475328	-1.231285888
Trees	Siparunaceae	*Siparuna* sp.	-0.092653888	0.212806353	-1.623847366
Trees	Siparunaceae	*Siparuna cuspidata*	-1.022091389	-0.289633225	0.237528078
Trees	Siparunaceae	*Siparuna decipiens*	-2.317506477	-0.336602725	-1.469543294
Trees	Siparunaceae	*Siparuna glycycarpa*	-0.555072322	-0.534725831	0.510548468
Trees	Siparunaceae	*Siparuna guianensis*	-0.799824444	-0.530842285	-0.564238114
Trees	Siparunaceae	*Siparuna sarmentosa*	-1.110553235	-1.063852548	-1.261984533
Trees	Elaeocarpaceae	*Sloanea* sp.	0.602991767	-0.441237744	1.737836734
Trees	Elaeocarpaceae	*Sloanea excelsa*	-0.901152243	-0.875040951	-1.766197669
Trees	Elaeocarpaceae	*Sloanea floribunda*	1.032655884	0.445703826	1.034253856
Trees	Elaeocarpaceae	*Sloanea guianensis*	1.011117029	0.537505755	0.588617037
Trees	Elaeocarpaceae	*Sloanea latifolia*	0.459878611	2.358902731	1.32516236
Trees	Elaeocarpaceae	*Sloanea nitida*	1.74991228	-0.633473318	0.416602925

