

## Distribution of pteridophyte communities along environmental gradients in Central Amazonia, Brazil

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**Abstract** Extrapolation of local abundance–environment relationships to broader scales provides species distribution models used for conservation planning. We investigated the importance of environmental heterogeneity and geographic distance on pteridophyte species spatial distribution on 38 plots of 250 × 2.5 m distributed over 90 km<sup>2</sup> in Central Amazon. Inclusion of canopy openness in our models increased the capacity of predicting community composition even under the narrow range of canopy openness found in our plots. Nevertheless, there was still a large amount of unexplained variance (55–65%). The response of the community to the light gradient was hierarchical and we did not find evidences of light partitioning. Most species were concentrated in low light plots but a few common and abundant occurred along the entire gradient. Soil properties were the major determinants of community composition. Contrary to similar studies, slope was not a good predictor of pteridophyte community composition, indicating that this relationship may be site-specific. There was no correlation between floristic distances and geographic distances. We concluded that mesoscale turnover is low, although locally environmental variation determines high turnover of species. Studies among different Amazonian physiognomies tend to find high levels of beta-diversity. However, coarse comparisons can not reveal subtle patterns that are relevant for biodiversity conservation planning. This study found

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some important changes on pteridophyte community within the same type of forest, mainly related to environmental heterogeneity, even in narrow ranges of environmental variation.

**Keywords** Beta diversity · Canopy openness · Dispersal limitation · Environmental heterogeneity · Ferns · Soil characteristics · Tropical forest · Turnover · Understorey

### Abbreviations

BDFFP	Biological Dynamics of Forest Fragments Project
INPA (The portuguese acronym for National Institute of Amazonian Research)	Instituto Nacional de Pesquisas da Amazônia
RAPELD	Inventory method that accommodates two sampling scales, Rapid Assessment surveys (RAP) and Long-Term Ecological Research (PELD, the Brazilian acronym for LTER)
CAPES	Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
PCoA	Principal coordinates analysis
ANOVA	Analyses of variance
GPS	Global positioning system

### Introduction

The development of predictive models of species distributions based on local surveys has wide management applications for conservation biology, biogeography and climate change studies (Balmford and Gaston 1999; Guisan and Zimmermann 2000; Guisan and Thuiller 2005). Regional conservation planning requires basic information on the abundance and distribution of species combined with environmental information that allows the extrapolation of local abundance-environment relationships to broader scales.

Factors determining the distribution of plant species vary from biogeographic to microenvironmental scales. The most common environmental variables related to floristic composition from local to regional scales are soil characteristics (e.g. nutrients content and texture), topography, (Svenning 1999; Pitman et al. 2001; Condit et al. 2002; Tuomisto et al. 2003a, b; Vormisto et al. 2004; Svenning et al. 2006), moisture availability and the length of the dry period (ter Steege et al. 2003; Engelbrecht et al. 2005). Few studies included light availability as a predictor of tropical community variation at the mesoscale (but see Jones et al. 2006). Solar radiation at ground level is influenced quantitatively and qualitatively by canopy structure (Chazdon et al. 1996), and no more than 4% of sunlight reaches the ground of tropical forests (Chazdon and Fetcher 1984; Clark 2002). Understorey plants in these forests are adapted to low levels of light incidence (Chazdon et al. 1996), and minimum light levels are required for germination and photosynthesis. On the other hand, high levels of irradiance can cause chlorophyll oxidation and reduction of photosynthetic efficiency (Sonoike 1996) and therefore limit the occurrence of most pteridophyte species.

The opening of gaps in a forest causes a local input of light, driving microclimate changes and shifts in the composition of species. Nevertheless, the integration of these local processes to larger temporal or spatial scales is rarely investigated. Especially for pteridophytes, the importance of light in determining species distribution at mesoscale in

tropical old-growth forests has not received much attention. Laboratory approaches provide insights on physiological mechanisms regulating species distribution, but suffer the limitation of being restricted to the responses of individual species under controlled conditions.

