# Broad Scale Distribution of Ferns and Lycophytes along Environmental Gradients in Central and Northern Amazonia, Brazil

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## Abstract:

Establishing which factors determine species distributions is of major relevance for practical applications such as conservation planning. The Amazonian lowlands exhibit considerable internal heterogeneity that is not apparent in existing vegetation maps. We used ferns as a model group to study patterns in plant species distributions and community composition at regional and landscape scales. Fern species composition and environmental data were collected in 109 plots of 250 m x 2 m distributed among four sites in Brazilian Amazonia. Interplot distances varied from 1 to ca. 670 km. When floristically heterogeneous datasets were analyzed, the use of an extended Sørensen dissimilarity index rather than the traditional Sørensen index improved model fit and made interpretation of the results easier. Major factors associated with species composition varied among sites, difference in cation concentration was a strong predictor of floristic dissimilarity in those sites with pronounced heterogeneity in cation concentration. Difference in clay content was the most relevant variable in sites with uniform cation concentrations. In every case, environmental differences were invariably better than geographic distances in predicting species compositional differences. Our results are consistent with the ideas that 1) the relative predictive capacity of the explanatory variables depends on the relative lengths of the observed gradients and 2) environmental gradients can be hierarchically structured such that gradients occur inside gradients. Therefore, site-specific relationships among variables can mask the bigger picture and make it more difficult to unravel the factors structuring plant communities in Amazonia.

Key-words: dispersal limitation; environmental factors; extended dissimilarities; pteridophytes; species turnover; Sørensen index; tropical forest; understory

IDENTIFYING AND UNDERSTANDING PATTERNS IN HOW SPECIES ARE DISTRIBUTED IS ESSENTIAL FOR CONSERVATION PLANNING, AND BIOGEOGRAPHICAL RESEARCH HAS LONG BEEN RECOGNIZED AS FUNDAMENTAL FOR THE ELABORATION OF CONSERVATION STRATEGIES IN THE AMAZON BASIN (RYLANDS 1990, GUISAN & ZIMMERMANN 2000). The Amazonian lowlands, including forests in non-inundated areas (terra firme), exhibit considerable internal heterogeneity that is not apparent in existing vegetation maps (Emilio *et al.* 2010). These maps (e.g., Capobianco *et al*. 2001, IBGE 2004) are therefore insufficient when the goal is to preserve a representative mosaic of Amazonian habitats and the species they harbour. General knowledge of the distribution of the Amazonian biota is still limited: collection density is low, and most collections come from only a few localities (Nelson *et al.* 1990, Hopkins 2007). Moreover, there is no consensus on the role of environmental factors in predicting species composition at different spatial scales. Complete inventories of all species in Amazonia are impossible due to the high species richness. Therefore, mapping the distribution of organismal diversity and evaluating the representativeness of protected areas are in practice dependent on the use of surrogate taxa and the modelling of species–environment relationships (Margules *et al.* 2002, Ruokolainen *et al.* 1997, 2007).

The balance between the relative importance of stochastic and environmental factors can be expected to change with both the spatial scale considered and the degree of environmental variation in the area of interest (Costa *et al.* 2005, Jones *et al.* 2006, 2008, Karst *et al.* 2005, Ruokolainen *et al.* 1997, 2007, Tuomisto *et al.* 2003a, b, c, Zuquim *et al.* 2009). At biogeographical scales, species present in one region may be absent from another because they have never managed to disperse there. In environmentally heterogeneous areas, species present in some localities may be absent from others because conditions there are not favourable. Dispersal limitation causes spatial autocorrelation in species distributions. Separating this effect from the effect of environmental heterogeneity is difficult, because environmental variables are often spatially autocorrelated as well. Environmental features have been consistently found to be important predictors of changes in plant species composition in neotropical forests (Phillips *et al.* 2003, Tuomisto *et al.* 2003a, b, c, Costa *et al.* 2005, Kinupp & Magnusson 2005, Jones *et al.* 2006, Ruokolainen *et al.* 2007, Zuquim *et al.* 2009). Even though it is obvious that no plant species can grow in all environmental conditions, establishing which environmental factors are most important for species distributions is not easy, and requires repeated inventories made in different areas.

The present knowledge on plant species distribution patterns in terra firme forests of Amazonia comes mostly from the western part of the basin, where the concentration of exchangeable bases in the soil has consistently emerged as one of the most important environmental factors associated with turnover in plant community composition at landscape to regional scales (Tuomisto & Poulsen 1996, Duivenvoorden 1995, Tuomisto *et al.* 2002, 2003a, b, c, Phillips *et al.* 2003, Vormisto *et al.* 2004, Higgins *et al.* 2011). In central Amazonia, floristic studies have mainly addressed local to mesoscales (0-100 km$^2$), and in these studies soil clay content has emerged as especially important (Laurance *et al.* 1999, Costa *et al.* 2005, Kinupp & Magnusson 2005, Castilho *et al.* 2006).

In studies on tropical plant communities, a large part of the variation in species turnover usually remains unexplained (Duivenvoorden *et al.* 2002, Tuomisto *et al.* 2003a, c, Vormisto *et al.* 2004, Jones *et al.* 2006). It is possible that the unexplained variation is truly stochastic and unstructured (and hence not describable by a predictive model), but the proportion of unexplained variation can also be inflated for technical reasons, such as sampling error, inadequate analytical tools and the omission of one or more relevant predictors. In the present paper, we attempt to eliminate one problem related to the analytical tools, namely the saturation of compositional dissimilarity at a fixed maximum value when sampling units share no species.

Both the relative importances of spatial vs. environmental factors, and the relative importance of each environmental factor in determining species distributions, differ among spatial scales and plant groups (Duivenvoorden *et al.* 2002, Phillips *et al.* 2003, Tuomisto *et al.* 2003a, b, c, Normand *et al.* 2006). This affects decisions on which predictors to use for planning and management in each scale and region. In this study, we address patterns in plant species distribution at the community level and the relationships with edaphic and climatic variables at broad (distances exceeding 600 km) and landscape (distances of 7-15 km) scales. We also explore the effects of using extended instead of traditional compositional dissimilarities in the analyses. This study focuses on ferns and lycophytes, but the results are probably indicative of patterns in other plant groups as well (Tuomisto *et al.* 2003a, b, c, Ruokolainen *et al.* 1997, 2007, Duque *et al.* 2005, Jones *et al.* 2008).

## METHODS

STUDY SITES – The study was carried out at four sites in central and northern Brazilian Amazonia, in the States of Amazonas and Roraima (Fig. 1). Forest structure varies from dense lowland tropical forest to white sand forest (*campinaranas*) and shrublands (*campinas*). The sites are located from 90 to ca. 670 km apart. Three sites are located to the north of the Amazon River and are within protected areas. One site is located to the south of the Amazon River along the BR-319 highway, and lacks protection status, so it is prone to threats such as deforestation and selective logging. All the sites are subject to long-term research by Brazilian Biodiversity

Research Program (PPBio), and therefore have a permanent inventory plot system. The study sites are described below in geographical order, from north to south, with additional information given in Table 1.

**Viruá National Park (Viruá):**

Viruá National Park is located in the State of Roraima, ca. 150 km to the south of Boa Vista. It comprises a mosaic of poorly-drained sandy flat areas and higher areas with clayey soils. Physiognomies vary from white-sand grasslands and shrublands (*campinaranas gramíneo-lenhosas e arbustivas*) and white-sand forests (*campinarana arbórea*) to lowland ombrophilous dense forest (IBGE 2004). The plots were installed in the northeastern area of the park in a permanent study grid of PPBio.

**Uatumã Biological Reserve (Uatumã):**

The Uatumã Biological Reserve is located ca. 120 km north of Manaus, next to the Balbina Hydroelectric Dam on the Uatumã River. The reserve is covered by sub-montane ombrophilous dense forest (IBGE 2004). The reserve is in a geologically complex area in the contact zone between the pre-Cambrian Barreiras formation and the Paleozoic formation (Irion 1978). The plots were installed in the southernmost part of the reserve in a permanent study grid of PPBio,

**Reserves of the Biological Dynamics of Forest Fragments Project (BDFFP):**

The site is situated about 60 km to the north of Manaus city and the plots were divided between three continuous forest reserves along a branch of Manaus – Boa Vista Highway (Km 41, Cabo Frio and Gavião). Each reserve comprises ca. 12 km$^2$ of *terra firme* tropical rain forest (lowland ombrophilous dense forest; IBGE 2004). Soils are characterized by kaolinitic clays on plateaus and at higher elevations, grading to sandy podzols at lower elevations, as is typical in the Manaus region. They are derived from highly weathered tertiary fluvio-lacustrine deposits and are acidic and poor in nutrients (Chauvel *et al.* 1987).