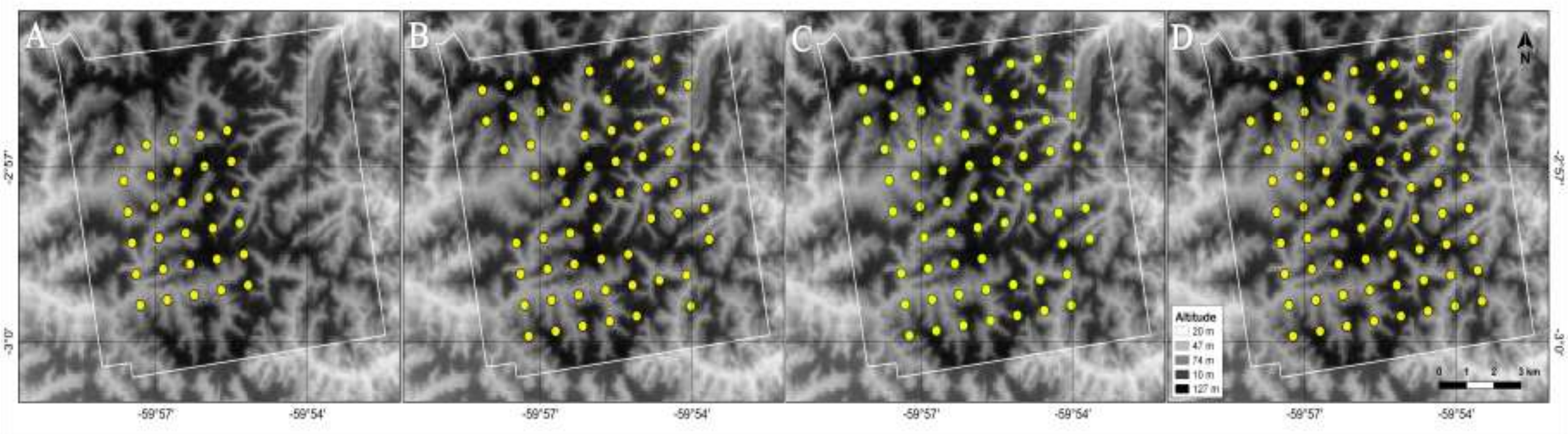
Trees	Elaeocarpaceae	*Sloanea pubescens*	0.461015214	-0.088459865	-1.097343474
Trees	Elaeocarpaceae	*Sloanea rufa*	-0.783003624	-0.756262729	-1.378551721
Trees	Elaeocarpaceae	*Sloanea schomburgkii*	-0.88365384	2.93809379	-0.896321176
Trees	Elaeocarpaceae	*Sloanea* sp.1	-0.973820915	0.608945285	0.59890293
Trees	Elaeocarpaceae	*Sloanea* sp.2	-0.802090664	-0.416665275	-0.383456906
Trees	Elaeocarpaceae	*Sloanea synandra*	0.547667453	-0.251592161	0.923679688
Palms	Arecaceae	*Socratea exorrhiza*	2.649562392	-0.170806858	-0.125342918
Trees	Moraceae	*Sorocea* sp.	-1.212184925	-1.3420849	-0.28941654
Trees	Moraceae	*Sorocea guilleminiana*	-1.793486797	-1.241831487	-1.682259697
Herbs	Rapateaceae	*Spathanthus unilateralis*	1.414673018	-0.08330975	-3.657234267
Herbs	Rapateaceae	*Spathelia excelsa*	-0.576422746	-0.730576596	-0.096904208
Trees	Malvaceae	*Sterculia* sp.	-0.285287983	-0.71313453	1.086266879
Trees	Malvaceae	*Sterculia duckeana*	1.255709802	-0.3699548	0.003194925
Trees	Malvaceae	*Sterculia excelsa*	-1.003582474	-0.1208253	-0.438730218
Trees	Malvaceae	*Sterculia frondosa*	1.244871026	-0.638876609	0.146283247
Trees	Malvaceae	*Sterculia pruriens*	0.499058878	-0.314410817	-0.642750282
Trees	Fabaceae	*Stryphnodendron*	-0.606913727	-1.064376265	-0.989004706
Trees	Fabaceae	*Stryphnodendron guianense*	-0.646459862	0.112300632	0.169624439
Trees	Fabaceae	*Stryphnodendron paniculatum*	-1.079333491	-0.880671857	-1.278249635
Trees	Fabaceae	*Stryphnodendron pulcherrimum*	-0.876562231	-0.229592495	-1.042169897
Trees	Fabaceae	*Stryphnodendron racemiferum*	-2.561345546	-1.023409118	-1.273129149
Trees	Fabaceae	*Swartzia* sp.	0.954368856	-0.637482994	0.727694448
Trees	Fabaceae	*Swartzia arborescens*	-0.144678596	-0.663838926	0.310275959
Trees	Fabaceae	*Swartzia brachyrachis*	-0.797861205	-0.29415078	0.592343943
Trees	Fabaceae	*Swartzia corrugata*	0.157936379	-0.138662937	0.558440623
Trees	Fabaceae	*Swartzia cuspidata*	1.648955612	-0.758525877	0.832957995
Trees	Fabaceae	*Swartzia ingifolia*	-2.015358687	-0.835573271	-1.264489556
Trees	Fabaceae	*Swartzia lamellata*	-0.536875276	-0.890293107	-1.419053201
Trees	Fabaceae	*Swartzia oblanceolata*	1.05039844	-0.24251323	1.125395941
Trees	Fabaceae	*Swartzia panacoco*	2.135835784	2.710449597	0.542300748

