Local Hydrological Conditions Explain Floristic Composition in Lowland Amazonian Forests

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ABSTRACT

Amazonian forests harbor a large variety of understory herbs adapted to areas with different hydrological conditions, ranging from welldrained to seasonally flooded forests. The presence versus absence of flooding forms the extremes of a hydrological gradient, with various intermediate conditions, such as seasonal soil waterlogged areas, in between. We investigated the relationship between understory herbs and hydrological conditions in Central Amazonian forests using eighty-eight 250×2 m plots distributed along a 600-km transect. Hydrological conditions were determined regionally by precipitation and locally by topographic conditions based on drainage potential, flooding height and soil permeability (sand content). Soil cation concentration was used as a proxy for soil fertility. The floristic dissimilarities among plots were visualized by Nonmetric Multidimensional Scaling, and simple and multiple regressions were used to identify the best predictor of herb species composition. Local drainage potential was more important in determining herb species composition than soil fertility or precipitation at non-flooded and flooded sites. Flooded sites comprised a very distinctive herb species composition within this flat regional landscape with moderate amounts of soil fertility variation (0.09–2.280 cmol(+)/kg). Hydrological models that consider local water conditions explained the largest part of herb species composition. Therefore, predictions of species distribution based on large-scale climatic variables may underestimate the favorable area for understory herbs if the variation on local hydrological conditions is not considered.

Abstract in Portuguese is available in the online version of this article.

Key words: drainage potential; environmental gradients; Purus-Madeira; soil fertility; understory herbs; vertical distance to the nearest drainage.

DESPITE BEING A MAIN FOCUS OF BIODIVERSITY RESEARCH, the factors driving species distributions are still under debate (Tuomisto et al. 2003, Costa et al. 2005, Zuquim et al. 2012). Many studies have focused on soil fertility (Gentry & Emmons 1987, Poulsen & Balslev 1991, Ruokolainen et al. 2007) and topography (Tuomisto et al. 1995, Tuomisto & Poulsen 2000) as the main predictors of herb community composition among large regions of nonflooded forests in the Amazon basin. In general, non-flooded forests have been largely recognized as being different from forests subject to seasonal flooding (Wittmann et al. 2006). The presence of prolonged flooding and its complete absence define the extremes of a hydrological gradient. Although gradients in types of flooding exist (Prance 1979), intermediate hydrological conditions such as seasonal soil waterlogged areas have been less studied and, little is known about the effect of hydrological conditions on floristic composition in these environments.

Hydrological conditions for plants can be assessed either directly by measuring soil-water availability (Jirka *et al.* 2007, Comita & Engelbrecht 2009) or indirectly by estimating soil drainage (Tuomisto & Ruokolainen 1994), topographical position (Clark *et al.* 1998, Tuomisto & Poulsen 2000, Vormisto *et al.* 2004) or, at a regional scale, precipitation (Clinebell et al. 1995). In Central Amazonia, a mosaic of forests with different hydrological conditions can be found, from seasonally inundated to terra firme (non-inundated) forests. In the vicinity of large rivers, forests can be subject to flooding for more than 200 d per year (Wittmann et al. 2004). Flooding also occurs near small to mediumsized streams, where flooding events last only one to a few days. Under these conditions, seasonal soil waterlogging takes place. The floristic composition of seasonally flooded areas along large rivers is known to be highly influenced by the duration and depth of flooding (Wittmann et al. 2006, Parolin et al. 2010). Less is known about composition of plants nearby small to mediumsized streams where flooding is not as extreme as in the vicinity of large rivers. In these areas, floristic composition has been observed to change according to the distance from a watercourse (Drucker et al. 2008, Costa et al. 2009), suggesting that water conditions also play an important role in determining plant assemblages in small and mid-sized riparian zones. At the other extreme, in non-flooded forests, drought can be a strong determinant of plant compositional patterns (Engelbrecht & Kursar 2003, Bunker & Carson 2005, Nepstad et al. 2007).

