The role of topographic-derived hydrological variables in explaining plant species distributions in Amazonia

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ABSTRACT

In Amazonian terra-firme non inundated forests, local floristic composition and species occurrence are explained by water availability as determined by topographic conditions. Topographic complexity can render these conditions quite variable across the landscape and the effects on plant ecological responses are difficult to document. We used a set of topographically defined hydrological metrics to evaluate community composition and single-species responses of four plant groups [pteridophytes (ferns and lycophytes), Melastomataceae, palms (Arecaceae) and Zingiberaceae] to topographic conditions in the middle Juruá River region, in western Brazilian Amazonia. The area spans two geological formations (Içá and Solimões) with contrasting topography. River terraces are also found along the main rivers in the area. Local topographic conditions were approximated by height above the nearest drainage (HAND), slope, and Strahler´s drainage order, all obtained from a SRTM digital elevation model (DEM). Data were analyzed using linear and generalized linear mixed models and regression trees. HAND was most successful in explaining floristic variability for all plant groups, except for Melastomataceae, and was more important in the hilly Içá formation than in the Solimões. Individual occurrences of 57% species were predicted by at least one of the topographic variables, suggesting a marked habitat specialization along topographic gradients. For these species, response models using SRTM-DEM-derived variables gave similar results than models using field-measured topography only. Our results suggest that topographical variables estimated from remote sensing can be used to predict local variation in the structure of plant communities in tropical forests.

KEYWORDS: DEM, geological formations, HAND, vegetation mapping

O papel de variáveis hidrológicas derivadas da topografia em explicar a distribuição de espécies de plantas na Amazônia

RESUMO

Nas florestas de terra firme não inundáveis da Amazônia, a composição florística e a ocorrência de espécies podem ser explicadas pela disponibilidade hídrica relacionada com a topografia. Dada a complexidade topográfica, a disponibilidade de água pode ser bastante variável e seus efeitos na resposta das plantas, difícil de documentar. Neste estudo avaliamos as respostas individuais de espécie de quatro grupos de plantas [pteridófitas (samambaias e licófitas), Melastomataceae, palmeiras (Arecaceae) e Zingiberaceae] às condições topográficas na região do médio Rio Juruá, no oeste da Amazônia brasileira. A área abrange duas formações geológicas (Içá e Solimões) com topografias contrastantes. Terras fluviais também são encontrados ao longo dos rios principais. As condições topográficas foram medidas usando a altura acima da drenagem mais próxima (HAND), declividade e orden de drenagem de Strahler, todas obtidas a partir de um modelo digital de elevação SRTM-DEM. Os dados foram analisados usando modelos lineares generalizados mistos e árvores de regressão. HAND foi a principal variável explicativa da composição florística para todos os grupos de plantas, exceto Melastomataceae, tendo maior efeito na formação Içá do que na Solimões. Ocorrências individuais de 57% das espécies foram explicadas por pelo menos uma das variáveis, sugerindo uma especialização marcada de habitat ao longo de gradientes topográficos. Para essas espécies, modelos usando variáveis derivadas do SRTM-DEM deram resultados semelhantes aos modelos usando apenas a topografia medida em campo, o que indicam que variáveis topográficas derivadas do SRTM-DEM podem ser usadas para prever variações locais na estrutura de comunidades de plantas em florestas tropicais.

PALAVRAS-CHAVE: DEM, formações geológicas, HAND, mapeamento de vegetação

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INTRODUCTION

Answering general questions on plant species distribution in Amazonia has been hampered by the lack of detailed information on how the species niche is constrained by environmental conditions (Tuomisto et al. 2019). In particular, soil nutrient concentration and water availability are important determinants of plant species distributions and floristic composition. Several studies show that occurrence and abundance of Amazonian plant species vary along gradients of soil nutrient concentration (Ca, Mg, K, Na) and available phosphorus (Tuomisto et al. 1998; 2016; Costa et al. 2005; Higgins et al. 2011; Zuquim et al. 2012; Baldeck et al. 2016; Cámara-Leret et al. 2017). Floristic composition also varies along topographical gradients from hilltops to valley bottoms (Tuomisto et al. 1995; Tuomisto and Poulsen 2000; Poulsen et al. 2006) because topographic units (i.e., bottomlands, slopes and hilltops or plateaus) differ substantially in water availability (Nobre et al. 2011). As topography and soil nutrients can be correlated due to topographically controlled soil formation, plant species may respond to both, as they are exposed to geochemical sedimentary layers with different nutrient concentration at different topographical positions (Tuomisto and Ruokolainen 1994, Vormisto et al. 2004; Baldeck et al. 2013; Chauvel et al. 1987; Osher and Buol 1998; Chadwick and Asner 2016). Yet floristic changes in topographic gradients are less obvious than soil gradients due to the absence of a metric that allows cross-scale comparisons of topographic conditions.

In Amazonia large areas are seasonally inundated on the river floodplains, which makes them ecologically and floristically distinct from areas of terra firme (Campbell et al. 1986; Balslev et al. 1987; Gentry 1988; Wittmann et al. 2013). In terra firme forests, environmental gradients are often defined by topographic variation. Topography, in turn, is a proxy for several environmental conditions that are important determinants of species distribution (Vormisto et al. 2004; Moeslund et al. 2013). Especially drainage has a clear relation to local topography, determining water availability as lower areas have higher water availability due to proximity to the water table and due to runoff of rainwater from higher areas (Fan et al. 2019). These characteristics make it possible to use topography as a practical surrogate of water availability on the terrain (Hätjema and Mitchell-Brucker 2005; Rennó et al. 2008; Costa et al. 2022).

Direct measurements of soil water availability or water table depth are time-consuming and very much affected by weather conditions during and just before measurement. In fact, few studies on plant species distribution in Amazonian terra firme have correlated such measurements with plant species distribution (e.g., Jirka et al. 2007; Guimaraes et al. 2021). Instead, topographic variation has been used as a surrogate for local hydrological conditions when addressing changes in local floristic composition, either by measuring topographic variation in the field (Tuomisto et al. 1995; Tuomisto and Poulsen 2000; Drucker et al. 2008; Costa et al. 2009), or by making a simple (and subjective) classification of topographic units (e.g., plateaus, slopes and valleys) into hydromorphic environments (Kahn and de Castro 1985; Svenning 1999; Drucker et al. 2008). In the absence of field measured topography, topographic metrics derived from digital elevation models (DEMs) have been applied as determinants of floristic composition. Out of these metrics, the algorithm HAND (height above the nearest drainage, Rennó et al. 2008) has stood out as a proxy for topographically defined hydrological conditions in terrains with relatively homogeneous soil conditions (Moulatlet et al. 2014; Schietti et al. 2014), but in terrains with highly heterogeneous soil conditions, its applicability has not been evaluated yet.