**BR-319 Highway, km 220 (BR-319):**

The site is situated ca. 200 km to the south of Manaus near km 220 of the BR-319 Highway (Manaus-Porto Velho). The road lies in the interfluve between the Purus and Madeira Rivers and is mainly covered by lowland ombrophilous dense forest (IBGE 2004). The plots are installed on Pleistocene sediments of the Solimões formation. The topography is flat, and small variations in relief (1 to 3 m) promote the occurrence of temporary ponds.

DATA COLLECTION: SAMPLING DESIGN - A total of 109 plots of 250 m x 2 m were sampled (38 plots in BDFFP, 30 in Viruá, 30 in Uatumã and 11 along the BR-319). Each plot followed the topographic contour to minimize internal heterogeneity in soil properties, which are often correlated with topographic position (Chauvel *et al.* 1987, Mertens 2004). The sampling design was based on the RAPELD methodology (Magnusson *et al.* 2005) and on Zuquim *et al.* (2007). The minimum distance between two plots was 1 km. In Viruá and Uatumã, the plots were distributed in regular grids of 5 km x 5 km. In BDFFP, the plots were distributed in three almost regular 3 km x 4 km grids and on the BR-319, the plots were located along two parallel trails of 5 km (Fig. 1). All the plots are part of the Brazilian Biodiversity Research Program (PPBio) network and the environmental and floristic data are publicly available (http://ppbio.inpa.gov.br/Eng/dadosinvent/).

DATA COLLECTION: FLORISTIC DATA – Inventories were focused on ground-rooted ferns and lycophytes, and included terrestrial, rupiculous and climbing individuals. Terrestrial individuals of species that mainly grow as epiphytes were included in the inventory, but epiphytic individuals were not. In each plot, all terrestrial, rupiculous and hemi-epiphytic fern and lycophyte individuals with at least one leaf (or stem in the case of lycophytes) longer than 10 cm were counted and identified. In the 38 plots of BDFFP, individuals with leaves between 5 and 10 cm were also included in the sample. Climbing individuals whose lowermost green leaves were higher than 2 m above ground were excluded because they are difficult to see from the ground. Each stem of *Selaginella* was counted as one individual in BDFFP, while in Viruá, Uatumã and BR-319, groups of stems closer than ca. of 30 cm to each other were considered as individuals. Voucher specimens were collected to verify the identities of the species. Full sets of the vouchers are deposited in Herbaria at the Instituto de Botânica de São Paulo (SP) and privately with the first author, and fertile duplicates at Instituto Nacional de Pesquisas da Amazônia (INPA), all in Brazil.

DATA COLLECTION: ENVIRONMENTAL DATA - Surface soil samples (topmost layer of the mineral soil sampled down to 5–10 cm depth) were taken every 50 m along the longer axis of each plot. In most sites, the six soil samples from the same plot were bulked into a single composite sample before laboratory analyses. In BDFFP, each sub-sample was analysed separately and the mean value per plot was used for each of the edaphic variables. Before laboratory analyses, the soil samples were cleaned of roots, air-dried and sieved through a 2 mm mesh. Analyses included soil texture (percentage of clay, silt and sand) and exchangeable bases (Ca, Mg, K, and Na using the Mehlich 1 method). All samples were analysed in the Thematic Laboratory of soils and plants at INPA.

Hemispherical photographs of the canopy were used to estimate the amount of light available in the understory. Percentage values of canopy openness were derived from digital images of the forest canopy taken at 50 to 100 cm above ground, under clouded conditions, in the early morning or late afternoon. Six images were taken in each plot at 50 m intervals. The photos were analyzed with the software Gap Light Analyzer (Frazer *et al.* 1999) by two different persons. To verify data consistency, 10 pictures were analysed by both persons. The correlation between their results (Pearson's $r = 0.98$) was considered sufficiently high for the purpose of the present paper. Three plots had to be excluded from analyses involving light because their hemispherical photos were overexposed. Geographical coordinates of the plots were taken using a Garmin 12XL GPS. Dry season length of each site was estimated based on Sombroek (2001). For BR-319, Sombroek (2001) gave the dry season length as 1–2 months, and 2 months was used in the analyses.

DATA ANALYSES – We used presence/absence instead of abundance data to minimize the influence of differences in plant sampling protocols among sites, especially different minimum size limits and differences in delimiting individuals in clonal *Selaginella* species. The total number of species ($\gamma$ richness) was calculated for each site. This was partitioned into two components, the mean species richness per plot ($\alpha$ richness) and the number of compositional units ($\beta$ richness = $\gamma/\alpha$). The latter is a measure of compositional heterogeneity and quantifies how many plots of mean species richness would be needed to accumulate the total species richness observed, if the plots shared no species (Tuomisto 2010).

To analyse the floristic data, we first calculated for each plot pair the Sørensen index, which quantifies the proportion of species shared between two plots (number of species shared divided by the average number of species present in the two plots). The Sørensen similarity index values were converted to dissimilarities (here called Sørensen dissimilarities) by subtracting from unity. When two sampling units share no species, the Sørensen dissimilarity between them necessarily equals the maximum value of unity no matter how large the actual ecological distance between the sampling units. This leads to distortions, such as the arch effect, that complicate the interpretation of ordination results in highly heterogeneous data. One solution that has been proposed to alleviate this problem is the step-across or extended dissimilarity method (Williamson 1978, Bradfield & Kenkel 1987, Belbin 1991, De´ath 1999). An extended dissimilarity measure is obtained between two sampling units that share no species (A and B) by using an intermediate sampling unit (C) as a stepping-stone, and calculating the sum of the dissimilarities A-to-C and C-to-B. More than one intermediate sampling unit can be used, and the smallest of the possible dissimilarities is then used. This method is theoretically appealing, because it allows compositional dissimilarity values to continue increasing with ecological distance beyond the distance at which no species are shared. Extended dissimilarities have as yet been little used in practical applications (but see Laitinen *et al.* 2007, Laitinen *et al.* 2008, Mahecha & Schmidtlein 2008). Here we report the results using the classical and extended dissimilarities in parallel to allow their comparison. Extended Sørensen dissimilarities were calculated using the method of De´ath (1999).

Principal Coordinates Analysis (PCoA) was applied to visualize floristic dissimilarities in ordination diagrams, both for all plots together and for each site separately. Multivariate multiple regressions were then carried out using the two first PCoA axes as dependent variables in order to test how well the community composition axes can be explained by environmental variables. The soil characteristics were synthesized into two variables: clay content (in %) and cation concentration (sum of the exchangeable bases Ca, Mg and K, in cmol(+)/kg; the concentration of Na in the soil samples was below detection level). Cation concentration was transformed before analysis by taking its natural logarithm.

To quantify to what degree variation in environmental and geographical distances can explain variation in species turnover between plots at different scales, multiple regression on dissimilarity matrices was used (Legendre *et al.* 1994). The Euclidean distance was used to quantify differences in environmental variables among plots. Geographical distances were log transformed before analysis and the resulting distances checked for linearity and homogeneity of variances with the floristic similarities. The unique and shared contributions of both kinds of explanatory data to explaining variation in the floristic dissimilarity matrix were quantified with variance partitioning (Borcard *et al.* 1992, Duivenvoorden *et al.* 2002, Tuomisto *et al.* 2003c). These analyses were carried out both for the whole dataset (102 plots; some plots had to be excluded because they had no ferns or because some environmental data were missing) and for each of the four sites separately. Dry season length was only used in analyses of the entire data set, because it did not vary within sites. Simple and partial Mantel tests were applied to quantify the correlations between geographical distances, differences in dry season length and dissimilarities in species composition of ferns and lycophytes.

We encountered no ferns or lycophytes in five of the 109 plots, and these were excluded from PCoA and Mantel tests. Ordinations and Mantel tests were made in the Vegan package (Oksanen *et al.* 2005) for R v. 2.6.2 (R Development Core Team 2008) and RStudio v. 0.92.44 (http://www.rstudio.org). Multiple regression on dissimilarity matrices were made using PERMUTE v.3.4 (http://www.bio.umontreal.ca/Casgrain/en/labo/permute/) and basic statistics were done in Systat 8.0 (Wilkinson 1998).