In dense tropical forests, estimation of understorey light availability is difficult, because of the temporal and spatial heterogeneity and the narrow range of variation of understorey light values. These may be the reasons why light is not usually included as a predictor of plant community composition at large scales. Coarse measures obtained with some simple methods (like densiometer measurement or the Canopy-scope method from Brown et al. 2000) cannot provide reliable information for the lower values (less than 20% of canopy openness) generally found in tropical forests (Roxburgh and Kelly 1995). Jones et al. (2006) found that canopy openness was moderately related to pteridophyte community differences at local scales. However, even the well-known local effect of gaps may not determine community structure at broader scales because gaps are unpredictably scattered in tropical terra firme forests. Nevertheless, part of the high percentage of unexplained variation of tropical plant communities composition (Duivenvoorden et al. 2002; Tuomisto et al. 2003a; Vormisto et al. 2004; Jones et al. 2006) may be due to the lack of inclusion of some relevant variables in the models. If light is an important factor affecting community structure in tropical rain forests at meso to regional scales, then predictive models would be improved with the inclusion of this variable.

Despite the known high tree alpha diversity in tropical forests (e.g. Ter Steege et al. 2003), Pitman et al. (2001) proposed that within terra firme forests, composition and structure of western Amazonian tree communities are relatively homogeneous. Additionally, low levels of plant beta diversity have been found by Condit et al. (2002) in Western Amazonia, but the authors were criticized for sampling Amazonian sites with small range of environmental differences (Ruokolainen and Tuomisto 2002). The variation of beta diversity in tropical forests can be attributed to environmental determinism and/or dispersal limitation. Several studies on pteridophyte communities have suggested that environmental models are consistently better predictors of beta diversity (Tuomisto et al. 2003a; Karst et al. 2005; Jones et al. 2006). However, at large scales (plots placed up to 1,400 km apart) a proportion of explained variance of pteridophyte distribution was exclusively related to geographic distance (Tuomisto et al. 2003a), partially supporting the importance of dispersal in structuring biological communities (Hubbell 2001). Karst et al. (2005) suggested that there is a balance between the relative importance of stochastic and environmental factors that depends on the spatial scale. For ferns, low turnover rates are expected in relatively homogeneous environments because the intense production of wind-dispersed spores may confer unusually high dispersal mobility (Page 2002). However, patterns at the mesoscale are still not well documented.

The aims of our study were (1) to determine if the inclusion of a measure of light availability increases the capacity to predict pteridophyte community composition at the mesoscale; and (2) to determine the main factors that influence beta diversity of pteridophyte communities at the scale of 90 km<sup>2</sup> of an Amazonian terra firme forest.

## Materials and methods

### Study site

The study was carried out in three continuous forest reserves of the Biological Dynamics of Forest Fragments Project (hereafter BDFFP) in Central Amazon, Brazil. Each reserve

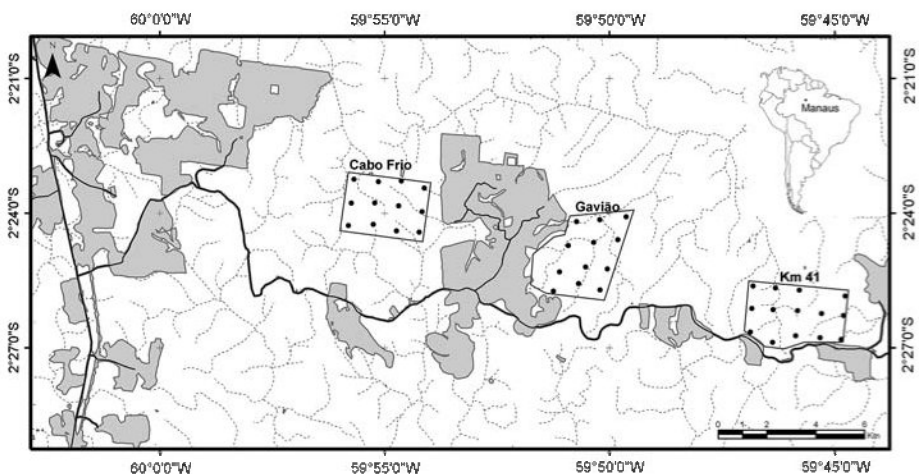
comprises nearly 12 km<sup>2</sup> of terra firme tropical rain forest, with a closed canopy 30–40 m high, with emergent trees up to 55 m high. The understorey is dominated by stemless palms. The mean annual rainfall is 2,200 mm and the mean annual temperature is 27°C (RADAMBRASIL 1978). Throughout this paper, we will consider as “local” the scale of each BDFFP reserve (1–5 km), and as “mesoscale” the total scale of the study (5–21 km). Regional refers to a scale larger than the 90 km<sup>2</sup> covered by this study.