Remote sensing data may help to fill the gap in environmental information needed to map species distribution at different scales (Rocchini et al. 2016). However, the association of environmental processes with species distribution from local to regional scales needs remote sensing data coupled with data on species occurrences that covers a large part of the environmental heterogeneity (Tuomisto et al. 2019). We used an extensive dataset of field measured topography in the western Brazilian Amazon to assess the ability of HAND and two other DEM-derived topographic metrics (i.e., the estimated topographic conditions) as proxies of local hydrological conditions to explain floristic composition and plant species distribution across two geological formations. We focused on four plant groups (pteridophytes, palms, Melastomataceae and Zingiberales) and addressed community and individual species responses to both field and DEM-derived topography. We specifically asked: i) whether species distributions of the different plant groups can be explained by the estimated topographic conditions; ii) what is the response magnitude and direction (i.e., positive, or negative) of individual species to the estimated topographic conditions; and iii) to which degree the species responses can be compared to local topographic measurements, i.e., if DEM-derived variables can replace topographic field measurements as useful metrics to be associated with floristics.

MATERIAL AND METHODS

Study Area

The study was conducted in western Amazonia in Brazil along the rivers Juruá and Tarauacá, with field sampling extending across 500 km (Figure 1). The study area is covered by continuous rainforest at an elevation range of 65–200 m.a.s.l. Mean annual rainfall is 2200 mm and annual mean temperature is 27 °C, with temperatures as low as 15 °C occurring during annual cold spells (Karger et al. 2017). The area is in a complex geological setting. The Içá and Solimões
floristic data

We use the same floristic data as Tuomisto et al. (2016). Floristic inventories were made at the 25-m subunit resolution within each transect. For pteridophytes, we registered all individuals with at least one green leaf (leafy stem in the case of lycophytes) longer than 10 cm, including epiphytes, hemiepiphytes and climbers if they had such leaves less than two meters above ground. All Melastomataceae individuals with post-cotyledon leaves were included. All Zingiberales individuals with a minimum height of 5 cm were recorded and, in the case of clonal species, bunches of leaves separated by at least 20 cm were considered as separate individuals. All palm individuals higher than 5 cm were included, but palm seedlings that could not be identified to species level were excluded. Each ramet in a clonal or colonial species was counted as an individual. Representative voucher specimens were deposited in the herbaria of the University of Turku, Finland (pteridophytes and Melastomataceae), University of Aarhus, Denmark (palms), Instituto Nacional de Pesquisas da Amazônia, Brazil (palms and Zingiberales) and Instituto de Botanica – Universidade de São Paulo, Brazil (pteridophytes and Melastomataceae). Pteridophytes and Melastomataceae were inventoried in all 71 transects, palms in 40 and Zingiberales in 39 (Supplementary Material, Table S1).

Topographic data

To place all transects on the same elevational and topographical framework, we used the digital elevation model (DEM) of the Shuttle Radar Topographic Mission (SRTM) with resolution of 1 arc sec (~30 m at the equator) to obtain elevation data for each 25-m subunit. Before extracting the SRTM elevation values for each subunit, we compared the SRTM-derived topographic profile of each transect with the corresponding field-measured true profile. This was done to account for possible errors associated with the measurements of transect coordinates. If there was a mismatch, we adjusted transect georeferencing to obtain the best possible match of

| Geological setting   | Number of transects | Field-measured topography (m) | HAND (m) | Slope (%) | SRTM (m) | Maximum Strahler’s drainage order |
|----------------------|---------------------|------------------------------|----------|-----------|----------|----------------------------------|
| Içá Formation        | 15                  | 14.69 (0 - 40.62)            | 12.71 (0.02 - 43.32) | 5.42 (1.21 - 7.94) | 155.56 (124.01 - 192.4) | 5                                 |
| Solimões Formation   | 23                  | 8.67 (0 - 28.74)             | 8.21 (0.02 - 31.64) | 3.74 (0-8.6) | 154.38 (125.26 - 187.76) | 4                                 |
| River terraces       | 33                  | 4.68 (0 - 16.73)             | 3.43 (0 - 19.7)    | 2.73 (0-7.15) | 119.26 (69 - 174.55) | 6                                 |

Floristic inventories were made at the 25-m subunit resolution within each transect. For pteridophytes, we registered all individuals with at least one green leaf (leafy stem in the case of lycophytes) longer than 10 cm, including epiphytes, hemiepiphytes and climbers if they had such leaves less than two meters above ground. All Melastomataceae individuals with post-cotyledon leaves were included. All Zingiberales individuals with a minimum height of 5 cm were recorded and, in the case of clonal species, bunches of leaves separated by at least 20 cm were considered as separate individuals. All palm individuals higher than 5 cm were included, but palm seedlings that could not be identified to species level were excluded. Each ramet in a clonal or colonial species was counted as an individual. Representative voucher specimens were deposited in the herbaria of the University of Turku, Finland (pteridophytes and Melastomataceae), University of Aarhus, Denmark (palms), Instituto Nacional de Pesquisas da Amazônia, Brazil (palms and Zingiberales) and Instituto de Botanica – Universidade de São Paulo, Brazil (pteridophytes and Melastomataceae). Pteridophytes and Melastomataceae were inventoried in all 71 transects, palms in 40 and Zingiberales in 39 (Supplementary Material, Table S1).

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the SRTM profile with the field-measured topography using an algorithm that optimized the search for initial points with similar topographic profiles. The initial SRTM profiles were based on the field-measured coordinates at the start and end points of each transect, as transects were assumed to be straight lines without major deviations. The coordinate correction procedure iteratively recalculated the start and end coordinates of each transect, such that the sum of the squared differences between field-measured and SRTM-derived topographic profiles were minimized. This was done with the constraint that the new coordinates could not be displaced by more than two SRTM pixels (approximately 60 m) from the original coordinates. In the next step, the new coordinates were used to assign coordinates for each 25-m subunit and to extract SRTM elevation values by bilinear interpolation. With this procedure, we had SRTM-derived topographic profiles that matched the topographies measured in the field. For five of the 71 transects (transects 780, 794, 806, 807 and 808) our algorithm failed to match with the topographic profiles within the range of 60 m and, therefore, these transects were not included in the final analysis. The R code for the algorithm can be found at (https://github.com/gamamo/Jurua-Hydro).

Based on the adjusted transect georeferencing, we calculated a single HAND value for each transect subunit. HAND is a topographic measure that equals the vertical distance (in meters) between a point of interest and the nearest watercourse (or point where the water table is assumed to be near the surface). Low HAND values correspond to moister sites close to the water table, and high HAND values to drier sites further above the water table. Since HAND is independent of absolute elevation, its values are comparable over large areas. We calculated HAND using a decision tree based on several topographic attributes extracted from the SRTM-DEM, including accumulated area, slope and curvatures, to determine the best drainage network for a given area.