## RESULTS

SPECIES DIVERSITY AND ENVIRONMENTAL CONDITIONS – In the 109 plots, we recorded 92 species of ferns and lycophytes (with two varieties of *Lindsaea lancea* being counted as species), representing 31 genera and 19 families (Appendix S1). The most frequent species in the dataset were *Trichomanes pinnatum* Hedw., found in 81 plots (88%), and *Lindsaea lancea* var. *lancea* (L.) Bedd and *Adiantum cajennense* Willd., both found in about 50% of the plots. A large percentage of the species (40%) occurred in only one or two plots. Five plots had no fern or lycophyte species, whereas the most species-rich plot had 27 species, with the mean being 7.8 species per plot. Of the four regions, Uatumã had the highest species richness both in total (γ = 62 spp *vs.* 9–33 in the other regions) and per plot (α = 13.7 spp/plot *vs*. 2–8.7 in the other regions; Table 1). The total species richness was almost identical in Viruá and BDFFP, even though BDFFP had more than four times as many species per plot. This is because Viruá was much more heterogeneous (β = 16.0 compositional units *vs.* 3.8), which is especially noteworthy because BDFFP was sampled with more plots. BR-319 was sampled with fewer plots than the other sites (11 vs. 30–38), so the small total number of species (γ = 9 spp) and limited compositional heterogeneity (β = 2.1) are partly sampling artefacts.

Cation concentration in the soil was less than 2 cmol(+)/kg in the vast majority of plots. Only two plots in Uatumã had values higher than this. Mean silt content was highest in the BR-319 plots. No linear correlation was found among the contents of clay, silt and cation concentration in the 109 plots. Mean canopy openness was between 2 and 13% in almost all plots, with just three plots in Viruá having canopy openness from 24 to 71%. Viruá differed from the other sites also in being more seasonal (dry season length of 5 months *vs.* 0-2 months in the other sites).

There was clear species turnover along the gradient of soil cation concentration (Fig. 2). Many species and some genera (such as *Diplazium*, *Pteris, Thelypteris*, *Mickelia* and *Bolbitis*) were restricted to the soils with the highest cation concentrations. Consequently, such plots had, in general, higher species richness than plots with lower soil cation concentrations.

FLORISTIC VARIATION ALONG ENVIRONMENTAL GRADIENTS - In all ordination diagrams, the relative positions of the plots seemed related to at least one environmental variable (Fig. 3). In the analysis of the full dataset, composition was related to all environmental variables included in the models. In Uatumã and Viruá, composition was best explained by ln(cation concentration) and canopy openness. Composition was related to clay content in all sites except Viruá, and this was the only significant relationship in BDFFP and BR-319. In these two sites, the proportion of variance in the first ordination axis values that was explained by the environmental variables (adjusted $R^2$) was much lower than that in the second axis. This indicates that some other factors than those measured in the present study were behind the primary compositional gradient in BDFFP and BR-319.

The effect of using extended rather than traditional Sørensen dissimilarities varied among the study sites. For three of the sites (Uatumã, BDFFP and BR-319), the ordination results (Fig. 3) were similar with either measure. In contrast, clearly different configurations of plots were obtained with the two dissimilarity measures for Viruá and the entire dataset. In both cases, the compositional relationships became easier to interpret when extended Sørensen dissimilarities were used. Correspondingly, for these two datasets, extending the Sørensen dissimilarities increased both the eigenvalue of the first PCoA axis and the degree to which variance in the axis values was explainable by environmental variables (Table 2). These results reflect differences in the degree of compositional heterogeneity in the corresponding datasets. In the entire dataset, mean Sørensen dissimilarity between plots was 0.73, and 27% of the dissimilarities had saturated to the maximum value of unity. In Viruá, mean Sørensen dissimilarity was 0.95 and saturation was 77%, whereas in the other three sites, mean Sørensen dissimilarity was 0.54–0.68 and saturation only 0–2%.

EXPLAINING VARIATION IN COMPOSITIONAL DISSIMILARITIES – Compositional dissimilarities in the full dataset were correlated with both log-transformed geographical distances and differences in dry season length (Table 3). Since geographical distances and differences in dry season length were themselves strongly correlated (Mantel's $r = 0.89$, $p<0.001$), partial correlation coefficients were clearly lower than simple ones but both were still significant (Table 3).

When multiple regression on dissimilarity matrices was done with the full dataset, the backward elimination procedure excluded the dissimilarity matrix based on clay content if classical Sørensen dissimilarities were used. Dissimilarity matrices based on dry season length, ln(cation concentration) and canopy openness were kept in the final model whether classical or extended Sørensen dissimilarities were used. The sites differed in which explanatory factors were kept in the final model (Fig. 4). The distance matrix based on clay content was a relevant variable in every site, and in BR-318 it was the only variable kept in the final model. In the models of the other sites, also cation concentration difference and geographical distance were retained. The models for Viruá and Uatumã retained difference in canopy openness. The results based on dissimilarity matrices (Fig. 4) paralleled those based on ordination axes (Table 2) in largely identifying the same environmental variables as important.

Environmental dissimilarities were better in predicting compositional dissimilarities than geographical distances were, both for the full dataset and for each site separately. The unique explanatory power of geographical distances was small in all multiple regression models. When geographical distance was retained in the models, its contribution went mainly to the shared component. The proportion of explained variance was higher for the extended Sørensen dissimilarities than for the classical Sørensen dissimilarities in the full dataset as well as within Viruá and Uatumã. In BR-319 and BDFFP, where the proportion of unexplained variance was especially large, it made little difference whether classical or extended Sørensen dissimilarities were used (Fig. 4).

## DISCUSSION

Our results indicate that the main factors driving fern community composition depend on the environmental heterogeneity of the study area and the spatial scale of sampling. Below, we discuss the relative importance of environmental factors and geographical distance (which can be thought to represent dispersal limitation) at different spatial scales.

MAJOR DETERMINANTS OF COMPOSITIONAL VARIATION – Among-species niche partitioning in relation to soil nutrients has been suggested as a mechanism that promotes speciation and regional co-existence of closely related species in tropical forests (Tuomisto *et al.*1998, Schulman *et al.* 2004, Fine *et al.* 2005, Tuomisto 2006, Jones *et al.* 2007). Further studies with explicit phylogenies and physiological studies are needed to confirm these hypotheses, but repeated field observations can also be used to test them. The results of the present study are in agreement with the proposition that specialisation and differentiation among plant species is an important factor behind compositional turnover along environmental gradients within tropical forests.

Earlier studies in neotropical rain forests have reached different conclusions on which environmental factors best explain floristic variation. Several studies have found climate important (Clinebell *et al.* 1995, ter Steege *et al.* 2003), whereas others have emphasised soil cation and clay content (Tuomisto & Poulsen 1996, Ruokolainen *et al.* 1997, 2007, Tuomisto *et al.* 2003a, b, c, Phillips *et al.* 2003, Jones *et al.* 2006) or soil clay content only (Costa *et al.* 2005, Zuquim *et al.* 2009). In the present study, we found that all three factors were important at the extent of all sites, but their explanatory powers differed among sites.

Soil cation concentration was the best predictor of floristic variation in the entire dataset and in Uatumã. In the other sites, clay content was the most important predictor. This is linked to the soil cation concentration varying most in Uatumã: the highest soil cation concentrations there were much higher than in any of the other sites, although the lowest values were very similar among sites. This caused more pronounced cation differences among plots in Uatumã than in the other sites. These results are consistent with the idea that the relative roles of explanatory variables depend on the observed lengths of the environmental gradients (Ruokolainen *et al.* 1997, 2007, McCoy 2002, Jones *et al.* 2006, Costa *et al.* 2009). Earlier studies that have found cation concentration to have poor explanatory power (Costa *et al.* 2005, Zuquim *et al.* 2009) were conducted in areas where soil cation concentration was more uniform than in the sites analysed here.