Soil-water availability is linked to the topographic profile of the terrain (Sollins 1998, Daws *et al.* 2002, Balvanera *et al.* 2010). Higher areas tend to be dryer than the lower areas because of

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the water runoff driven by gravitational potential, whereas lower areas tend to be moister because of the water input from higher sites and the proximity of the water table (Rennó et al. 2008). However, this association cannot be extended to large regions that differ in general elevation. The relationship between soilwater availability and topography becomes complex when wide, flat areas are compared with well-dissected terrains. Recently, a new analytical approach has provided a way to overcome this caveat by enabling inferences of hydrological properties through an estimation of the vertical distance of any site to the nearest drainage (Rennó et al. 2008). The vertical distance to the nearest drainage (VDND) provides an indirect measure of hydrological condition by relating topographic elevation values to the nearest drainage rather than the sea level. This approach creates topographic profiles of different geomorphologies that are comparable at regional scales. Schietti et al. (2013) applied this metric successfully to predict species composition in a 10×10 km landscape with a highly dissected topography. However, most of the Amazon basin is less dissected, and we do not know if topographically defined hydrological predictors are effective to detect patterns of species distribution in flatter landscapes.

In the flat plains of Central Amazonia, soils can be saturated by water even far away from streams and rivers (Sombroek 2000). This landscape is characterized by weathered soils of low cation concentration (Quesada et al. 2011) and high variation in the soil water table level. The geological history of such formations (Rossetti et al. 2005, Hayakawa et al. 2010) led to small variations in soil fertility and high variations of soil water conditions. This scenario allowed the investigation of herb species composition in a hydrological gradient that includes non-flooded, seasonal soil waterlogged and flooded sites under relatively homogeneous soil fertility over an extent of ca 600 km. Since herbs are sensitive to both hydrology (Gentry & Emmons 1987) and soil fertility (Zuquim et al. 2012), we hypothesize that the species composition of understory herbs is mainly structured by hydrological gradients when there is no prominent variation in soil fertility. We tested this hypothesis by analyzing the relative importance of soil fertility and hydrological conditions (as assessed from local drainage, topography, soil type and regional precipitation) as predictors of herb species composition.

METHODS

STUDY AREA.—The study was conducted between the Purus and Madeira Rivers in Central Amazonia along a 600-km section of the federal road BR-319 (Fig. S1). The dominant vegetation is dense tropical lowland forest in the northern part of the study area and open tropical lowland forests with the predominance of babaçu (*Orbygnia martiana*) and patauá (*Oenocarpus bataua*) palms in the old growth forests of the southern part (Brasil 1978). The climate is predominantly hot and moist with mean temperature in the coldest month superior to 18°C and mean annual precipitation varying from 2000 to 2700 mm (Brasil 1978). The number of dry months (precipitation below 100 mm) per year varies between one and five (Sombroek 2001). The topography is generally flat, and the most common landforms are low plateaus with poorly drained soils that can extend up to dozens of kilometers (mega-plateaus), slopes with well-drained soils (mega-slopes) and riverine terraces close to primary rivers (Brasil 1978). Riverine terraces are subject to frequent flooding caused by overflow of small streams. In the mega-plateaus, waterlogging or flooding occurs mainly because of soil saturation caused by heavy precipitation and consequently fluctuations in the water table level. Flooding can reach up to 5 m aboveground, as observed by the marks in tree trunks, and can last for several weeks. The main soil types are plinthosols on mega-plateaus and mega-slopes and fluvisols on terraces (Quesada *et al.* 2011).

SAMPLING DESIGN.—Understory herbs were sampled in 88 permanent plots distributed in nine of the 11 research sites that the Brazilian Biodiversity Research Program (PPBio) has established along the BR-319 road. Each site had two 5-km trails with ten plots distributed 1 km apart, following the RAPELD sampling design (Magnusson *et al.* 2005). Each plot had a 250 m long main axis oriented along the altitudinal terrain contour to minimize soil and topography variations and was 2 m wide.

INVENTORY OF UNDERSTORY HERBS .--- Inventories were mostly done during the dry season, between August and December of 2010. Herbs in Amazonia are mostly perennial and evergreen. Only saprophytes are seasonal, but these were not included in the sampling. All obligate understory terrestrial herbs (Poulsen 1996) taller than 5 cm and rooted within the plots were counted and identified. Epiphytes fallen to the ground and hemiepiphytes were not sampled. Since many herb species have vegetative propagation, we considered as individuals the groups of stems or leaves that were 20 cm apart from each other, following Costa et al. (2005). For species that form large mats which do not allow distinction of single individuals (e.g., Selaginella and Trichomanes), we considered each stem as an individual. The varieties of Lindsaea lancea (L.) Bedd. and Ischnosiphon puberulus Loes. were not considered as distinct taxonomic entities. Determinations were based on field guides (Zuquim et al. 2008, Costa et al. 2011), monographs (Andersson 1977, Hagberg 1990, Judziewicz et al. 1999, Prado 2005, Prado & Freitas 2005), comparison with voucher specimens at the INPA Herbarium, and consultation of specialists. Vouchers for each species and/or morphotypes were collected and all fertile material was deposited in the INPA Herbarium, Manaus.