To complement the HAND estimates, we derived two other topographic variables related to the local hydrological conditions, namely slope and stream order of the nearest drainage (according to Strahler 1957) from the SRTM-DEM. Slope is related to the overland and subsurface flow of water, and therefore it affects potential soil moisture, which is generally higher on gentler slopes. Strahler’s stream order is an estimate of the size of a water channel based on the same drainage network that was generated to calculate the HAND. In Amazonian forests, water table depth varies not only along topographic profiles, but also according to the distance to rivers of different drainage orders. Low values of Strahler’s drainage order are found often near the headwaters and indicate intermittent waterflow dominated by ground water streamflow. Strahler’s drainage order increases downstream and larger values indicate more continuous waterflow, the magnitude of which depends on the interplay between infiltration from large rivers and ground water depth (Miguez-Macho and Fan 2012).

**Data Analysis**

The floristic responses (community-level analysis) to the topographic predictors were assessed using regression models developed for each of the four plant groups separately. To use community data as the response variable, we reduced the dimensionality of the data through NMDS (non-metric multidimensional scaling) to two dimensions. A floristic dissimilarity matrix for each NMDS was calculated using the extended Sørensen dissimilarity. This is based on the classical Sørensen similarity index, but it uses intermediate plots as steppingstones to calculate dissimilarities between plots that do not share species, which facilitates relating long compositional gradients to environmental variables (De’ath 1999).

We modeled the relationship between the NMDS axes and the set of topographic variables using linear mixed models (LMM) with gaussian distribution. Each of the two NMDS axes for each of the four plant groups was used separately as a response variable. We built models that included as explanatory variables HAND, drainage order and slope, and models that included only field measured topography as explanatory variable. To assess how the set of topographic variables explained the distribution of each individual species, we used generalized linear mixed models (GLMM) with binomial distribution (presence-absence data). Species occurrences were the response variables, and the quadratic forms of HAND, slope and Strahler’s drainage order were the independent terms. We also built GLMMs that included only field measured topography as explanatory variable. For each individual species modelling, only transects within the same geological formation where a species had been registered were included in the species model to avoid overpredictions. We restricted our analysis to those species considered as frequent in the dataset, with at least 20 occurrences. Transect identity and transect affiliation to geological formation were set as random terms in all LMMs. The first aimed to account for the autocorrelation of sub-samples within transects; the second, to account for the marked differences in the environmental conditions of each geological formation. In GLMMs, only transect identity was set as a random term because the modelled species were rare in the three geological formations, so geological differences were not a relevant factor in the models.

In both community (LMM) and species-level models (GLMM), all variables were standardized by subtracting the mean and dividing by the standard deviation prior to the analyses to compare the effect sizes based on model
coefficients. For the models that contained HAND, slope and Strahler's order as variables, we applied a model selection procedure that started with a full model and then, models with different combination of the variables were compared using the dredge function of the R package MuMIn (Barton 2018). The best model was selected based on the Akaike Information Criteria (AIC). When more than one model had AIC < 2, the best model was determined as an average of their estimated standardized coefficients (Anderson and Burnham 2004), using the model.avg function of the R package MuMIn (Barton 2018). Model evaluation was done by comparing the model's AIC with a null model assuming no explanatory variables. Then, we evaluated the effect of the different variables in explaining each community composition (NMDS axes) or individual species occurrence in each model by comparing the magnitude and significance of the standardized beta coefficients of the final models. Coefficient values closer to 1 or -1 indicate stronger effect, whereas coefficient values closer to 0 indicate non-significant effects. The likelihood-ratio based pseudo-$R^2$ was reported individually for each model, with a maximum value of 1. LMM and GLMM using field measured topography as explanatory variable were also evaluated by comparing the model's AIC with a null model assuming no explanatory variable. All analyses were performed in the R statistical software (R Core Team 2020).

To evaluate the hierarchical importance of DEM-derived topographic variables in structuring plant communities in each geological formation, we used distance-based multivariate regression trees (MRT) (De’Ath 2002). We built MRT separately for each species group in each of the three geological surfaces (Solimões Formation, Içá Formation, and fluvial terrace). The two NMDS axes were set as dependent variables, and HAND, slope, and Strahler’s order as independent variables. MRTs were obtained by repeatedly splitting the observation units into two clusters that were determined by a break point in an environmental variable. Each split aimed to minimize the floristic differences between subunits in the same cluster, and at each level in the MRT, the variable that gives the minimum within-group sum of squared distance to the group mean was selected. This process was repeated with each sub-group of the previous step until each observation unit formed its own cluster.

We calculated dissimilarities using the Bray-Curtis index for occurrence data including all the species of each taxonomic group using the R package vegan (Oksanen et al. 2018). We used cross-validation to select the MRT with the smallest error (De’Ath 2002). The explained variation of the MRT is given by the residual error of the overall tree. MRTs were calculated using the functions of the R package mvpart (Therneau and Atkinson 2013).

RESULTS

Floristic composition

HAND was relevant to explain community composition of all plant groups except Melastomataceae (Figure 2a; Table S2). The effect was stronger for palms (b = -0.12) than for the other groups. Slope was only significant for pteridophytes (b = 0.04), and Strahler's drainage order was only significant for palms (b = 0.05). When NMDS axis 2 was the response variable (Figure 2b), HAND was still a significant variable for the same plant groups and had a strong effect for palms (b = -0.12). Strahler’s drainage order was significant for palms (b = 0.10) and Zingiberales (b = -0.03). Slope had a significant effect for palms (b = -0.06) and Zingiberales (b = -0.03).

Individual species responses

Individual species responses to DEM-derived topographic variables were variable (Figure 3; Supplementary Material, Table S2). Pteridophytes (81%) and palms (80%) had the highest proportion of species that responded to the variation in HAND. Pteridophyte and Melastomataceae species responded mostly negatively, i.e., the probability of species occurrence decreased with increasing HAND values (Figure 3). For palm species, 55% had a positive response, i.e., species occurrence probability increased with increasing HAND values. Slope and Strahler’s drainage order were significant in several models for all plant groups (Figure 3; Supplementary Material, Table S2). Model fit, as measured by the pseudo-$R^2$, varied from 0.05 – 0.45 in pteridophytes, 0.05 – 0.63 in Zingiberales, 0.05 – 0.45 in palms and 0.01 – 0.39 in Melastomataceae (Supplementary Material, Table S2). Out of the species restricted to a single geological formation, only one (Calathea neblinense - Zingiberales) had a positive relationship with HAND.