The ability to detect trends in species distributions depends on the spatial structure of the environment (Nekola & White 1999) and on the length of the environmental gradient studied. Within one site, the range of variation in environmental variables must logically increase as the area considered increases (environmental heterogeneity may remain the same, but cannot decrease with increasing area). However, when separate sites are compared, they may differ in environmental heterogeneity such that a large area in one site contains a smaller range of environmental variation than a smaller area in another site. Among our study sites, Uatumã showed a range of variation in soil cation concentration that was almost as large as the range in the entire data set, whereas the other sites were much more homogeneous in this respect. Consequently, the results of variance partitioning for the Uatumã data were similar to those for the entire data set. The other three sites comprised only a small part of the entire cation concentration gradient, so soil clay content emerged as the best environmental predictor, albeit with a low predictive power.

Plants need exchangeable bases to grow, so it is logical to expect cation availability to have a causal connection with plant species distributions. In contrast, clay is not a physiologically necessary substance, so its explanatory power comes from its correlations with factors like soil water holding capacity and drainage. When the environment is homogenous, biological interactions and stochastic factors can be expected to play a larger role in determining spatial patterns in species distribution than in environmentally heterogeneous areas. Many of these factors are difficult to observe and quantify, so their effects appear in the unexplained variation in statistical models.

GEOGRAPHICAL DISTANCES – Many studies looking at broad scales have found that floristic similarity between plots decreases with geographical distance (Nekola & White 1999, Duivenvorden *et al.* 2002, Condit *et al.* 2002, Tuomisto *et al.* 2003b, Vormisto et al. 2004, Normad et al. 2006), which has sometimes been interpreted as an indication that dispersal processes determine species distributions. At landscape scales, some studies have found distance decay of similarity (Tuomisto *et al.* 2003a) whereas others have not (Ruokolainen *et al.* 1997, Tuomisto *et al.* 2003c, Karst *et al.* 2005, Jones *et al.* 2006). There is strong evidence for dispersal limitation of fern spores at continental scales (Muñoz *et al.* 2004, Geiger *et al.* 2007), but to what extent this process determines patterns of species distribution in Amazonia is still unknown. Despite the high dispersal ability of fern spores, most spores fall close to the mother plant (Peck *et al.* 1990), so some spatial structure determined by dispersal limitation is to be expected.

The shared component in the multiple regression models is equally compatible with the hypothesis that species composition and environmental variables are independent of each other but co-vary because both are spatially autocorrelated, and the hypothesis that species composition has a causal relationship with spatially autocorrelated environmental variables. However, the unique explanatory power of geographical distances was very low in our analyses, both in comparison with the component co-explained by environmental differences and especially in comparison with the component uniquely explained by environmental differences. This suggests that dispersal limitation is not the main driver of fern species distributions in Amazonia.

CLASSIC AND EXTENDED SØRENSEN DISSIMILARITIES – The use of extended Sørensen dissimilarities instead of classic Sørensen dissimilarities strongly influenced the interpretation of results obtained for the entire dataset and for Viruá and Uatumã, where environmental and floristic heterogeneity was high. Extended Sørensen dissimilarities improved the visual interpretability of the ordination diagrams, increased the variation captured by ordination axes, and increased the total proportion of explained variance in multiple regression on dissimilarity matrices. The extended dissimilarity approach therefore proved useful in regions with high turnover of species among plots. In the sites with low species turnover (BDFFP and BR-319), extending the floristic dissimilarities had little effect on the results. As proposed by De´ath (1999), it therefore seems that when environmentally heterogeneous areas are covered, extended dissimilarities can facilitate the interpretation of results and provide more robust inferences about community turnover along external gradients than classical dissimilarities do.

Our results support the hypothesis that current environmental conditions are more important than dispersal limitation for fern species distributions and turnover in central and northern Amazonia. Both climate and soil properties (especially cation concentration) appear to be major drivers, but the heterogeneity created by them has a different spatial structure and is hence best observable at different spatial scales. In sites with uniform soil cation concentration, soil clay content emerged as important, which supports the idea that environmental gradients are hierarchically structured and gradients occur inside gradients (Costa *et al.* 2009). This causes site-dependent results that can mask the bigger picture of factors structuring plant communities in Amazonia.

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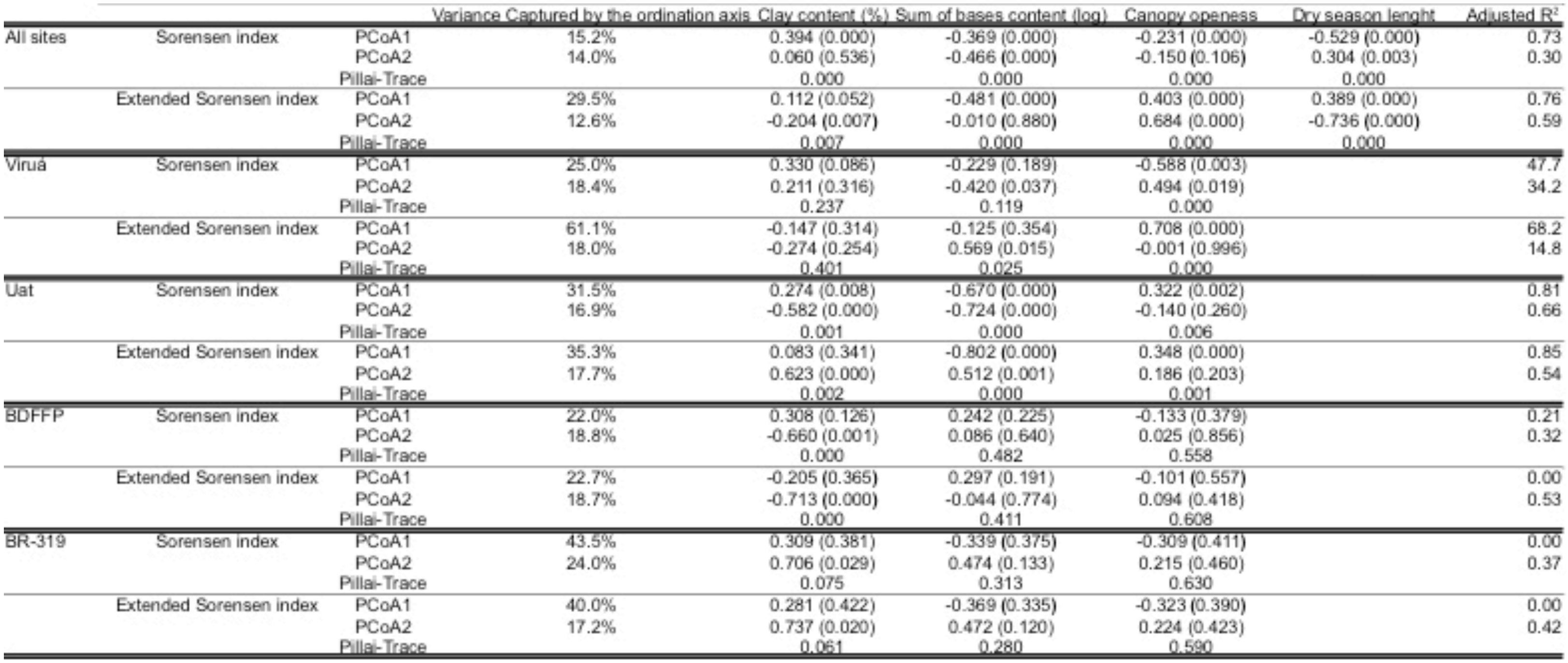
## TABLES

Table 1. Descriptive statistics of species richness and environmental variables in 109 plots in four study sites in central and northern Amazonia, Brazil. Mean ± standard deviation with range given in parentheses. Mean annual temperature is 26-28°C in all sites.  Dry season length is the number of consecutive months with mean precipitation less than 100 mm. Climatic and geomorphological data from RADAMBRASIL (1978) and Sombroek (2001).