Trees	Fabaceae	*Swartzia polyphylla*	1.867985173	-0.753359674	0.515967093
Trees	Fabaceae	*Swartzia recurva*	-3.084435968	-0.573397429	-0.215326067
Trees	Fabaceae	*Swartzia reticulata*	0.096328893	-0.186217255	-1.055989721
Trees	Fabaceae	*Swartzia schomburgkii*	2.185342362	-0.947526906	0.800063767
Trees	Fabaceae	*Swartzia tessmannii*	0.258970162	2.631672371	-0.017139059
Trees	Fabaceae	*Swartzia tomentifera*	-0.336143525	-0.573752796	-0.720697079
Trees	Fabaceae	*Swartzia ulei*	2.099590155	0.370138373	-0.674454707
Palms	Arecaceae	*Syagrus inajai*	-2.126192052	-0.390873567	-1.913359537
Trees	Clusiaceae	*Symphonia globulifera*	1.857078091	-0.717929492	0.802874849
Trees	Bignoniaceae	*Tabebuia serratifolia*	-1.367465592	-0.471485747	-1.732045678
Trees	Apocynaceae	*Tabernaemontana muricata*	-0.793688609	-0.350832551	-0.87923578
Trees	Fabaceae	*Tachigali* sp.	-1.101688638	0.138248348	-1.77547074
Trees	Fabaceae	*Tachigali venusta*	-1.98843	-0.315751019	-0.017842299
Trees	Sapindaceae	*Talisia* sp.	-0.377098577	0.259364046	0.710957197
Trees	Sapindaceae	*Talisia allenii*	0.132490302	0.247698296	0.149861112
Trees	Anacardiacee	*Tapirira guianensis*	-0.301723738	-0.03990982	0.819933536
Trees	Anacardiacee	*Tapirira retusa*	0.092885188	-0.988341819	-1.97037512
Trees	Dichapetalaceae	*Tapura amazonica*	-2.080020734	1.00397921	-2.064080311
Trees	Dichapetalaceae	*Tapura guianensis*	-0.644119761	-1.441125859	-2.208395821
Trees	Dichapetalaceae	*Tapura lanceolata*	0.612835582	-0.693874491	-4.266362016
Trees	Fabaceae	*Taralea oppositifolia*	1.802597262	-0.321832251	-0.81914246
Trees	Burseraceae	*Tetragastris panamensis*	-3.746596348	-0.514234679	-3.086033125
Trees	Malvaceae	*Theobroma subincanum*	0.761806122	2.149490425	-3.176876987
Trees	Malvaceae	*Theobroma sylvestre*	-2.73430651	0.612595186	-1.008814842
Trees	Sapindaceae	*Thyrsodium spruceanum*	-1.260792346	-0.438068832	-0.341974311
Trees	Sapindaceae	*Toulicia guianensis*	-1.343602729	-0.763619542	-0.157733243
Trees	Clusiaceae	*Tovomita* sp.	-1.136193478	-0.829561954	-2.075322757
Trees	Clusiaceae	*Tovomita amazonica*	-0.881412172	-0.859952811	-1.808281159
Trees	Clusiaceae	*Tovomita caloneura*	-0.694585563	-0.337162541	2.196654961
Trees	Clusiaceae	*Tovomita choisyana*	-0.29273064	-1.407654688	-1.782854262