ENVIRONMENTAL VARIABLES.—Hydrological conditions of plots were determined by local drainage potential (given by topography and soil type) and precipitation regime. Drainage potential of a given point of the terrain was calculated as the elevation difference between the point itself and the nearest point in the drainage to which the focal point is hydrologically connected. At local scales, the elevation above sea level (asl) is a good representation of the drainage potential (*i.e.*, high elevation sites are farther from the water table than low elevation sites), but at regional scales, sites with different elevation asl may have the same drainage potential (i.e., distance from water table). For this reason the terrain drainage potential can be assessed using VDND, which represents the distance of soil surface to the water table. We calculated VDND using a remote sensing based algorithm developed by Rennó et al. (2008), which combines a digital elevation model with a drainage network. We first generated different drainage network complexities from the SRTM digital elevational model (SRTM-DEM). These were validated with field observations of permanent and temporary streams made along 110 km of trails used to access the sampling plots. The best drainage network representing our study area had a contribution area of at least 50 raster cells (90 × 90 m) to initiate a drainage point (Threshold = 50, sensu Rennó et al. 2008). To estimate the VDND value for each plot, we took geographical coordinates every 10 m along the plots (except for the M01 plot where we took points every 50 m) with a Garmin 60X GPS. VDND values were extracted for the geographical coordinates of the plots and the mean vertical distance to nearest drainage was calculated. We truncated VDND values at a maximum of 15 m because only two plots had higher VDND values and both of them were in the same class of well-drained soils. Calculations were performed in IDL/ENVI (v. 4.7) software written by C. D. Rennó (available at http://www.dpi.inpe.br/~camilo/hand/hand_grid.sav).

Vertical distance to the nearest drainage values close to zero indicate areas where the water table is near the surface (saturated areas), whereas larger positive values indicate a larger vertical distance of the water table from the surface (well-drained areas). VDND is a stationary measure and represents the local draining potential of the terrain independently of the season. For thirteen plots placed in flooded areas the soil water conditions could not be described using VDND, which is meant to quantify the variation in water level below the soil surface, not aboveground. For these plots, we described the hydrological conditions by estimating flood depth by other means. In four plots, we installed leveloggers (LT Levelogger Junior M10/F30, Solinst) in the bottom of piezometers to measure the height of the water column. Piezometers are 7 m deep vertical tubes positioned in the initial point of each plot, approximately 0.5 m aboveground. Holes in lower part of the tubes allow water input and vertical water flow. Data were collected between June and July of 2011, when we observed the higher flooding in the study area. In nine plots, we inferred the height of the water column through the water marks left on tree trunks by the highest water level in the previous year. When more than one measure of flooding was available, we considered the highest flooding value registered. The complete gradient of local drainage was, therefore, the combination of VDND with the measurements of flooding height aboveground (leveloggers and water marks on tree trunks). Positive values of this gradient represent the vertical distance to the water table given by VDND and negative values represent the height of flooding aboveground (Fig. S2; Table S2).

Soil sand content was used as a proxy of water permeability, since water retention in the soil depends on its particle size (Marshall *et al.* 1996). Clay and silt hold more water than sand, which loses moisture because of the weaker forces retaining water in

the large spaces between the grains (Hacke et al. 2000). Physical and chemical soil properties were obtained for 87 of the 88 plots following PPBio's protocol (http://ppbio.inpa.gov.br/manuais). Soil samples were taken from the top 5 cm of mineral soil at 50 m intervals (six samples/plot) along the plot's long axis. The samples were air-dried, sieved through a 2 mm mesh and bulked to produce composite samples. The sand content of the soil samples was determined by the hydrometer method after treatment with physical and chemical dispersants to separate the particles (Donagema et al. 2011). Cations were extracted either by the KCl 1 N method (Ca⁺ and Mg⁺²) or by Mehlich's I extraction solution (K⁺) and their concentrations determined by atomic spectrometry. Na⁺ concentrations were below the spectrometer detection level. The soil cation concentration was used as a proxy for soil fertility, as it is, in general, closely related to cation exchange capacity, phosphorus concentration and total elemental composition (Quesada et al. 2010). Soil analyses were conducted on the Plant and Soil Thematic Laboratory at INPA.