| | **Viruá** | **Uatumã** | **BDFFP** | **BR-319** |
|---|---|---|---|---|

| | | | | |
|---|---|---|---|---|
| **Location** | 1.45ºN, 61.00ºW | 1.80ºS, 59.25ºW | 2.40ºS, 59.85ºW | 4.40°S, 60.95°W |
| **Mean annual precipitation** | 2300 mm | 2370 mm | 2200 mm | 2200 mm |
| **Altitude (m above sea level)** | 40–340 | 70–200 | 70–160 | 30–50 |
| **Plots** | 30 | 30 | 38 | 11 |
| **Species/plot (α)** | 2±1.7<br>(0 - 6) | 13.7±6.2<br>(4 - 27) | 8.7±4.3<br>(2 - 20) | 4.3±1.3<br>(2 – 6) |
| **Total species (γ)** | 32 | 62 | 33 | 9 |
| **Compositional units (β)** | 16.0 | 4.5 | 3.8 | 2.1 |
| **Clay content (%)** | 19.8±16.8<br>(0.5 – 57.8) | 45.3±22.9<br>(16.5 - 85.5) | 45.7±27.5<br>(5.7 - 81.9) | 24.6±4.9<br>(16.5 - 32.5) |
| **Silt content (%)** | 17.5±5.9<br>(4.8 – 32.3) | 15.5±10.4<br>(7.7 - 62.5) | 4.4±2.3<br>(0.31 - 10.0) | 57.2±7.7<br>(47.9 - 70.6) |
| **Ca+K+Mg (cmol(+)/kg)** | 0.35±0.23<br>(0.14 – 1.17) | 0.9±1.2<br>(0.16 - 5.68) | 0.46±0.2<br>(0.2 - 1.0) | 0.25±0.1<br>(0.14 – 0.42) |
| **Dry season lenght (months)** | 5 | 0 | 0 | 1 to 2 |
| **Canopy Openness** | 13.8±19.05<br>(4.4 – 71.1) | 4.4±0.72<br>(2.9 - 5.9) | 6.2±1.1<br>(7.4 - 4.2) | 4.5±0.9<br>(3.2 – 5.7) |

Table 2. Results from multivariate multiple regression analyses of fern and lycophyte plots in central and northern Brazilian Amazonia. An ordination axis from principal coordinates analysis (PCoA1 or PCoA2) is the dependent variable in each case. Compositional dissimilarities were quantified with the Sørensen or extended Sørensen dissimilarity in the full dataset of 102 plots and in each of four sites separately. Adjusted regression coefficients (with associated probabilities between brackets) and Pillai-Trace probabilities for the whole model are given.



| | | | Variance Captured by the ordination axis | Clay content (%) | Sum of bases content (log) | Canopy openess | Dry season lenght | Adjusted $R^2$ |
|---|---|---|---|---|---|---|---|---|
| All sites | Sorensen index | PCoA1 | 15.2% | 0.394 (0.000) | -0.369 (0.000) | -0.231 (0.000) | -0.529 (0.000) | 0.73 |
| | | PCoA2 | 14.0% | 0.060 (0.536) | -0.466 (0.000) | -0.150 (0.106) | 0.304 (0.003) | 0.30 |
| | | Pillai-Trace | | 0.000 | 0.000 | 0.000 | 0.000 | |
| | Extended Sorensen index | PCoA1 | 29.5% | 0.112 (0.052) | -0.481 (0.000) | 0.403 (0.000) | 0.389 (0.000) | 0.76 |
| | | PCoA2 | 12.6% | -0.204 (0.007) | -0.010 (0.880) | 0.684 (0.000) | -0.736 (0.000) | 0.59 |
| | | Pillai-Trace | | 0.007 | 0.000 | 0.000 | 0.000 | |
| Viruá | Sorensen index | PCoA1 | 25.0% | 0.330 (0.086) | -0.229 (0.189) | -0.588 (0.003) | | 47.7 |
| | | PCoA2 | 18.4% | 0.211 (0.316) | -0.420 (0.037) | 0.494 (0.019) | | 34.2 |
| | | Pillai-Trace | | 0.237 | 0.119 | 0.000 | | |
| | Extended Sorensen index | PCoA1 | 61.1% | -0.147 (0.314) | -0.125 (0.354) | 0.708 (0.000) | | 68.2 |
| | | PCoA2 | 18.0% | -0.274 (0.254) | 0.569 (0.015) | -0.001 (0.996) | | 14.8 |
| | | Pillai-Trace | | 0.401 | 0.025 | 0.000 | | |
| Uat | Sorensen index | PCoA1 | 31.5% | 0.274 (0.008) | -0.670 (0.000) | 0.322 (0.002) | | 0.81 |
| | | PCoA2 | 16.9% | -0.582 (0.000) | -0.724 (0.000) | -0.140 (0.260) | | 0.66 |
| | | Pillai-Trace | | 0.001 | 0.000 | 0.006 | | |
| | Extended Sorensen index | PCoA1 | 35.3% | 0.083 (0.341) | -0.802 (0.000) | 0.348 (0.000) | | 0.85 |
| | | PCoA2 | 17.7% | 0.623 (0.000) | 0.512 (0.001) | 0.186 (0.203) | | 0.54 |
| | | Pillai-Trace | | 0.002 | 0.000 | 0.001 | | |
| BDFFP | Sorensen index | PCoA1 | 22.0% | 0.308 (0.126) | 0.242 (0.225) | -0.133 (0.379) | | 0.21 |
| | | PCoA2 | 18.8% | -0.660 (0.001) | 0.086 (0.640) | 0.025 (0.856) | | 0.32 |
| | | Pillai-Trace | | 0.000 | 0.482 | 0.558 | | |
| | Extended Sorensen index | PCoA1 | 22.7% | -0.205 (0.365) | 0.297 (0.191) | -0.101 (0.557) | | 0.00 |
| | | PCoA2 | 18.7% | -0.713 (0.000) | -0.044 (0.774) | 0.094 (0.418) | | 0.53 |
| | | Pillai-Trace | | 0.000 | 0.411 | 0.608 | | |
| BR-319 | Sorensen index | PCoA1 | 43.5% | 0.309 (0.381) | -0.339 (0.375) | -0.309 (0.411) | | 0.00 |
| | | PCoA2 | 24.0% | 0.706 (0.029) | 0.474 (0.133) | 0.215 (0.460) | | 0.37 |
| | | Pillai-Trace | | 0.075 | 0.313 | 0.630 | | |
| | Extended Sorensen index | PCoA1 | 40.0% | 0.281 (0.422) | -0.369 (0.335) | -0.323 (0.390) | | 0.00 |
| | | PCoA2 | 17.2% | 0.737 (0.020) | 0.472 (0.120) | 0.224 (0.423) | | 0.42 |
| | | Pillai-Trace | | 0.061 | 0.280 | 0.590 | | |

Table 3. Simple and partial Mantel tests between compositional dissimilarities of ferns and lycophytes, log-transformed geographical distances and dry season length in 104 plots in central and northern Amazonia, Brazil. Statistical significance of the correlation estimated with Monte Carlo permutation using 1000 permutations.

| | Index of floristic dissimilarity | |
|---|---|---|
| | Sørensen | Extended Sørensen |
| Log(Geographic distance) | 0.53*** | 0.36*** |
| Dry season length | 0.52*** | 0.41*** |
| Log(Geographic distance), with dry season length partialled out | 0.18*** | 0.01 |
| Dry season length with log(geographic distance) partialled out | 0.13*** | 0.19*** |

APPENDIX

The following supplementary material is available for this article

Table S1: List of fern and lycophyte species found in 109 plots in four regions within central and northern Amazonia, Brazil. Frequency is the number of sites or plots in which a species was observed. Epiphytic individuals were not included in the inventory, but terrestrial individuals of mostly epiphytic species were.

| Family | Species | Main habit | Frequency (sites) | Frequency (plots) |
|---|---|---|---|---|
| Aspleniaceae | Asplenium laetum Sw. | Terrestrial/rupiculous | 2 | 6 |
| | Asplenium serratum L. | Epiphytic | 1 | 1 |
| | Asplenium stuebelianum Hieron. | Terrestrial/rupiculous/ epiphytic | 1 | 1 |
| Blechnaceae | Salpichlaena hookeriana (Kunze) Alston | Terrestrial (twining leaves) | 1 | 2 |
| | Salpichlaena volubilis (Kaulf.) J. Sm. | Terrestrial (twining leaves) | 1 | 1 |
| Cyatheaceae | Cyathea microdonta (Desv.) Domin | Terrestrial | 1 | 6 |
| | Cyathea pungens Domin | Terrestrial | 1 | 8 |
| | Cyathea sp. A | Terrestrial | 1 | 2 |
| | Cyathea sp. B | Terrestrial | 1 | 1 |
| Dryopteridaceae | Bolbitis semipinnatifida (Fée) Alston | Terrestrial/rupiculous | 2 | 4 |
| | Cyclodium guianense (Klotzsch) L. D. Gómez | Terrestrial/rupiculous | 1 | 2 |
| | Cyclodium meniscioides (Willd.) C. Presl | Terrestrial/climbing | 2 | 12 |
| | Mickelia guianensis (Aubl.) R. C. Moran et al. | Terrestrial/climbing | 1 | 14 |
| | Mickelia lindigii (Mett.) R. C. Moran et al. | Terrestrial/climbing | 1 | 1 |
| | Mickelia nicotianifolia (Sw.) R. C. Moran et al. | Terrestrial/rupiculous/ climbing | 1 | 2 |
| | Polybotrya caudata Kunze | Terrestrial/climbing | 1 | 11 |
| | Polybotrya sessilisora R. C. Moran | Terrestrial/climbing | 2 | 25 |
| Hymenophyllaceae | Davalliopsis elegans (Rich.) Copel. | Terrestrial | 2 | 7 |
| | Trichomanes cellulosum Klotzsch | Terrestrial | 1 | 5 |
| | Trichomanes cristatum Kaulf. | Terrestrial | 1 | 1 |
| | Trichomanes diversifrons (Bory) Mett. ex Sadeb | Terrestrial | 1 | 2 |
| | Trichomanes martiusii C. Presl | Terrestrial | 3 | 6 |
| | Trichomanes pinnatum Hedw. | Terrestrial | 4 | 81 |
| | Trichomanes trollii Bergdolt | Terrestrial | 1 | 3 |
| | Trichomanes vittaria DC ex Poir. | Terrestrial | 2 | 7 |
| | Vandeboschia radicans (Sw.) Copel. | Climbing | 1 | 1 |