Trees	Clusiaceae	*Tovomita schomburgkii*	-0.541357668	-0.573841888	-1.980444518
Trees	Burseraceae	*Trattinnickia* sp.	-0.895466811	-0.407860501	0.659887465
Trees	Burseraceae	*Trattinnickia burserifolia*	-1.001183872	-0.93696226	-0.011556763
Trees	Burseraceae	*Trattinnickia glaziovii*	-0.945424962	-0.441928287	-0.057808844
Trees	Burseraceae	*Trattinnickia peruviana*	-1.621638769	-0.549230403	-1.549282941
Trees	Burseraceae	*Trattinnickia rhoifolia*	-0.79494987	0.217443527	-1.233309537
Trees	Meliaceae	*Trichilia* sp.	-1.415691559	-0.936136329	-2.510844092
Trees	Meliaceae	*Trichilia* aff. *schomburgkii*	-0.952704131	0.122590692	-0.278590306
Trees	Meliaceae	*Trichilia cipo*	-1.038073267	-0.206338953	-1.300646045
Trees	Meliaceae	*Trichilia micrantha*	-1.246920909	-0.152626515	-0.754598411
Trees	Meliaceae	*Trichilia pallida*	-1.61486559	-0.413611884	1.272554933
Trees	Meliaceae	*Trichilia schomburgkii*	-0.855812057	-0.385340659	-0.733674488
Trees	Meliaceae	*Trichilia septentrionalis*	-1.568952064	-0.010830455	-1.057310672
Ferns	Hymenophyllaceae	*Trichomanes cellulosum*	0.774586529	-0.541928437	-2.19644505
Ferns	Hymenophyllaceae	*Trichomanes elegans*	-0.798835646	-1.212010605	-1.263164136
Ferns	Hymenophyllaceae	*Trichomanes pinnatum*	-2.420697483	1.425287425	-3.304258084
Ferns	Hymenophyllaceae	*Trichomanes* sp.1	-3.190779139	-1.226961319	-3.308036089
Ferns	Hymenophyllaceae	*Trichomanes trollii*	-0.263386674	3.840000789	-1.847255121
Ferns	Tectariaceae	*Triplophyllum dicksonioides*	-3.050164823	1.317453106	-2.79934101
Trees	Moraceae	*Trymatococcus amazonicus*	-3.069194109	0.815524293	-2.309752825
Lianas	Bignoniaceae	*Tynanthus panurensis*	-1.511263461	-0.719735322	-1.843007607
Trees	Annonaceae	*Unonopsis* sp.	-0.920799563	-0.554855379	0.638930994
Trees	Annonaceae	*Unonopsis duckei*	-2.230182431	-1.276048124	-2.535624383
Trees	Annonaceae	*Unonopsis stipitata*	-1.868952455	-0.489851092	-0.699873087
Trees	Humiriaceae	*Vantanea* sp.	1.907169382	0.749253644	0.09071856
Trees	Humiriaceae	*Vantanea guianensis*	0.278387025	-0.731060512	-0.596387087
Trees	Humiriaceae	*Vantanea macrocarpa*	-1.088128711	-0.618825107	0.182192072
Trees	Humiriaceae	*Vantanea micrantha*	-1.31561532	-0.245516942	-1.024896746
Trees	Humiriaceae	*Vantanea parviflora*	1.301997706	0.071517345	-1.344876411
Trees	Fabaceae	*Vatairea paraensis*	2.308896264	-0.690162815	1.575787416

Trees	Fabaceae	*Vatairea sericea*	-1.708457528	-1.368855967	-1.619124298
Trees	Myristicaceae	*Virola* sp.1	1.80172201	-0.670786755	-0.035664163
Trees	Myristicaceae	*Virola caducifolia*	0.310029212	-0.101639538	2.210278569
Trees	Myristicaceae	*Virola calophylla*	0.988771288	1.616373616	-1.24099599
Trees	Myristicaceae	*Virola guggenheimii*	-0.286558387	0.713902286	-2.101907352
Trees	Myristicaceae	*Virola mollissima*	-1.777640218	-0.902795993	-1.484635158
Trees	Myristicaceae	*Virola multicostata*	-0.738189259	-0.544185294	-1.897404335
Trees	Myristicaceae	*Virola multinervia*	-1.471648586	-0.290182012	-0.494101143
Trees	Myristicaceae	*Virola pavonis*	1.311766892	-0.401699992	-2.267809311
Trees	Myristicaceae	*Virola* sp.2	0.594355735	-0.366221237	-1.281715282
Trees	Myristicaceae	*Virola theiodora*	-1.481091055	-0.626676589	0.722971793
Trees	Myristicaceae	*Virola venosa*	-2.478460201	0.158997853	-2.554347468
Trees	Lamiaceae	*Vitex sprucei*	1.249255458	-0.242088755	-3.441177804
Trees	Lamiaceae	*Vitex triflora*	-0.751047109	-0.226498503	0.47924463
Trees	Vochysiaceae	*Vochysia* sp.	-1.264171454	-0.072152907	-0.895316215
Trees	Vochysiaceae	*Vochysia biloba*	-0.332187403	1.135856517	0.307153964
Trees	Vochysiaceae	*Vochysia rufescens*	-0.946038071	-0.037996346	-0.151401429
Trees	Vochysiaceae	*Vochysia* sp.2	-0.392643761	0.109650892	-0.454973664
Trees	Fabaceae	*Vouacapoua pallidior*	0.420038886	3.139338145	-2.695130701
Trees	Rubiaceae	*Warszewiczia schwackei*	-1.206993658	0.632425069	-1.686463567
Trees	Annonaceae	*Xylopia* sp.	1.903652884	-0.488380118	1.33277281
Trees	Annonaceae	*Xylopia amazonica*	-0.299083337	0.468111524	-0.387835397
Trees	Annonaceae	*Xylopia benthamii*	2.373417669	-0.987288139	-0.528127966
Trees	Annonaceae	*Xylopia nitida*	0.242160146	-0.385343827	-0.285691846
Trees	Annonaceae	*Xylopia parviflora*	-0.688227302	2.559058527	1.310357997
Trees	Annonaceae	*Xylopia polyantha*	-0.164950294	0.303058294	1.816717768
Trees	Fabaceae	*Zygia racemosa*	-4.331918178	-1.355643445	-3.300990952
Trees	Fabaceae	*Zygia ramiflora*	-2.044062299	-0.873740787	-0.158110487