Precipitation data for each site was downloaded from the Worldclim data base with 30 arc-sec (\sim 1 km) resolution (Hijmans *et al.* 2005). We used the bioclimatic variable precipitation on the driest quarter of the year as a proxy for rain seasonality, as suggested by Leigh (2004).

DATA ANALYSIS .- Plots were ordered according to dissimilarities in their species composition using Nonmetric Multidimensional Scaling (NMDS). Ordinations were carried in one to four dimensions and the decrease in stress was used to decide on the dimensionality to be used. Three plots were excluded from the analysis as outliers: two of them were placed in areas affected by recent fire and one was in a secondary forest. Ordinations with all plots (N = 85) were used to detect compositional patterns along the whole gradient of local hydrological conditions, and separate ordinations for the non-flooded plots (N = 72) and flooded plots (N = 13) were performed to understand compositional patterns within these categories separately. Ordinations were carried out both for quantitative (species abundances) and qualitative (presence-absence, hereafter: occurrence) data. Species abundances were first relativized by dividing the number of individuals of a species by the total number of individuals in the corresponding plot. Dissimilarities were calculated with the Kulczynski metric (Legendre & Legendre 1998).

The NMDS ordination axes, which represent species composition, were used as dependent variables in regression analyses. The explanatory variables were drainage potential (VDND combined with flooding level), precipitation (precipitation of the driest quarter of the year), soil cation concentration and soil permeability (sand content). To test our hypothesis that the herb species composition is structured by hydrological gradients when there is no prominent variation in soil fertility, we performed simple and multiple regressions (Table 1). The complete multiple regression models included all four environmental variables (drainage potential, precipitation, soil cation concentration and soil permeability). In the first step, complete and simple models were used to test the effect of the full set of environmental variables and the

| Model | Models and variables | Ν | Plot conditions | Transformations |
|------------------------------|--|----|-------------------------|-----------------------|
| 1. Complete model | $A = a + DP \times b_1 + SP \times b_2 + SCC \times b_3 + PR \times b_4$ | 85 | Flooded and non-flooded | Ln (6 + DP), Ln (SCC) |
| 2. Complete model | $A = a + DP \times b_1 + SP \times b_2 + SCC \times b_3 + PR \times b_4$ | 72 | Non-flooded | |
| 3. Complete hydrologic model | $A = a + \mathrm{DP} \times b_1 + \mathrm{SP} \times b_2 + \mathrm{PR} \times b_3$ | 85 | Flooded and non-flooded | |
| 4. Complete hydrologic model | $A = a + \mathrm{DP} \times b_1 + \mathrm{SP} \times b_2 + \mathrm{PR} \times b_3$ | 72 | Non-flooded | |
| 5. Predictive model | $A = a + \mathrm{DP} \times b_1 + \mathrm{PR} \times b_2$ | 85 | Flooded and non-flooded | Ln (6 + DP) |
| 6. Predictive model | $A = a + \mathrm{DP} \times b_1 + \mathrm{PR} \times b_2$ | 72 | Non-flooded | |
| 7. Simple hydrologic model | $A = a + \mathrm{DP} \times b_1$ | 85 | Flooded and non-flooded | |
| 8. Simple hydrologic model | $\mathcal{A} = a + \mathrm{DP} \times b_1$ | 72 | Non-flooded | |

TABLE 1. Simple and multiple regression models, their respective variables and transformations. A, compositional ordination axis; DP, drainage potential; PR, Precipitation; SCC, Soil cation concentration; SP, soil permeability.

specific effect of drainage potential to explain herb species composition. In the second step, we tested the predictive power of models including two hydrological variables that can be obtained from remote sensing (precipitation and drainage potential) when applied for regional scales. The Pillai-Trace statistic was used to evaluate the effect of the independent variables on the set of the ordination axes in the multivariate tests. This statistic has been recommended to multivariate tests because it is the least sensitive to violations of assumptions (Olson 1976). Non-linear functions $(y = a^{(-b \times X)} \text{ or } y = \frac{a_X}{1 + b_X})$ were used to adjust the relationship between the compositional ordination axes and the drainage potential gradient. Data transformation was needed to linearize some relationships for multiple regressions, as indicated in Table 1. An examination of collinearity among the variables in the multiple regressions was performed with the Variance Inflation Factor (Dormann et al. 2013)

Community patterns and the limits of species distributions were evaluated by direct gradient analysis. In this analysis, species were ordered along the hydrological gradient by the mean value of the gradient in the plots where the species occurred. Data analysis was conducted in R v. 2.13.0 (R Development Core Team 2010), with additional functions from the package *vegan* (Oksanen *et al.* 2007).