| | | | | |
|---|---|---|---|---|
| Lindsaeaceae | Lindsaea divaricata Klotzsch | Terrestrial | 2 | 3 |
| | Lindsaea dubia Spreng. | Terrestrial | 1 | 6 |
| | Lindsaea falcata Dryand. | Terrestrial | 3 | 44 |
| | Lindsaea guianensis (Aubl.) Dryand. | Terrestrial | 3 | 9 |
| | Lindsaea lancea var. elatior ( Kunze ) K.U.Kramer | Terrestrial | 1 | 1 |
| | Lindsaea lancea var. lancea (L.) Bedd. | Terrestrial | 4 | 55 |
| | Lindsaea portoricensis Desv. | Terrestrial | 1 | 1 |
| | Lindsaea sp. A | Terrestrial | 1 | 1 |
| | Lindsaea sp. B | Terrestrial | 1 | 7 |
| | Lindsaea sp. C | Terrestrial | 1 | 1 |
| Lomariopsidaceae | Cycopeltis semicordata (Sw.) J. Sm. | Terrestrial | 1 | 1 |
| | Lomariopsis japurensis (Mart.) J. Sm. | Terrestrial/climbing | 1 | 20 |
| | Lomariopsis prieuriana Fée | Terrestrial/climbing | 3 | 50 |
| | Nephrolepis rivularis (Vahl) Mett. ex Krug | Epiphytic | 1 | 2 |
| Marattiaceae | Danaea leprieurii Kunze | Terrestrial | 2 | 8 |
| | Danaea nodosa (L.) Sm. | Terrestrial | 1 | 4 |
| | Danaea trifoliata Kunze | Terrestrial | 2 | 16 |
| Metaxyaceae | Metaxya rostrata C. Presl | Terrestrial | 3 | 20 |
| Polypodiaceae | Campyloneurum repens (Aubl.) C. Presl | Epiphytic | 1 | 6 |
| | Microgramma persicariifolia C. Presl | Epiphytic | 1 | 2 |
| Pteridaceae | Adiantopsis radiata (L.) Fée | Terrestrial | 1 | 1 |
| | Adiantum argutum Splitg. | Terrestrial | 1 | 8 |
| | Adiantum cajennense Willd. | Terrestrial | 3 | 54 |
| | Adiantum cinnamomeum Lellinger & J. Prado | Terrestrial | 1 | 3 |
| | Adiantum dolosum Kunze | Terrestrial | 1 | 3 |
| | Adiantum glaucenscens Klotzsch | Terrestrial | 2 | 5 |
| | Adiantum humile Kunze | Terrestrial | 1 | 7 |
| | Adiantum latifolium Lam. | Terrestrial | 1 | 1 |
| | Adiantum latifoliumXobliquum | Terrestrial | 1 | 2 |
| | Adiantum lucidum (Cav.) Sw. | Terrestrial | 1 | 1 |
| | Adiantum multisorum Sampaio | Terrestrial | 1 | 2 |
| | Adiantum obliquum Willd. | Terrestrial | 2 | 15 |
| | Adiantum paraense Hieron. | Terrestrial | 3 | 30 |
| | Adiantum petiolatum Desv. | Terrestrial | 2 | 4 |
| | Adiantum pulverulentum L. | Terrestrial | 2 | 3 |
| | Adiantum terminatum Kunze ex Miq. | Terrestrial | 2 | 14 |
| | Adiantum tomentosum Klotzsch | Terrestrial | 2 | 14 |
| | Adiantum sp. A | Terrestrial | 1 | 1 |
| | Adiantum sp. B | Terrestrial | 1 | 1 |
| | Pityrogramma calomelanos (L.) Link | Terrestrial | 1 | 1 |
| | Pteris pungens Willd. | Terrestrial | 1 | 1 |
| | Pteris tripartita Sw. | Terrestrial | 1 | 1 |

| | | | | |
|---|---|---|---|---|
| Saccolomataceae | Saccoloma inaequale (Kunze) Mett. | Terrestrial | 2 | 8 |
| Schizaeaceae | Actinostachys pennula Hook. | Terrestrial | 1 | 5 |
| | Lygodium volubile Sw. | Terrestrial (twining leaves) | 2 | 6 |
| | Schizaea elegans (Vahl) Sw. | Terrestrial | 3 | 5 |
| | Schizaea incurvata Schkuhr | Terrestrial | 1 | 1 |
| Selaginellaceae | Selaginella amazonica Spring | Terrestrial | 1 | 5 |
| | Selaginella asperula Spring | Terrestrial | 1 | 1 |
| | Selaginella breynii Spring | Terrestrial | 2 | 3 |
| | Selaginella palmiformis Alston ex Crabbe & Jermy | Terrestrial | 1 | 1 |
| | Selaginella parkeri (Hook . & Grev.) Spring | Terrestrial | 1 | 8 |
| | Selaginella pedata Klotzsch | Terrestrial | 2 | 51 |
| | Selaginella sp. A | Terrestrial | 1 | 1 |
| Tectariaceae | Tectaria incisa Cav. | Terrestrial | 1 | 6 |
| | Triplophyllum crassifolium Holttum | Terrestrial | 1 | 12 |
| | Triplophyllum dicksonioides (Fée) Holttum | Terrestrial | 2 | 31 |
| | Triplophyllum funestum (Kunze) Holttum | Terrestrial | 2 | 29 |
| | Triplophyllum glabrum J. Prado & R. C. Moran | Terrestrial | 1 | 6 |
| | Triplophyllum hirsutum (Holttum) J. Prado & R. C. Moran | Terrestrial | 2 | 16 |
| | Triplophyllum sp. A | Terrestrial | 1 | 2 |
| Thelypteridaceae | Thelypteris abrupta (Desv.) Proctor | Terrestrial | 1 | 5 |
| | Thelypteris macrophylla (Kunze) C. V. Morton | Terrestrial | 1 | 1 |
| | Thelypteris poiteana (Bory) Proctor | Terrestrial/rupiculous | 1 | 3 |
| Woodsiaceae | Diplazium cristatum (Desr.) Alston | Terrestrial | 1 | 1 |
| | Diplazium grandifolium (Sw.) Sw. | Terrestrial | 1 | 1 |

FIGURE LEGENDS

Figure 1. Location of the four study sites and 109 plots (black dots) in central and northern Amazonia, Brazil. The dots indicating plot locations are scaled to reflect mean cation concentration (sum of exchangeable bases, Ca+K+Mg) in soil samples taken from the plots. Black lines are boundaries between countries or states and gray lines represent rivers.

Figure 2. Occurrence of fern and lycophyte species along the soil cation concentration gradient in 104 plots in central and northern Amazonia, Brazil. The plots are listed in the order of increasing mean cation concentration, and the species in the order of decreasing mean cation concentration in the plots where the species was observed. Note that the rate of change in cation concentration along the x axis is not constant, as there are many plots with relatively similar intermediate cation concentrations. The 50 species presented were randomly chosen from the 92 observed species. For a full list of species, see Table S1 in Appendix 1.