The soils in Central Amazonia are kaolinitic clays on plateaus and higher elevations, grading to sandy Podzols at lower elevations (Chauvel et al. 1987). They are classified as yellow latosols and white quartzose sands according to the Brazilian soil classification system (Embrapa 1999) and derive from highly weathered tertiary fluvio-lacustrine deposits (Chauvel et al. 1987). The soils are typically acidic and poor in nutrients such as phosphorus, copper, calcium and potassium (Chauvel et al. 1987).

### Data collection

Thirty eight 2.5 × 250 m<sup>2</sup> plots were located with a minimum distance of 1 km between each plot in three reserves of the BDFFP (Fig. 1). The establishment of plots separated by a minimum distance of 1 km avoided environmental autocorrelation, as environment is frequently spatially structured (Legendre et al. 2002). Each plot followed the topographic contour. Soil properties inside plots tend to be relatively homogeneous, since in Central Amazon soil texture is highly correlated with topographic position (Chauvel et al. 1987; Mertens 2004). The sampling design was based on the RAPELD methodology (Magnusson et al. 2005).

All terrestrial and hemiepiphyte pteridophyte individuals with at least one leaf longer than 5 cm were counted and identified. Climbing individuals whose lowermost green leaves were higher than 2 m above ground were not considered because they are difficult to visualize from the ground, especially small individuals. *Selaginella* species were excluded



**Fig. 1** Location of plots (black dots) on three reserves of continuous forest of the Biological Dynamics of Forest Fragments Project. White areas are continuous forest, gray areas are pasture or secondary growth, dark lines represent roads, dotted lines represents rivers

because they form large clumps and individuals could not be distinguished in the field. Voucher collections are deposited in the INPA Herbarium in Manaus, Brazil.

Data on terrain slope, properties of surface soil (the top 5 cm after removing the litter cover) and canopy openness were obtained every 50 m along the long axis of each plot. Averages of the 6 measurements were used to represent each variable in each plot. Terrain slope was measured with a Suunto clinometer, perpendicular to the main plot axis. Percentage values of canopy openness were derived from digital images of the forest canopy taken with a hemispherical lens attached to a digital camera and tripod. Images were taken 50 cm above ground, between 5:30 and 8:30 and between 16:00 and 18:00, to avoid sun brightness on higher leaves and direct light on the lens. Images were analyzed with the software Gap Light Analyzer (Frazer et al. 1999). The six surface soil samples obtained were bulked to produce a composite sample for each plot. Before the analyses, samples were cleaned of roots, air-dried and sieved through a 2 mm sieve. Analyses included soil texture (percentage of clay, silt and sand), pH and macronutrients (Ca, Mg, K, and Na). Soil analyses were done in the Soil Laboratory of the Agronomy Department at INPA. Soil samples with previously known values of physicochemical parameters were simultaneously analyzed to control for laboratory errors. Geographic coordinates of plots were taken at the starting points of the plots, using a GPS Garmin 12XL.

#### Data analysis

Soil properties were represented by two variables: texture and exchangeable bases. Clay content was highly inversely correlated to the sand content ( $r = -0.99$ ) and was used as a measure of soil texture. Exchangeable bases were calculated by the sum of the amount of Ca, K and Mg (mg/kg). Sodium was not included because the levels were too low to be detected. Differences in environmental variables among reserves were tested with analyses of variance (ANOVA).

There was no correlation between geographical distances among plots and their dissimilarity in canopy openness (Simple Mantel test,  $P = 0.56$ ,  $r = 0.03$ ,  $n = 37$ ), clay content ( $P = 0.057$ ,  $r = 0.06$ ,  $n = 38$ ) or slope ( $P = 0.612$ ,  $r = 0.02$ ,  $n = 38$ ). On the other hand, the content of exchangeable bases ( $P < 0.001$ ,  $r = 0.20$ ,  $n = 38$ ) was spatially structured and differed significantly between reserves (ANOVA,  $F = 6.02$ ,  $P = 0.006$ ).