RESULTS

We sampled 31,362 individuals belonging to 148 morphospecies (Table S1). 3432 (10.9%) of the stems were not included in the analyses because of uncertainties on identifications caused by mixed collections and misidentification of different morphospecies under the same field name. Thirty-eight species and morphotypes were sampled only once and represented 25.5 percent of the registered taxa. *Ischnosiphon puberulus* Loes., *Heliconia acuminata* A. Rich., *Calathea altissima* Horan. and *Trichomanes pinnatum* Hedw. were found in more than 70 percent of the plots. Direct gradient analysis showed that more species were restricted to the flooded areas and attained high abundances in the flooded plots (Fig. S3). In the non-flooded areas, species composition changed gradually along the hydrological gradient, and this change was mostly associated with the abundances (rather than occurrence) of species.

CORRELATIONS AMONG ENVIRONMENTAL VARIABLES.—Hydrological variables were weakly or not at all correlated with soil variables (VDND × sand content: r = 0.24, VDND × soil cation concentration: r = -0.23, VDND × total phosphorus: r = -0.32, precipitation × sand content: r = -0.35, precipitation × soil cation concentration: r = 0.14, precipitation × total phosphorus: r = -0.04). The multiple correlations within models were also low (VIF < 1.3).

The variation in soil cation concentration in our entire dataset ranged from 0.09 to 2.280 cmol(+)/kg. Four plots found in flooded areas had higher soil cation concentration than 0.650 cmol (+)/kg, which is the upper limit of the range of cation concentration found in non-flooded areas (0.090–0.650 cmol(+)/kg). The correlation between VDND and soil cation concentration excluding these four plots was even weaker (VDND × soil cation concentration: r = -0.20). Therefore, the effects of hydrological variables were not confounded with fertility effects in the results.

DISTRIBUTION OF UNDERSTORY HERBS ALONG ENVIRONMENTAL GRADIENTS.-The complete model for the entire hydrological gradient, which included soil cation concentration, drainage potential, soil permeability and precipitation (model 1 in Table 1), explained 49 percent of the floristic variation when abundance data were used and 53 percent when occurrence data were used (Table 2). The best predictor of herb species composition was drainage potential, followed by precipitation. Soil cation concentration and soil permeability had only weak predictive power. Even when only non-flooded plots were analyzed (model 2 in Table 1), drainage potential and precipitation were more important predictors of floristic composition than soil cation concentration and permeability. This was the case for both abundance and occurrence data (Table 2). The pure hydrological models confirmed drainage potential as a more important predictor for floristic composition than soil permeability or precipitation (Table 3). These results were otherwise the same for flooded and nonflooded plots, but for the latter, precipitation had relevant predictive power for occurrence data (models 3 and 4 in Table 1).

DISTRIBUTION OF UNDERSTORY HERBS ALONG HYDROLOGICAL GRADIENTS.—The relationship between herb species composition and drainage potential (models 7 and 8) was not linear, but the

| TABLE 2. | Standardized regression | <i>coefficients</i> (b | s _{std}) and respectiv | e probabilities | associated to | the multiple | e regressions | between . | species c | romposition | and the | environmental | variables |
|----------|--------------------------|------------------------|----------------------------------|-----------------|-------------------|--------------|----------------|-----------|-----------|--------------|-----------|---------------|-----------|
| | represented by drainage | potential (DP) |), soil permeability | (SP), soil cat | ion concentration | 1 (SCC), p | recipitation (| PR) and | Nonmet | ric Multidii | mensional | Scaling (NM | DS). The |
| | table summarizes the res | ults of the mod | dels 1 and 2. | | | | | | | | | | |