Figure 2. Output of the LMM for plant community data from the middle Juruá River (western Brazilian Amazon). Standardized slope coefficients and the standard error (horizontal bars) of the LMMs are shown for all variables used to model species occurrence with the NMDS axis 1 (A) and 2 (B). Coefficients different from zero are associated with significant effects. SDO = Strahler’s drainage order.
**Table 2.** Summary of linear mixed models for plant communities along the middle Juruá River (western Brazilian Amazon) showing the results of model selection of the response of community composition (MDS1 and MDS2) to DEM-derived topographic metrics (HAND, slope and Strahler’s drainage order (SDO)) and to field measured topography (Topo). The fit of the best models, alongside the null model assuming no explanatory variables (intercept-only), are shown for every response variable. Null models are shown separately for models with DEM-derived variables (Null) and for models with field measured topography (Null Topo). Response variables with null values are those for which the null model AIC was lower than for any model that included the variable.

| Plant group | Response variable | Model | df | LogLink | AIC | ΔAICc |
|-------------|------------------|-------|----|---------|-----|-------|
| Pteridophytes | MDS1 | HAND + Slope | 6 | -344.158 | 700.4 | 0 |
| | | Null | 4 | -355.615 | 719.3 | 18.88 |
| | | Topo | 5 | -324.770 | 659.6 | 0 |
| | | Null Topo | 4 | -355.615 | 719.3 | 59.67 |
| | MDS2 | HAND | 5 | -509.064 | 1028.2 | 0 |
| | | Null | 4 | -545.529 | 1099.1 | 70.91 |
| | | Topo | 5 | -492.247 | 994.5 | 0 |
| | | Null Topo | 4 | -545.529 | 1099.1 | 104.55 |
| Zingiberales | MDS1 | HAND + Slope | 6 | -344.158 | 700.4 | 0 |
| | | Null | 5 | -355.615 | 719.3 | 18.88 |
| | | Topo | 5 | -324.770 | 659.6 | 0 |
| | | Null Topo | 4 | -355.615 | 719.3 | 59.67 |
| | MDS2 | Null | 4 | -348.856 | 705.8 | 0 |
| | | Null Topo | 4 | -348.856 | 705.8 | 0 |
| Palms | MDS1 | HAND | 5 | -309.746 | 629.6 | 0 |
| | | Null | 4 | -316.312 | 640.7 | 11.11 |
| | | Topo | 5 | -299.290 | 608.7 | 0 |
| | | Null Topo | 4 | -316.312 | 640.7 | 32.02 |
| | MDS2 | Null | 4 | -348.856 | 705.8 | 0 |
| | | Null Topo | 4 | -348.856 | 705.8 | 0 |
| Melastomataceae | MDS1 | Null | 4 | -695.057 | 1326.1 | 0 |
| | | Topo | 5 | -657.789 | 1326.1 | 1.5 |
| | | Null Topo | 4 | -659.057 | 1326.1 | 0.52 |
| | MDS2 | Null | 4 | -798.735 | 1605.5 | 0 |
| | | Null Topo | 4 | -798.735 | 1605.5 | 0 |

**Congruence with field measured topography**

Overall, LMM and GLMM with field-measured topography as the sole explanatory variable had similar AIC values than models with DEM-derived topographic variables (Table 2, Supplementary Material, Figures S1, S2; Table S2). At the species level, the difference between the AICs, as assessed with an ANOVA, was not significant for any plant group (pteridophytes: p = 0.985, Zingiberales: p = 0.958, palms: p = 0.964, Melastomataceae: p = 0.927) (Supplementary Material, Figure S3).

**Regression trees**

Regression trees (Figure 4) showed that, in the river terraces, the main floristic differences for each species group were explained by drainage (pteridophytes, palms and Zingiberales, MRT residual errors = 0.87, 0.78 and 0.62, respectively) and slope (Melastomataceae, MRT residual error = 0.85). HAND was the variable that caused the main division of the MRT for the Íca Formation for all plant groups (MRT residual error: pteridophytes = 0.84, Zingiberales = 0.93, palms = 0.66, Melastomataceae = 0.94). In the Solimões Formation, the main division for all plant groups was associated with HAND (pteridophytes and Melastomataceae, MRT residual error = 0.88 and 0.96, respectively) and drainage (Zingiberales and palms, MRT residual error = 0.82 and 0.51, respectively).

**DISCUSSION**

HAND explained species composition of all plant groups, suggesting that this variable detected the influence of hydrological conditions as determined by topographic gradients. The underlying mechanisms to explain species distribution along topographic gradients are possibly related to species tolerance to desiccation or waterlogging. Desiccation is often associated with the distance to the water table on hilltops, while waterlogging is more common in areas close to the water table in local topographic bottomlands (Lopez and Kursar 1999; Parent et al. 2008; Oliveira et al. 2018; Fontes et al. 2020; Garcia et al. 2022).

Slope was also a significant variable to explain the floristic composition of pteridophytes (NMDS 1) and palms and...
Zingiberales (NMDS 2). The response of these plant groups to slope might reflect the strong slope gradient of the study area. Along topographic profiles, the slope angle indicates the capacity of the soil to retain moisture that infiltrates from precipitation (Rennó et al. 2008). On steep slopes, high lateral and sub superficial runoff diminish water infiltration, which is a limiting factor to plants that do not have deeper roots to anchor and access moisture from deeper soil layers (Fan et al. 2019). On the other hand, steep slopes do not accumulate as much litter as flat areas, so the lack of litter facilitates the establishment of seedlings of plants that do not have large nutrient reserves, such as the pteridophytes (Rodrigues and Costa 2012).

We found a significant effect of Strahler’s order in explaining floristic composition for palms (NMDS 1 and NMDS 2) and for Zingiberales (NMDS 2) in models where HAND also had a significant effect, suggesting that species responses to the modelled hydrological conditions were also related to the complementary effect of HAND in the gradient of drainage order formed along a watershed. Close to the watershed exit, bottomlands get inundated by rainwater because water infiltration is low when the soils are saturated due to the inundations of the large rivers (Miguez-Macho and Fan 2012). At the headwaters, the influence of low Strahler’s order rivers on the soil saturation is dependent on terrain slope. While flat terrains can get frequently moist, in bottomlands of the areas with more pronounced slopes, the soil does not stay saturated after a rainfall because the small rivers have relatively low influence on soil saturation (Fan et al. 2013).