Quantitative and qualitative composition of the plots were reduced to fewer dimensions with Principal Coordinates Analyses (PCoA), applied over an association matrix calculated with the Bray-Curtis index for quantitative data or its analogue (Sørensen index) for qualitative data. Quantitative data were standardized by sampling units to proportions of the total number of individuals. The first and second PCoA axes explained 42.2% and 20.3% of the variance on the distance matrix based on quantitative data, respectively. Qualitative composition was based on presence-absence data; the first and second axes explained 37.4% and 27.2% of the variance. When analyzing presence/absence data, greater importance is given to rare species, while patterns evaluated with abundance data tend to be more related to the most abundant species.

The first two axes of PCoA were used as dependent variables in inferential tests. Multivariate multiple linear regressions were used to test the effects of environmental variables (soil texture, exchangeable bases, terrain slope and canopy openness) on community composition axes. This statistical approach is analogous to a redundancy analysis (RDA, Legendre and Legendre 1998) performed after the main patterns of composition have been synthesized by ordination. It was chosen because it allows testing the two main ordination axes, which represent most of the variation in composition, as dependent variables in the

same model. However, the contribution of each of the independent variables to the total explained variance can no longer be separated. The separate contribution of independent variables to community composition can roughly be estimated by multiple regressions with each ordination axis. Soil pH was correlated with clay content (Pearson correlation =  $-0.619$ ) and was not included in the model. Canopy openness data were log transformed to achieve linearity. One plot had to be excluded from all analyses that include canopy openness due to absence of data.

Simple Mantel tests were carried out to determine whether the floristic distances and the environmental distances between all paired plots were correlated with their geographic distances. The floristic distance matrix was constructed using the Bray-Curtis Index after site-based standardization. Significance of correlations was based on 1,000 permutations of the model. PCoA analyses and Mantel tests were performed with the PATN package (Belbin 1992) and inferential tests with Systat 8.0 (Wilkinson 1998).

## Results

### General diversity and environmental conditions

Thirty six species of pteridophytes were found in the plots, 87.5% terrestrial and 12.5% hemiepiphytes. The family with the highest number of species was Hymenophyllaceae. *Trichomanes pinnatum* Hedw. and *Lindsaea lancea* (L.) Bedd. were found in all plots. The species *Adiantum obliquum* Willd., *Cyathea surinamensis* (Miq.) Domin, *Salpichlaena hookeriana* (Kunze) Alston, *Schizaea stricta* Lellinger, *Trichomanes arbuscula* Desv., *T. cristatum* Kaulf. and *T. martiusii* C. Presl. were found only in one plot, and comprised 17.5% of the total of species sampled (see Appendix 1). The ranges of variation of soil texture, exchangeable bases and terrain slope were broad, while canopy openness data had little variation among plots (Table 1).

### Turnover of species and factors influencing pteridophyte community structure

Spatial processes did not structure the pteridophyte community at the scale of the study ( $90 \text{ km}^2$ ), as floristic distances between plots were not correlated with the geographic distances between them (Simple Mantel test,  $P = 0.095$ ,  $r = -0.051$ ). However, environmental variables predicted 38.1% and 51.5% of the variance in pteridophyte community composition captured by PCoA axes, for quantitative or qualitative data, respectively (Table 2). Community composition was related to soil texture and canopy openness, for either quantitative or qualitative data. Slope affected the qualitative, but not the quantitative composition. The amount of exchangeable bases in the soil significantly affected the quantitative,

**Table 1** Descriptive statistics of environmental variables of the plots on the reserves of BDFFP, Manaus, Brazil

	Clay content (%)	Exchangeable bases (mg/kg)	Terrain slope (°)	Canopy openness (%)
<i>N</i> of cases	38	38	38	37
Minimum–maximum	>0 to <100	48.70–204.34	0.67–23.17	4.18–8.30
Mean $\pm$ SD	52 $\pm$ 36	100.94 $\pm$ 38.73	9.39 $\pm$ 6.40	6.21 $\pm$ 1.07