| Data type | Axis | DP | SP | SCC | PR | \mathbb{R}^2 |
|--------------------------|--------------|-----------|--------------|--------------|-----------|----------------|
| All the plots $(N = 85)$ | 5) | | | | | |
| Quantitative | NMDS 1 | 0.730**** | -0.198^{*} | -0.204^{*} | -0.092 | 0.49 |
| | NMDS 2 | 0.092 | -0.134 | 0.196 | -0.315*** | 0.10 |
| | Pillai-Trace | 0.452*** | 0.122* | 0.054 | 0.329*** | |
| Qualitative | NMDS 1 | 0.166*** | -0.088 | 0.105 | -0.066 | 0.53 |
| | NMDS 2 | 0.027 | 0.096 | -0.208 | 0.239* | 0.04 |
| | Pillai-Trace | 0.582*** | 0.059 | 0.124* | 0.385*** | |
| Non-flooded plots (1 | N = 72) | | | | | |
| Quantitative | NMDS 1 | 0.242* | -0.040 | -0.207 | 0.399*** | 0.24 |
| | NMDS 2 | -0.239* | -0.074 | -0.053 | 0.523*** | 0.26 |
| | Pillai-Trace | 0.163* | 0.168* | 0.065 | 0.549*** | |
| Qualitative | NMDS 1 | -0.156 | 0.184 | 0.007 | 0.773*** | 0.47 |
| | NMDS 2 | -0.447*** | 0.032 | -0.046 | 0.221 | 0.15 |
| | Pillai-Trace | 0.264*** | 0.186** | 0.127 | 0.717*** | |

*P < 0.05; **P < 0.01, ***P < 0.001.

TABLE 3. Standardized regression coefficients (b_{std}) and respective probabilities associated to the multiple regressions relating the compositional axes to drainage potential (DP) and precipitation (PR), soil permeability (SP) and Nonmetric Multidimensional Scaling (NMDS). The table summarizes the results of the models 3 and 4.

| Data type | Axis | DP | SP | PR | R^2 |
|------------------|-------------------|----------------|--------|--------------|-------|
| All the plots (N | V = 85) | | | | |
| Quantitative | NMDS 1 | 0.688*** | -0.184 | -0.124 | 0.42 |
| | NMDS 2 | -0.143^{*} | -0.163 | -0.280^{*} | 0.07 |
| | Pillai-Trace | 0.451*** | 0.122* | 0.323*** | |
| Qualitative | NMDS 1 | 0.763*** | -0.091 | -0.064 | 0.55 |
| | NMDS 2 | 0.081 | 0.127 | 0.202 | 0.01 |
| | Pillai-Trace | 0.583*** | 0.057 | 0.403*** | |
| Non-flooded p | lots ($N = 72$) | | | | |
| Quantitative | NMDS 1 | 0.294** | -0.012 | 0.343** | 0.21 |
| | NMDS 2 | -0.225^{*} | -0.067 | 0.508*** | 0.27 |
| | Pillai-Trace | 0.159* | 0.157* | 0.508*** | |
| Qualitative | NMDS 1 | -0.158 | 0.183 | 0.775*** | 0.48 |
| | NMDS 2 | -0.434^{***} | 0.038 | 0.208 | 0.16 |
| | Pillai-Trace | 0.254*** | 0.184 | 0.703*** | |
| | | | | | |

*P < 0.05; **P < 0.01, ***P < 0.001.

best adjustment was a negative exponential function (Fig. 1A and B). The exponential decay models provided the best adjustments for both abundance and occurrence data ($R^2 = 0.47$, P < 0.001 and $R^2 = 0.62$, P < 0.001, respectively), since the floristic variation was higher in the flooded part of the gradient but stabilized toward the non-flooded part (Fig. 1A and B). Flooding height effect explained 67 percent of the variation in species composition (occurrence data) among plots subject to flooding (Fig. S4). On

the other hand, floristic composition in non-flooded plots, when analyzed separately, had a weak linear relationship with drainage potential ($R^2 = 0.11$, P < 0.005) for abundance data (Fig. 1C), but no significant relationship for occurrence data (Fig. 1D).

Despite the importance of flooding for floristic composition, most of our sites were not flooded. At non-flooded sites, the model including drainage potential and precipitation (model 6 in Table 1) explained approximately 22 percent of the floristic variation in the abundance data and 46 percent in the occurrence data (Table 4). Precipitation was more important than local drainage potential for the occurrence data. Local drainage was associated with the second axis of the NMDS ordination, whereas precipitation was associated with the first one. This effect was not so clear when all plots were included (model 5).