Figure 3. Ordination (PCoA) diagrams of 104 2 m x 250 m plots in central and northern Amazonia, Brazil, based on the species composition of ferns and lycophytes. Panels A) and F) show ordination of all plots from all sites. Other panels show plots from one site each. A–E) Ordination based on the classical Sørensen index (Class); F–J) Ordination based on the extended Sørensen index (XD). Dot sizes according to the values of the main environmental gradient related to the first two axes of PCoA: Ln(cation concentration) in All sites and Uatumã; % of Canopy openness in Viruá and % of Clay content in BDFFP and BR 319. For the range of the environmental variables, see Table 1. The variances explained by each axis are given in Table 2.

Figure 4. Relative contributions of different factors to explaining variation in species turnover of ferns and lycophytes in 102 plots from central and northern Amazonia. The diagrams show results of multiple regression on dissimilarity matrices, where the variance of the compositional dissimilarity matrix is partitioned into fractions uniquely and jointly explained by environmental and geographical distances. Explanatory variables that had statistically significant contributions after backward elimination are listed to the right of each diagram. *Geog. dist.* is the matrix of log-transformed geographical distances, and the other explanatory distance matrices are based on canopy openness (*canopy*), log-transformed concentration of exchangeable bases (*cation*), clay content (*clay*), and dry season length (*dry season*). The fractions of variance in the floristic dissimilarity matrix are as follows: Black = uniquely explained by the environmental distances; dark gray = jointly explained by the environmental and geographical distances; white = uniquely explained by the geographical distances; light gray = unexplained by the available variables.

Figure 1

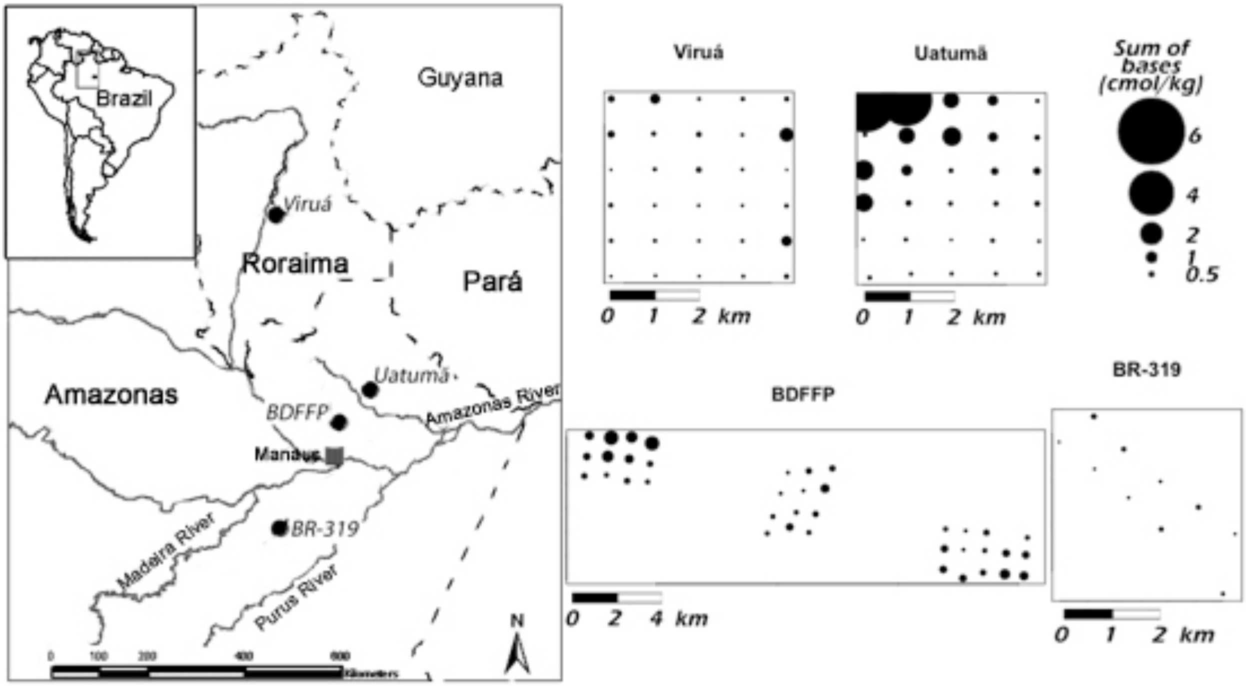

Brazil
Guyana
Roraima
Pará
Amazonas
Viruá
Uatumã
BDFFP
Manaus
BR-319
Amazonas River
Madeira River
Purus River
N
0 100 200 400 600 Kilometers
Viruá
Uatumã
Sum of bases (cmol/kg)
6
4
2
1
0.5
0 1 2 km
0 1 2 km
BDFFP
0 2 4 km
BR-319
0 1 2 km