Fig. S1 Ducke Reserve in the Central Amazon, Brazil. Darker colors represent higher areas (*plateaus* and *vertentes*) and lighter colors represent lower areas (*baixios*). White line countours the Reserve limits and yellow dots indicate the locations of the 250 m transect permanent plots on a 1 km equidistant sampling grid where it were sampled the lifeforms of A: Lianas, B: Herbs , C: Ferns, D: Trees, palms and shurbs.



CONCLUSÃO GERAL

Existem muitos trabalhos sobre a especialização de espécies, sendo esse um tema recorrente na literatura desde o início do século passado. As medidas de especialização geralmente usam a abundância maior das espécies em certos locais como um indicativo de que a espécie é especialista (naquele mesmo local). Essa é uma maneira pouco eficiente de se avaliar especialização na Amazônia, cujas comunidades são compostas majoritariamente por espécies pouco abundantes. Dessa forma, o índice de especialização adaptado do Standard Effect Size, usado nesse trabalho, parece funcionar muito bem também para esse tipo de comunidade, dado que utiliza medidas do desvio padrão da ocorrência, comparado com um modelo nulo. A principal vantagem desse modelo é que ele pode ser calculado para espécies com poucas ocorrências.

A especialização nos gradientes que medimos varia entre as formas de vida estudadas e não seguem o padrão de biomassa (espécies maiores não são necessariamente mais generalistas que as menores). Isso deve se dar ao fato de que cada forma de vida parece viver em uma faixa variável de tolerância no gradiente. Acreditamos que samambaias, por exemplo, devem tolerar faixas muito maiores do gradiente de soma de bases do que aquele encontrado na área de estudo. Além disso, formas de vida de tamanho intermediário, como as lianas e as palmeiras, foram muito congruentes às respostas aos gradientes, principalmente aos de fertilidade. Essas formas de vida já foram consideradas muito congruentes em gradientes topográficos e também bons substitutos para a comunidade de plantas (veja Landeiro et al. 2012 – referenciado no artigo).

As formas de vida responderam de forma diferente aos três gradientes analisados e, samambaias e árvores, foram aqueles que tiveram diferenças significativas entre os três. A água (HAND) gerou mais especialização na maioria das formas de vida, indicando que é um importante gerador de especialização nas comunidades vegetais. Discordando de nossas hipóteses, o HAND foi o maior gerador de especialização comparado ao fósforo e à soma de bases, dois dos mais importantes nutrientes para as plantas e também muito escassos nos solos da Amazônia Central. Apesar de água estar disponível na maior parte do ano, com uma curta estação seca, algumas espécies parecem ou não tolerar a falta de água nos lugares mais altos (platôs) ou não conseguir lidar com a anóxia e outras adversidades das áreas mais facilmente alagáveis (baixios).

Sugerimos que outros trabalhos busquem entender como as espécies se especializam em certas faixas de gradientes e, como essa especialização difere entre os diferentes grupos funcionais dentro das assembleias comumente estudadas. Além disso, sugerimos o uso mais frequente do HAND nos trabalhos de ecologia, visto que é um excelente preditor da comunidade de plantas e seus aspectos intrínsecos em mesoescala.