**Table 2** Standard partial regression coefficients for each variable included in the multivariate multiple linear regression models, and probabilities associated (inside brackets)

	Variance captured by the ordination axis (%)	Clay content (%)	Base cation content	Slope	Log canopy openness	R <sup>2</sup>
Quantitative composition	PCoA1	-0.647 (0.002)*	0.318 (0.119)	-0.101 (0.548)	-0.322 (0.031)*	0.353
	PCoA2	0.143 (0.437)	0.455 (0.020)*	-0.167 (0.290)	0.009 (0.947)	0.438
	Pillai-trace	(0.005)*	(0.037)*	(0.526)	(0.095)	0.381 (0.000)*
Qualitative composition	PCoA1	-0.168 (0.356)	0.056 (0.763)	0.385 (0.017)*	-0.521 (0.000)*	0.453
	PCoA2	-0.749 (0.000)*	-0.142 (0.367)	-0.192 (0.152)	0.018 (0.876)	0.602
	Pillai-trace	(0.000)*	(0.669)	(0.056)	(0.001)*	0.515 (0.000)*

Probabilities associated with the Pillai-trace statistic represent the summed effect of variables over the two ordination axes

\*P < 0.05



but not the qualitative composition (Table 2). There was a gradual turnover of pteridophyte community composition along the gradient of base content (Fig. 2a), but community composition along the clay content gradient suggests a hierarchical structure (Fig. 2b) with most of the species concentrated in one extreme of the gradient and a few species occurring across the entire gradient.

#### Light as a predictor of pteridophyte community composition

The percentage of variance of the quantitative pteridophyte community composition (represented by the PCoA axis1) explained by environmental variables increased from 25.9% to 35.3% with the inclusion of a surrogate measure for understorey light as a predictor. The effect was stronger for qualitative data, with  $R^2$  increasing from 18.4% to 45.3% with the addition of canopy openness in the linear model. Despite the low values of canopy openness found in all plots, in the relatively more open plots, the community primarily comprised the most common species (*Lindsaea lancea*, *Adiantum cajennense* Willd. and *Trichomanes pinnatum*). The abundance of these species had no apparent relationship with the light level. Many more species were present in the darker plots, and therefore, the pteridophyte community had an overall hierarchical structure on the light gradient, with the composition of lighter plots being a subset of darker plots (Fig. 3).

### Discussion

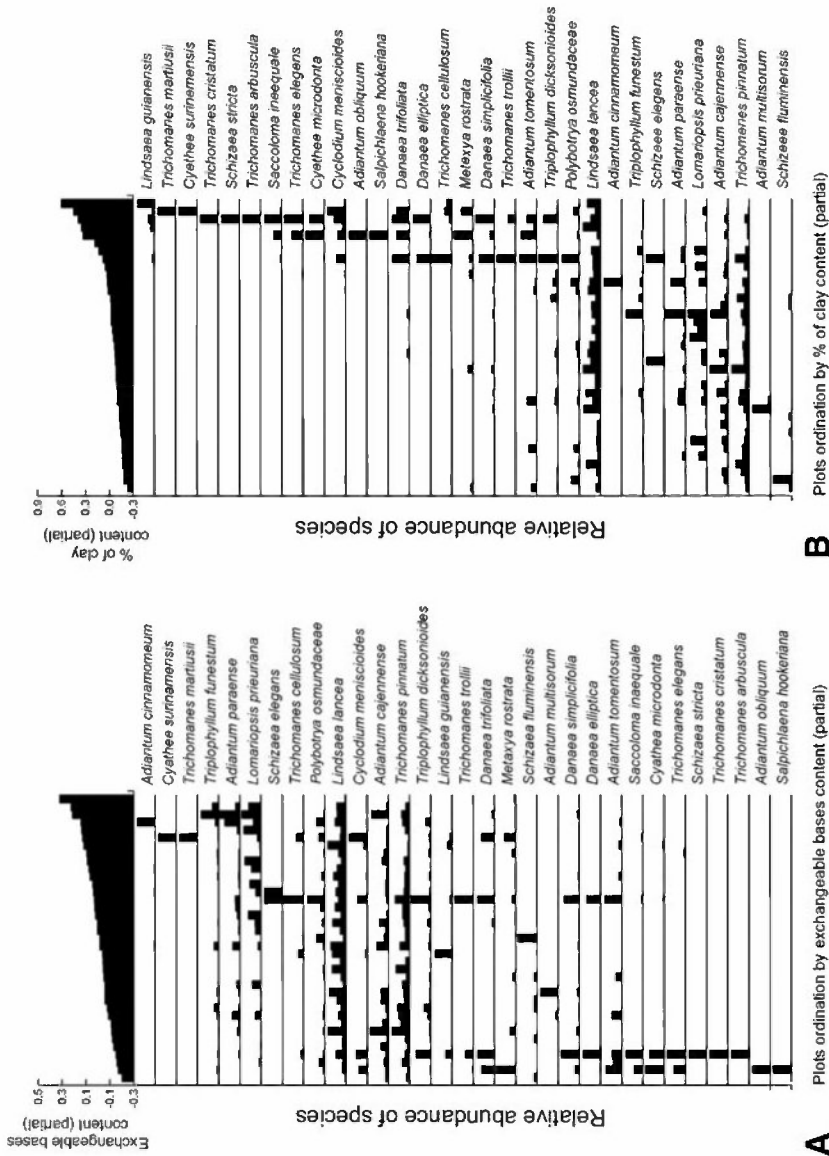
Systematic conservation planning requires information on the spatial distribution of species. The most widely applied approaches on conservation planning are based on modelling distribution of species to infer general patterns of biodiversity indicators such as species richness (Zaniewski et al. 2002) but Ferrier et al. (2002) suggests an alternative approach based on modelling at community level. Both approaches are based on extrapolation of local surveys to non-surveyed areas using environmental variables as predictors and demand a deeper knowledge of the biodiversity-environment relationship. The present study analyzed the importance of some possible predictors of community composition.