DISCUSSION

HERB DISTRIBUTION VERSUS HYDROLOGY .- Local drainage explained the largest part of the variation in herb composition in a flat regional landscape with small variation in soil fertility. It has been assumed that hydrological conditions drive herb species composition at local to meso-scales, although this has only been indirectly concluded through the association of herb species composition and topography (Tuomisto & Ruokolainen 1994, Tuomisto & Poulsen 2000, Salovaara et al. 2004, Drucker et al. 2008). We show through a novel hydrological approach that this relationship is also valid at regional scales. Our results support the assumption that hydrologically similar environments can have similar species composition even if separated by many kilometers. Similar results were found for woody plants in floodplain forests (ter Steege et al. 2000, Wittmann et al. 2006). Here, we extend this finding for herbs and to a gradient from non-flooded to seasonally flooded areas.



FIGURE 1. Relationship between the herb composition, reduced to one Nonmetric Multidimensional Scaling (NMDS) ordination axis and the drainage potential based on quantitative (A and C) and qualitative data (B and D). The complete gradient of local hydrological conditions is considered in A and B. Only non-flooded plots are considered in C and D. The dashed lines separate flooded and non-flooded plots.

| TABLE 4. | Standa | ordized regressio | n coeffic | cients (| o _{std}) and resp | ective probabilities a | ssociatea |
|----------|----------|-------------------|-----------|----------|-----------------------------|------------------------|-----------|
| | to the r | multiple regressi | ions rela | ating th | e composition | al axes to drainage | potential |
| | (DP), | precipitation | (PR) | and | Nonmetric | Multidimensional | Scaling |
| | (NML | DS). The table . | summar | rizes th | e results of th | e models 5 and 6. | |

| Data type | Axis | DP | PR | \mathbb{R}^2 |
|--------------------|-----------------|-----------|--------------|----------------|
| All the plots $(N$ | = 85) | | | |
| Quantitative | NMDS 1 | 0.639*** | -0.056 | 0.40 |
| | NMDS 2 | -0.187 | -0.221^{*} | 0.07 |
| | Pillai-Trace | 0.446*** | 0.354** | |
| Qualitative | NMDS 1 | 0.739*** | -0.031 | 0.53 |
| | NMDS 2 | 0.115 | 0.156 | 0.01 |
| | Pillai-Trace | 0.581*** | 0.408*** | |
| Non-flooded plo | ts ($N = 72$) | | | |
| Quantitative | NMDS 1 | 0.291*** | 0.348 | 0.22 |
| | NMDS 2 | -0.239* | -0.537*** | 0.23 |
| | Pillai-Trace | 0.158* | 0.528*** | |
| Qualitative | NMDS 1 | -0.121 | 0.697*** | 0.46 |
| | NMDS 2 | -0.428*** | 0.195 | 0.16 |
| | Pillai-Trace | 0.253*** | 0.701*** | |

*P < 0.05; **P < 0.01, ***P < 0.001.

Several authors have suggested that soil fertility is the main determinant of herb distribution in well-drained forests of Amazonia (Gentry & Emmons 1987, Vormisto *et al.* 2000, Costa et al. 2005). However, this association depends on the relative breadth of soil fertility (Pansonato et al. 2013) and hydrological gradients in the study area. Soils of Central Amazonia are mostly cation-poor; the cation concentrations in our soil samples from the Purus-Madeira region ranged from 0.09 to 2.28 cmol(+)/kg. The low range of cation concentration indicates a narrow gradient of soil fertility in comparison with the gradient found in Western Amazonia by Ruokolainen et al. (2007), where soil cation content ranged from 0.13 to 14.53 cmol(+)/kg. In the Purus-Madeira region, soil fertility and hydrological conditions were weakly correlated, and our models confirmed the importance of hydrological conditions as predictors of species composition, even when the relatively cation-rich alluvial soils near the Solimões River were included in the analysis (plots M01 and M02 in Fig. S1). Despite the importance of soil nutrients in other areas, hydrological conditions were an important factor for species composition of herbs in our study area. Flooded areas, for example, had a very distinctive herb composition even when the flood was at low depth (<0.3 m). The seasonality of flooding allows fast growing species to establish and reproduce during the dry season. For plants with shallow roots, such as understory herbs, small variations in local water availability are relevant, since their roots are restricted to the surface soil layer. We conclude that hydrological conditions are the primary constraint on herb species composition when soil fertility variation is moderate.