The occurrence of 57% of the species in all plant groups was predicted using the DEM-derived variables. The models met some of our expectations. Species such as *Mickelia nicotianifolia*, *Campyloneurum fuscosquamatum* (pteridophytes), *Astrocaryum ulei* (palm) and *Clidemia epiphytica* (Melastomataceae) are commonly found in bottomlands and were correctly modelled to be negatively related to HAND, while *Oenocarpus bataua* (palm), commonly found on hilltops in western Amazonia, were correctly modelled to be positively related to HAND. Also, *Calathea altissima* (ginger) has been described as common species on steep slopes and our models predicted its occurrence correctly. Habitat specialization related to topographic
position was reported before for many palms (Svenning 1999; Vormisto et al. 2004), pteridophytes (Tuomisto and Ruokolainen 1994; Tuomisto et al. 1995; 1998; Zuquim et al. 2012), Melastomataceae (Tuomisto and Ruokolainen 1994) and Zingiberales (Costa et al. 2005). These previous studies have used field-measured topographical variables, which accurately reflect slope and relative topographic position, but do not contain information about distance to water table and cannot be correlated across study areas. Our models using DEM-derived topography metrics were similar to models using field measured topography as explanatory variables at both community and species level, which is consistent with the idea that specialization to local topography might be related to species tolerance to water availability. However, as soil conditions were not evaluated in our study, the usefulness of DEM-variables as surrogates of field measured topography still requires further investigation.

Floristic patterns differed between geological formations. In the Içá Formation, HAND was the most important predictor of floristic composition for all the plant groups. This result may have been an effect of the Içá Formation being hillier, with a wider range of environmental conditions from lower to higher topographic positions relative to the Solimões Formation or the river terraces. Water availability likely changes for plants growing in different parts of this topographic gradient. Moreover, other soil conditions related to water availability may explain species distribution. Soils of the Içá Formation and river terraces in high topographic positions have coarser texture (Tuomisto et al. 2016) and may dry out faster than those in lower topographic levels. In the Solimões Formation and river terraces, finer sediments prevail.
and the water table is superficial, so that water availability is not a limiting factor for plants in dry periods. This would explain why drainage order was so important to explain floristic composition in the river terraces.

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Moulatlet et al. The role of topographic-derived hydrological variables in explaining plant species distributions in Amazonia

**Figure S1.** Comparison between generalized linear mixed models built at species-level with DEM-derived topographic metrics (Hydrology) and with field measured topography (Topography) from transects along the middle Juruá River (western Brazilian Amazon). A – Distribution of AIC values for each plant group; B – Comparison between AICs for each modelled species. Pearson’s R = 0.99.

**Figure S2.** Comparison between generalized linear mixed models built at species-level with DEM-derived topographic metrics (Hydrology) and with field measured topography (Topography) for each species of each plant group sampled in transects along the middle Juruá River (western Brazilian Amazon). The results of Hydrological vs. Topographic models are connected for each individual species.
Figure S3. Presence of one selected species (vertical bars) of each plant group sampled in the set of transects along the middle Juruá River (western Brazilian Amazon). The transect (250 m total length) is divided in 20 subunits of 25 m each. Solid lines correspond to the field measured topographic profiles. Dashed lines correspond to the calculated HAND values. Species occurrence probabilities according to the field measured topography and to HAND are shown in the right column. Both variables are standardized by subtracting the mean and dividing by the standard deviation.
Table S1. Number of plant species used in each model and the corresponding number of transects and subunits within transects along the middle Juruá River (western Brazilian Amazon). Values within parenthesis indicate the number of species significantly associated to at least one hydrological variable in GLMM.

| Plant group             | Community level analysis | Species level analysis |
|-------------------------|--------------------------|------------------------|
|                         | Species | Transects | Subunits | Species | Transects | Subunits |
| Pteridophytes           | 170     | 58        | 1160     | 50 (33)  | 39        | 711      |
| Zingiberales            | 115     | 32        | 632      | 60 (36)  | 39        | 711      |
| Palms                   | 62      | 33        | 660      | 39 (25)  | 39        | 711      |
| Melastomataceae         | 149     | 58        | 1055     | 39 (14)  | 32        | 582      |

Table S2. Summary of generalized linear mixed models (GLMM) for individual plant species sampled in transects along the middle Juruá River (western Brazilian Amazon). Coefficients of each model (at logit scale) are shown with the respective standard errors (SE), p-values and pseudo-$R^2$. The numbers 1 and 2 after each variable’s name refer to the linear and squared terms, respectively. AIC values are shown for the models with DEM-derived topographic variables (AIC DEM) and for the models with field measured topography (AIC Topo).

| Plant group/species       | Species code | Variable | Coefficient | SE   | p    | AIC DEM | AIC Topo | Pseudo $R^2$ |
|---------------------------|--------------|----------|-------------|------|------|---------|----------|--------------|
| Pteridophytes             |              |          |             |      |      |         |          |              |
| Adiantum humile           | Adian.humi   | HAND1    | -57.78      | 20.44| 0    | 290.6   | 302.1    | 0.298        |
|                           |              | HAND2    | -37.12      | 15.73| 0.02 |         |          |              |
| Adiantum obliquum         | Adian.obli   | HAND1    | -17.1       | 7.92 | 0.03 | 461.2   | 454.2    | 0.082        |
|                           |              | HAND2    | -13.74      | 6.81 | 0.04 |         |          |              |
| Adiantum paraense or A. tuamistoanum | Adian.p.t | HAND1 | 8.51       | 3.16 | 0.01 | 649.4   | 648      | 0.069        |
| Adiantum petiolatum       | Adian.peti   | Slope2   | 15.6        | 7.54 | 0.04 | 134.5   | 131.1    | 0.128        |
|                           |              | SDO2     | -23.07      | 9.67 | 0.02 |         |          |              |
|                           |              | HAND1    | 28.88       | 6.67 | 0    |         |          |              |
| Adiantum terminatum       | Adian.ter   | HAND1    | -6.17       | 0.38 | 0    | 705.3   | 698.9    | 0.156        |
|                           |              | HAND2    | -4.05       | 0.49 | 0    |         |          |              |
| Adiantum tomentosum       | Adian.tome   | SDO1     | -3.19       | 0    | 0    |         |          |              |
|                           |              | SDO2     | 5.59        | 0    | 0    |         |          |              |
| Asplenium pearcei         | Asple.pear   | SDO2     | 9.21        | 3.27 | 0    | 707.9   | 707.4    | 0.088        |
|                           |              | HAND2    | -8.96       | 4.02 | 0.03 |         |          |              |
| Bolbitis nicotianifolia  | Bolbi.nico   | HAND1    | -18.55      | 6.95 | 0.01 | 160.2   | 140      | 0.193        |
| Campylophoneum fucosquamatum | Campy.fusc | SDO1     | 31.47       | 6.26 | 0    | 461.9   | 460.6    | 0.278        |
|                           |              | HAND1    | -71.07      | 22.74| 0    |         |          |              |
| Cnemidaria ewanii         | Cnemi.ewan   | Slope1   | -11.78      | 5.67 | 0.04 | 172.2   | 178.9    | 0.112        |
|                           |              | HAND1    | -22.93      | 5.66 | 0    |         |          |              |
| Cysteia andina           | Cyath.andi   | Slope2   | -19.19      | 8.12 | 0.02 | 141.4   | 139.7    | 0.244        |
| Cysteia lasiosora        | Cyath.lasi   | HAND1    | -17.02      | 4.92 | 0    | 141.4   | 450.4    | 0.447        |
|                           |              | HAND2    | 8.5         | 3.49 | 0.02 |         |          |              |
| Cysteia trailii          | Cyath.trai   | HAND1    | 29.7        | 12.57| 0.02 | 209.9   | 218.4    | 0.443        |
|                           |              | HAND2    | 18.18       | 8.92 | 0.04 |         |          |              |
| Cyclodium meniscioides   | Cyclo.meni   | HAND1    | -12.45      | 4.89 | 0.01 | 422.7   | 431.2    | 0.217        |
|                           |              | HAND2    | 12.5        | 4.07 | 0    |         |          |              |
| Danacea subgen. Anthrodanaea | Danae.b.g | SDO2     | 15.52       | 6.89 | 0.02 | 276.5   | 276.2    | 0.158        |
### Table S2. Continued.