Figure 2

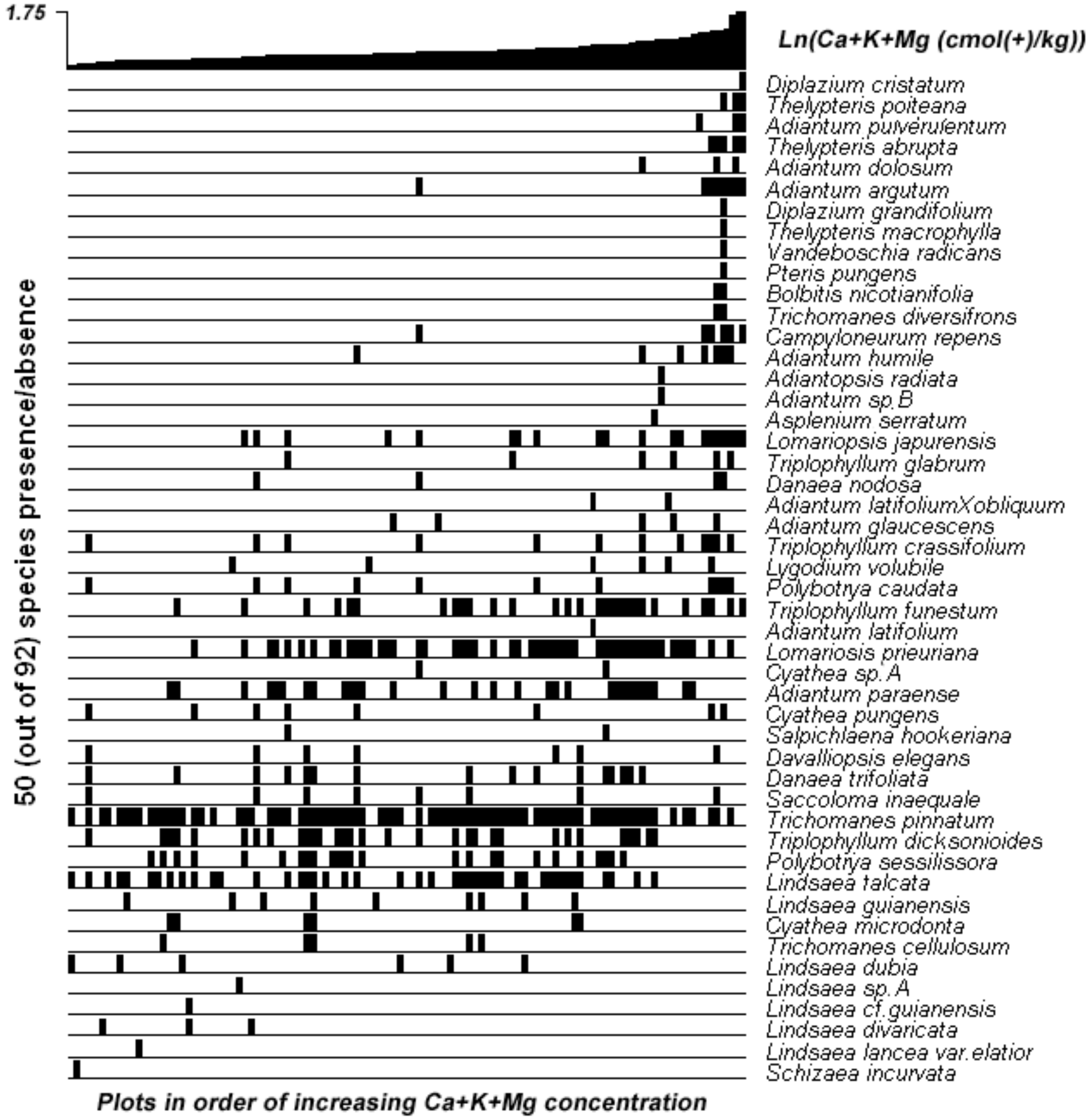

1.75
Ln(Ca+K+Mg (cmol(+)/kg))
50 (out of 92) species presence/absence
Diplazium cristatum
Thelypteris poiteana
Adiantum pulverulentum
Thelypteris abrupta
Adiantum dolosum
Adiantum argutum
Diplazium grandifolium
Thelypteris macrophylla
Vandeboschia radicans
Pteris pungens
Bolbitis nicotianifolia
Trichomanes diversifrons
Campyloneurum repens
Adiantum humile
Adiantopsis radiata
Adiantum sp.B
Asplenium serratum
Lomariopsis japurensis
Triplophyllum glabrum
Danaea nodosa
Adiantum latifoliumXobliquum
Adiantum glaucescens
Triplophyllum crassifolium
Lygodium volubile
Polybotrya caudata
Triplophyllum funestum
Adiantum latifolium
Lomariosis prieuriana
Cyathea sp.A
Adiantum paraense
Cyathea pungens
Salpichlaena hookeriana
Davalliopsis elegans
Danaea trifoliata
Saccoloma inaequale
Trichomanes pinnatum
Triplophyllum dicksonioides
Polybotrya sessilissora
Lindsaea falcata
Lindsaea guianensis
Cyathea microdonta
Trichomanes cellulosum
Lindsaea dubia
Lindsaea sp.A
Lindsaea cf.guianensis
Lindsaea divaricata
Lindsaea lancea var.elatior
Schizaea incurvata
Plots in order of increasing Ca+K+Mg concentration

Figure 3

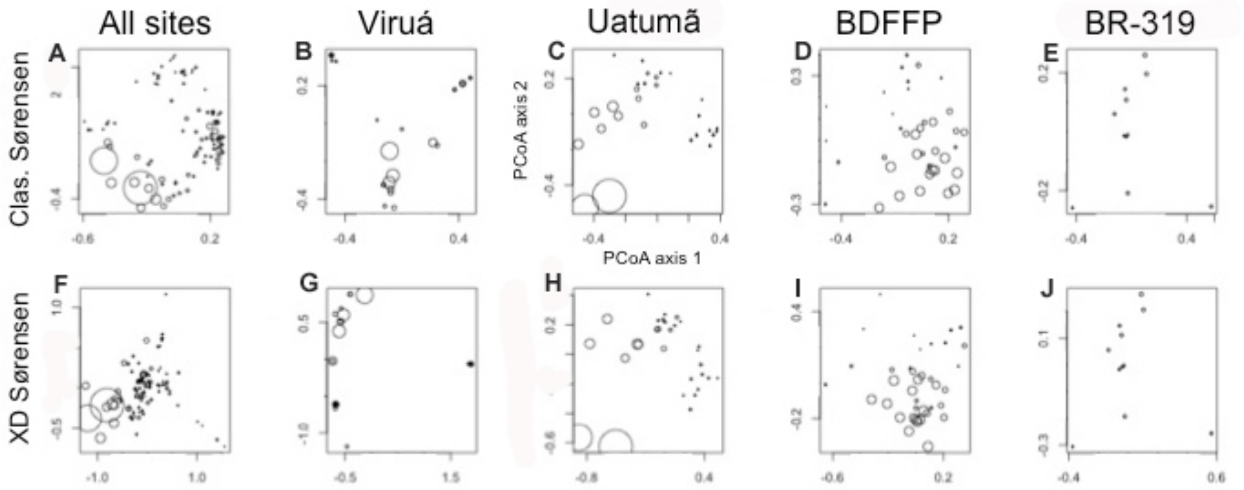
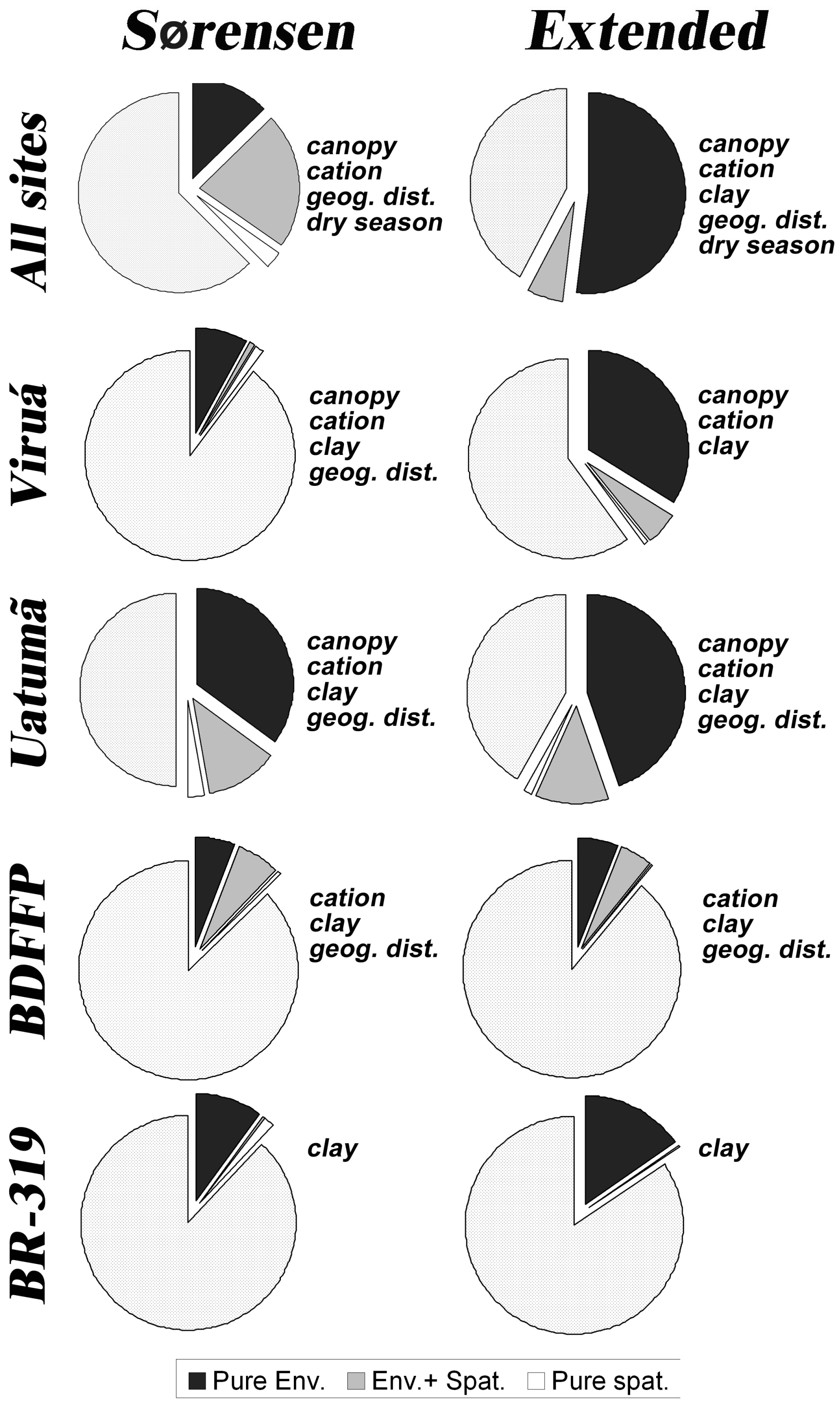

All sites
Viruá
Uatumã
BDFFP
BR-319
A
B
C
D
E
F
G
H
I
J
Clas. Sørensen
XD Sørensen
PCoA axis 2
PCoA axis 1
-0.6
0.2
-0.4
0.4
0.3
-0.3
-1.0
1.0
-0.5
0.5
1.5
-0.8
-0.6
0.1
0.6

Figure 4


Sørensen
Extended
All sites
canopy
cation
geog. dist.
dry season
canopy
cation
clay
geog. dist.
dry season
Viruá
canopy
cation
clay
geog. dist.
canopy
cation
clay
Uatumã
canopy
cation
clay
geog. dist.
canopy
cation
clay
geog. dist.
BDFFP
cation
clay
geog. dist.
cation
clay
geog. dist.
BR-319
clay
clay
Pure Env.
Env.+ Spat.
Pure spat.