LOCAL HYDROLOGICAL CONDITIONS AS PREDICTOR OF SPECIES COMPOSITION AT REGIONAL SCALES .- Local drainage potential was more important for herb species composition than our estimate of precipitation. The secondary role of precipitation in our models contrasted with its importance for regional scale (Gentry 1988, Clinebell et al. 1995, ter Steege et al. 2003). The determination of the relative importance of precipitation versus local water availability is not easy, as data on the latter have not previously been available at extents comparable to those where precipitation data has been used. SRTM data coupled with VDND made topographical data available to investigate variation in local drainage. Our results showed that hydrologically similar environments may result in similar species composition even under different precipitation regimes. However, our study area did not include any climatically dry forests, so our findings should not be overextrapolated. Soil water availability depends on precipitation, and in dry forests, environments might be hydrologically similar only a part of the year. Evaluating the relative importance of precipitation would necessitate the inclusion of climatically drier areas in the hydrological gradient, although the local effects would possibly remain. Further studies on the role of local water availability in predicting the distribution of other groups of plants might clarify the predictive power of this variable and its relative importance compared to precipitation.

One of the main limitations of broad-scale predictive distribution models at the community and species level is the difficulty to include predictors of local environmental conditions that affect the occupation of sites (Ferrier *et al.* 2002, Pearson & Dawson 2003). There are no complete maps of these predictors at the required spatial scales. Local hydrological models for predicting species distribution at regional scales, such as the one developed by Rennó *et al.* (2008) are good options to detect subtle changes in community composition. The VDND model is applicable for any scale using geoprocessing techniques, provided that a field validation of drainage position is conducted. The results of our study extend to regional scales according to Schietti *et al.* (2013), who reported that VDND predicts up to 82 percent of the distribution of different groups of plants (trees, lianas, palms, shrubs and herbs) at a lowland non-inundated forest, north of the Amazon River.

Vertical distance to the nearest drainage was effective in detecting local hydrological conditions in non-flooded areas since it uses site-independent gravitational potential for terrain description and a robust method for separation of well-drained from waterlogged areas (Rennó *et al.* 2008). The prediction of the abundance of the herb assemblage in non-flooded areas by the VDND shows that herb species composition followed topography, as reported by Tuomisto and Poulsen (2000), Costa *et al.* (2005) and Drucker *et al.* (2008). However, the seasonality of flooded areas cannot be mapped exclusively with VDND and field measurements of flood height were needed for these sites. An extension of the algorithm to calculate flooding and then recalculate VDND values based on flood heights is currently being developed. If effective, it will further expand the applicability of this predictor to map species distributions.

IMPLICATIONS: CLIMATIC CHANGES AND CONSERVATION OF UNDERSTORY HERBS .- Long dry seasons may lead to long-term shifts in species composition in tropical forests (Condit 1998, Malhi et al. 2009). Local effects of extended droughts have been registered for shrubs (Condit et al. 1995), trees and lianas (Nepstad et al. 2007) and seedlings (Bunker & Carson 2005). Some authors have already registered death or a decrease in entire herb populations in years with unusually long dry seasons (Freiberg & Turton 2007, Schleuning et al. 2008). Parolin et al. (2010) suggested that drought can be more stressful for plants adapted to flooding than the flood itself. This is why a decrease in water availability in the soil might increase the short-term costs of metabolic regulation for species, leading to a rapid loss of water through stomata. We expect that more frequent prolonged dry seasons will modify the herb assemblages along the current hydrological gradient. Species adapted to wetter areas may have population decrease if no suitable habitat is available within dispersal distance.

Climate change scenarios for Amazonia indicate a trend toward increased dry season intensity and, consequently, water deficit of the forests (Aragão *et al.* 2014). Our results suggest that hydrological models that consider local water availability have predictive power to explain herb species composition. However, the drainage potential that support different sets of species are not homogeneously distributed on the landscape but are somewhat related to geomorphology. Therefore, conservation of areas that have potential to harbor the diversity of understory herbs should include physiographic units with wet conditions, to where species could eventually move if the climate gets drier.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Grid locations which are part of the Brazilian Biodiversity Research Program between the River Purus and Madeira.

FIGURE S2. Distribution of VDND values.

FIGURE S3. Relative abundance of species ordered along the hydrological gradient in 88 plots along the BR-319 road.

FIGURE S4. Relationship between herb species composition and flooding height.

TABLE S1. Morphospecies list and respective abundances.

TABLE S2. Elevation average values of SRTM-DEM, VDND and VDND with flooding for all plots.

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