| Plant group/species | Species code | Variable | Coefficient | SE  | p    | AIC DEM | AIC Topo | Pseudo R² |
|---------------------|--------------|----------|-------------|-----|------|---------|----------|-----------|
| Danaea leprieurii   | Danae.lepr   | Slope1   | 12.42       | 4.45| 0.01 | 498     | 509      | 0.278     |
|                     |              | SDO1     | -15.16      | 5.55| 0.01 |         |          |           |
| Didymochloaena truncatula | Didym.trun | SDO1     | -7.55       | 0   | 0    | 147     | 143.2    | 0.347     |
|                     |              | SDO2     | 15.41       | 0   | 0    |         |          |           |
|                     |              | HAND1    | -19.74      | 0.01| 0    |         |          |           |
|                     |              | HAND2    | -5.12       | 0.01| 0    |         |          |           |
| Lindsaea lancea var. lancea | Linds.lanc.l | Slope1   | -16.9       | 6.53| 0.01 | 618.5   | 622.3    | 0.217     |
| Lomariopsis japurensis | Lomar.japu  | HAND1    | -16.96      | 4.2 | 0    | 653.8   | 626.9    | 0.309     |
|                     |              | HAND2    | -11.79      | 3.69| 0    |         |          |           |
| Metaxyra parkeri    |              | HAND1    | 23.63       | 6.21| 0    |         |          |           |
|                     |              | HAND2    | -8.32       | 3.68| 0.02 |         |          |           |
| Polybotrya caudata  | Polyb.caud   | HAND1    | -9.66       | 4.34| 0.03 | 169.9   | 165      | 0.184     |
| Polybotrya crassirhizoma | Polyb.cras | Slope1   | 62.81       | 22.53| 0.01 | 145.8   | 166.6    | 0.398     |
|                     |              | Slope2   | 57.96       | 21.94| 0.01 |         |          |           |
|                     |              | HAND1    | -270.21     | 133.56| 0.04 |         |          |           |
| Polybotrya pubens   | Polyb.pube   | Slope1   | 16.66       | 4.87| 0    | 470.4   | 466.6    | 0.390     |
|                     |              | SDO2     | 15.86       | 6.17| 0.01 |         |          |           |
|                     |              | HAND1    | -19.48      | 4.78| 0    |         |          |           |
| Saccoloma inaequale | Sacco.inae   | Slope2   | 11.06       | 3.7 | 0    | 658.5   | 663      | 0.265     |
|                     |              | SDO1     | -12.74      | 4.8 | 0.01 |         |          |           |
|                     |              | SDO2     | 12.86       | 3.78| 0    |         |          |           |
|                     |              | HAND1    | -11.51      | 4.13| 0.01 |         |          |           |
|                     |              | HAND2    | -7.86       | 3.5 | 0.02 |         |          |           |
| Salpichlaena volubilis | Salpi.volu  | HAND1    | -15.01      | 4.74| 0    | 320     | 312.4    | 0.134     |
| Selaginella parkeri  | Selag.park   | HAND1    | 13.08       | 3.78| 0    | 420.7   | 425      | 0.122     |
| Thelypteris abrupta  | Thely.abru   | Slope2   | 8.48        | 3.5 | 0.02 | 148.9   | 158      | 0.373     |
| Trichomanes elegans  | Trich.eleg   | HAND1    | -16.8       | 4.42| 0    | 487.8   | 476.1    | 0.109     |
| Trichomanes pinnatum | Trich.pinn  | Slope1   | 12.59       | 4.75| 0.01 | 729.5   | 741.6    | 0.276     |
|                     |              | SDO1     | -10.84      | 3.89| 0.01 |         |          |           |
| Trichomanes sp. 1   | Trich.sp1    | HAND1    | -36.98      | 0   | 0    | 452.3   | 446.8    | 0.271     |
|                     |              | HAND2    | -2.03       | 0   | 0    |         |          |           |
| Trichomanes sp. 4   | Trich.sp4    | HAND1    | 7.5         | 3.48| 0.03 | 656.7   | 646.4    | 0.188     |

### Zingiberales

| Plant group/species | Species code | Variable | Coefficient | SE  | p    | AIC DEM | AIC Topo | Pseudo R² |
|---------------------|--------------|----------|-------------|-----|------|---------|----------|-----------|
| Calathea altissima  | cala.alti    | Slope2   | 15.74       | 5.68| 0.01 | 694.1   | 703.8    | 0.316     |
| Calathea curaraya   | cala.cura    | Slope2   | -19.85      | 9.38| 0.03 | 136.8   | 136.4    | 0.513     |
| Calathea fragilis   | cala.frag    | Slope1   | 12.86       | 5.01| 0.01 | 171.6   | 175.7    | 0.120     |
| Calathea neblinense | cala.nebl    | SDO1     | -37.95      | 16.82| 0.02 | 129     | 129.3    | 0.293     |
|                     |              | HAND1    | 54.81       | 17.84| 0    |         |          |           |
| Calathea sp. 26     | cala.sp26    | Slope2   | 9.15        | 4.47| 0.04 | 171     | 166.4    | 0.293     |
| Calathea sp. 32     | cala.sp32    | Slope1   | 66.29       | 24.3 | 0.01 | 93      | 97.2     | 0.3       |
Table S2. Continued.

| Plant group/species | Species code | Variable | Coefficient | SE  | p    | AIC DEM | AIC Topo | Pseudo R² |
|---------------------|--------------|----------|-------------|-----|------|---------|----------|-----------|
| Calathea sp. 36     | cala.sp36    | HAND1    | -18.56      | 7.21| 0.01 | 163.9   | 162.8    | 0.086     |
|                     |              | SDO1     | 3.42        | 0   | 0    |         |          |           |
|                     |              | SDO2     | 12.95       | 0   | 0    |         |          |           |
| Calathea sp. 38     | cala.sp38    | HAND1    | -13.68      | 4.65| 0    | 110.6   | 112      | 0.392     |
| Calathea sp. 39     | cala.sp39    | Slope2   | 14.84       | 7.04| 0.04 | 259.1   | 260.3    | 0.135     |
| Calathea sp. 4      | cala.sp4     | HAND1    | 26.74       | 5.31| 0    | 289.7   | 285.6    | 0.414     |
| Calathea straminea  | cala.stra    | HAND2    | -10.55      | 3.49| 0    | 486.2   | 466.1    | 0.402     |
| Calathea variegata  | cala.vari    | Slope1   | -11.46      | 5.33| 0.03 | 136     | 138.5    | 0.269     |
| Calathea zingiberina| cala.zing    | HAND1    | 21.33       | 3.82| 0    | 435.4   | 432.6    | 0.246     |
| Chamaecostus sp. 1  | cham.sp1     | Slope2   | 8.68        | 3.37| 0.01 | 126.7   | 117.2    | 0.255     |
| Costus lasius       | cost.lasi    | HAND1    | -10.59      | 4.93| 0.03 | 491.6   | 477.4    | 0.054     |
| Heliconia acuminata | heli.acum    | HAND1    | -24.47      | 11.86| 0.04| 239.5   | 240.1    | 0.064     |
| Heliconia juruana   | heli.juli    | Slope1   | -18.98      | 7.02| 0.01 | 298.3   | 300.9    | 0.212     |
| Heliconia spathocircinata | heli.spat | HAND1 | -6.48 | 3.14 | 0.04 | 203.6 | 191.1 | 0.075     |
| Heliconia striata   | heli.stri    | HAND1    | -50.69      | 23.17| 0.03| 186.5   | 188      | 0.406     |
| Heliconia tenebrosa | heli.tene    | HAND1    | -7.45       | 3.11| 0.02 | 855.1   | 841.9    | 0.168     |
| Heliconia velutina  | heli.velu    | SDO2     | 22.96       | 7.49| 0   | 405.5   | 402.6    | 0.422     |
| Ischnosiphon hirsutus| isch.hirs   | HAND1    | -10.56      | 4.18| 0.01| 701.7   | 692      | 0.234     |
| Ischnosiphon killipi | isch.kill  | HAND1    | 14.21       | 5.71| 0.01| 188     | 187.1    | 0.08      |
| Ischnosiphon lasiocoleus | isch.lasi | HAND1   | 26.97       | 12.45| 0.03| 205.1   | 200.7    | 0.533     |
| Ischnosiphon longiflorus | isch.long | HAND1   | 10.68       | 3.12| 0   | 633     | 200.7    | 0.13      |
| Ischnosiphon puberulus | isch.pube | HAND1    | -10.66      | 3.9  | 0.01| 705.3   | 700.7    | 0.219     |
| Ischnosiphon sp. 1  | isch.sp1     | HAND1    | -15.82      | 7.28| 0.03| 579.8   | 575.7    | 0.208     |
|                     |              | HAND2    | -14.94      | 6.14| 0.01|         |          |           |
| Monophyllanthus araracuarensis | mono.arar | Slope1 | -13.09     | 6.46| 0.04| 236.9   | 231.5    | 0.626     |
| Monotagma contrariosum | mono.cont | HAND2   | -88.59      | 33.05| 0.01| 149.8   | 152.1    | 0.28      |
| Monotagma exile     | mono.exil    | SDO1     | -13.6       | 6.4  | 0.03| 345.2   | 344.8    | 0.286     |
|                     |              | HAND1    | 14.75       | 5.03| 0   |         |          |           |
| Monotagma secundum  | mono.sp5     | Slope2   | 10.94       | 5.25| 0.04| 343.9   | 342.7    | 0.47      |
| Monotagma sp. 5     | mono.sp5     | HAND1    | -22.74      | 8.79| 0.01|         |          |           |
| Monotagma tomentosum| mono.tome    | SDO2     | 12.96       | 6.27| 0.04| 320.3   | 312.1    | 0.094     |
| Phenakospermum guyanensis | phen.guya | Slope1 | 9.44        | 3.42| 0.01| 687.3   | 689.1    | 0.227     |
| Renealmia breviscopia | rene.brev  | HAND1    | -21.07      | 7   | 0    | 280.4   | 283      | 0.09      |
| Renealmia sp. 4     | rene.sp4     | HAND1    | -18.42      | 6.61| 0.01| 112.8   | 111      | 0.213     |
| Palms               |              |          |             |     |      |         |          |           |
| Astrocaryum gynacanthum | astrgyna  | HAND1    | 7.46        | 3.3 | 0.02| 725.1   | 720.1    | 0.306     |
|                     |              | HAND2    | -6.47       | 2.75| 0.02|         |          |           |
Table 2. Continued.

| Plant group/species          | Species code | Variable | Coefficient | SE  | p     | AIC DEM | AIC Topo | Pseudo R² |
|------------------------------|--------------|----------|-------------|-----|-------|---------|----------|-----------|
| *Astrocaryum ulei*           | astrulei     | HAND1    | -21.45      | 6.95| 0     | 588.1   | 577.1    | 0.275     |
| *Attalea butyracea*          | attabuty     | HAND2    | 13.02       | 5.64| 0.02  | 237.2   | 231.5    | 0.304     |
| *Attalea maripa*             | attamari     | SDO1     | 12.61       | 4.16| 0     | 603.9   | 613.8    | 0.181     |
|                              |              | HAND1    | -14.33      | 4.99| 0     |         |          |           |
| *Bactris acanthocarpa*       | bactacan     | HAND1    | 23.07       | 5.11| 0     | 431.4   | 406.1    | 0.223     |
|                              | bactbifi     | Slope1   | -66.11      | 27.72| 0.02 |         |          |           |
| *Bactris bifida*             | bactbifi     | SDO1     | -22.17      | 9.37| 0.02  | 286.9   | 296.6    | 0.444     |
|                              |              | bachtirt | 8.02        | 0.47| 0     | 466.7   | 462.2    | 0.056     |
|                              |              | Slope1   | -4.94       | 1.35| 0     |         |          |           |
|                              |              | Slope2   | -6.23       | 0.09| 0     |         |          |           |
|                              |              | SDO1     | -3.4        | 0   | 0     |         |          |           |
|                              |              | SDO2     | 6.88        | 0   | 0     |         |          |           |
| *Bactris hirta*              | bacthirt     | HAND1    | 8.02        | 4.16| 0     | 816.1   | 813.4    | 0.213     |
|                              |              | Slope1   | -20.51      | 9.32| 0.03  | 346.3   | 338.8    | 0.447     |
|                              |              | Slope2   | -2.63       | 0.09| 0     |         |          |           |
|                              |              | SDO1     | -3.4        | 0   | 0     |         |          |           |
|                              |              | SDO2     | 6.88        | 0   | 0     |         |          |           |
| *Bactris killipii*           | bactkill     | HAND1    | 20.89       | 4.25| 0     | 430.2   | 404.6    | 0.272     |
| *Bactris maraja*             | bactmara     | HAND1    | -8.72       | 3.61| 0.02  | 816.1   | 813.4    | 0.213     |
|                              |              | HAND2    | -7.95       | 3.25| 0.01  |         |          |           |
| *Bactris simplicifrons*      | bactsimp     | HAND1    | 13.18       | 3.67| 0     | 628.7   | 631.6    | 0.053     |
| *Bactris sphaerocarpa*       | bactspha     | HAND1    | 10.82       | 4.52| 0.02  | 460.6   | 458.3    | 0.362     |
| *Desmoncus giganteus*        | desmgiga     | HAND1    | -21.45      | 10.36| 0.04  | 313.3   | 320.8    | 0.026     |
|                              | dessmi       | SDO2     | 14          | 5.28| 0.01  | 432.5   | 426.8    | 0.115     |
|                              |              | HAND2    | -21.6       | 8.52| 0.01  |         |          |           |
| *Euterpe precatoria*         | euteprec     | HAND1    | -11.72      | 3.14| 0     | 824     | 821.1    | 0.201     |
| *Geonoma bronniartii*        | geonbron     | Slope1   | -20.51      | 9.32| 0.03  | 346.3   | 338.8    | 0.447     |
| *Geonoma deversa*            | geondeve     | HAND1    | 9.42        | 3.32| 0     | 797.7   | 796      | 0.198     |
| *Geonoma macrostachys*       | geonmacr    | SDO1     | -7.04       | 3.32| 0.03  | 707.4   | 701.9    | 0.324     |
| *Geonoma maxima*             | geonmaxi     | SDO1     | -11.28      | 3.9 | 0     | 708.9   | 697.6    | 0.309     |
|                              |              | HAND1    | 19.04       | 4.07| 0     |         |          |           |
| *Iriartea deltoidea*         | iriadelt     | SDO1     | -11.45      | 4.16| 0.01  | 641.5   | 642.3    | 0.207     |
|                              |              | SDO2     | -21.91      | 5.31| 0     |         |          |           |
|                              |              | HAND1    | -10.67      | 0   | 0     |         |          |           |
|                              |              | HAND2    | -10.76      | 0   | 0     |         |          |           |
| *Lepidocaryum tenue*         | lepitenu     | SDO2     | -96.38      | 35.05| 0.01  | 73.5    | 81.2     | 0.393     |
| *Oenocarpus bacaba*          | oenobaca     | HAND1    | 30.36       | 6.6 | 0     | 277.6   | 271.6    | 0.239     |
| *Oenocarpus balickii*        | oenobali     | HAND1    | 34.08       | 11.98| 0     | 146.3   | 151.4    | 0.093     |
| *Oenocarpus bataua*          | oenobata     | SDO2     | -10.13      | 4.21| 0.02  | 615.7   | 603.4    | 0.371     |
|                              |              | HAND1    | 15.28       | 5.47| 0.01  |         |          |           |
| *Phytelephas macrocarpa*     | phytrmacr    | Slope1   | -10.13      | 4.02| 0.01  | 160.9   | 156.2    | 0.306     |
| *Socratea exorrhiza*         | socrexor     | HAND1    | -6.08       | 2.89| 0.04  | 904.3   | 901.9    | 0.104     |

**Melastomataceae**

| Adelobotrys marginata        | Ade.marg     | HAND1    | -38.66      | 10.59| 0     | 137.2   | 128.6    | 0.393     |
| Bellucia sp. 1               | Bel.1        | SDO1     | 9.18        | 3.79| 0.02  | 210.2   | 210.5    | 0.015     |
| Clidemia epiphytica          | Cli.epip     | HAND1    | -28.01      | 8.47| 0     | 194.2   | 180.6    | 0.058     |

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### Table S2. Continued.

| Plant group/species       | Species code | Variable | Coefficient | SE  | p   | AIC DEM | AIC Topo | Pseudo R² |
|---------------------------|--------------|----------|-------------|-----|-----|---------|----------|-----------|
| Clidemia septuplinervia   | Cli.sept     | HAND1    | -21.94      | 0.87| 0   | 132.3   | 113.9    | 0.114     |
|                           |              | HAND2    | -16.3       | 0.02| 0   |         |          |           |
|                           |              | SDO1     | -10.77      | 0   | 0   |         |          |           |
|                           |              | SDO2     | -23.49      | 0   | 0   |         |          |           |
| Leandra sp. 20            | Lea.20       | HAND1    | -26.5       | 7.37| 0   | 111     | 109.1    | 0.395     |
| Leandra sp. 21            | Lea.21       | HAND1    | -16.86      | 5.17| 0   | 305.6   | 298.2    | 0.237     |
| Leandra candelabrum       | Lea.cand     | SLOPE1   | 13.5        | 5.39| 0.01| 234.9   | 238.5    | 0.025     |
|                           |              | HAND1    | -15.02      | 6.8 | 0.03|         |          |           |
| Miconia sp. 68            | Mic.68       | SLOPE2   | 7.73        | 3.38| 0.02| 340.6   | 339.6    | 0.058     |
| Miconia lourteigiana      | Mic.lour     | SLOPE1   | -14.74      | 0   | 0   | 202.8   | 198.2    | 0.04      |
| Miconia prasina           | Mic.pras     | HAND1    | -14.19      | 5.2 | 0.01| 434.2   | 427.8    | 0.142     |
|                           |              | HAND2    | 8.89        | 3.86| 0.02|         |          |           |
| Miconia spennerostachya   | Mic.spen     | SLOPE2   | 7.03        | 3.05| 0.02| 142.7   | 141.3    | 0.173     |
| Miconia tormentosa        | Mic.tome     | HAND1    | -15.48      | 5.92| 0.01| 451.1   | 450.3    | 0.166     |
| Tococa sp. 2              | Toc.2        | SDO2     | -35.87      | 13.73| 0.01| 351.6   | 355.6    | 0.101     |
| Tococa ulei               | Toc.ulei     | HAND1    | -8.92       | 3.87| 0.02| 445.4   | 435.3    | 0.01      |
|                           |              | SDO1     | 6.74        | 0   | 0   |         |          |           |
|                           |              | SDO2     | 0.66        | 0   | 0   |         |          |           |