#### Light as a predictor of pteridophyte community composition

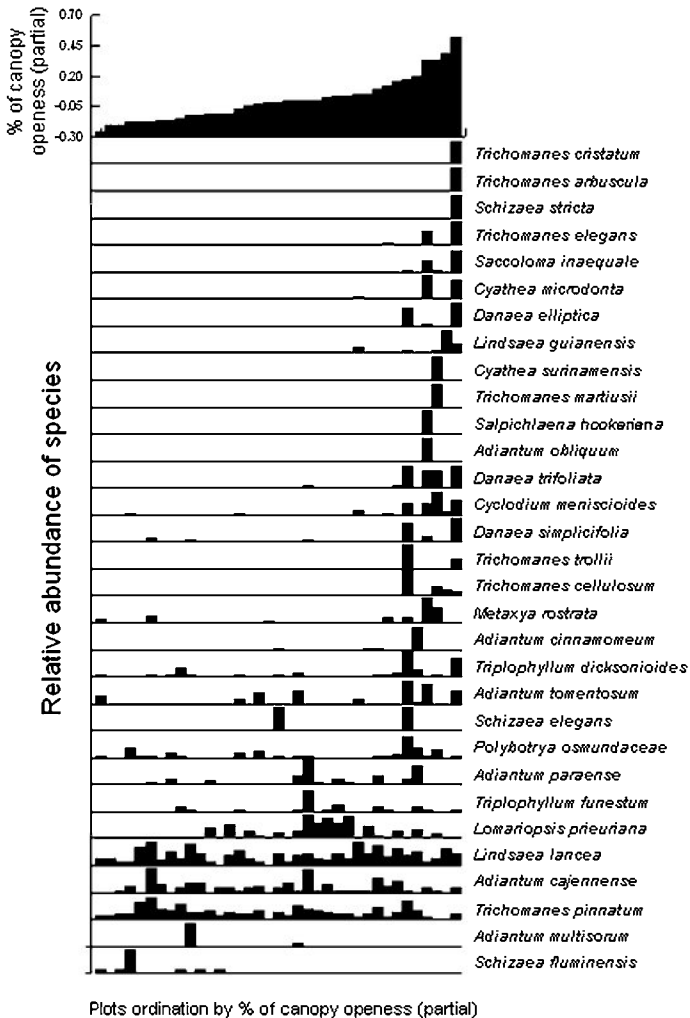
In studies of plant community composition, generally a large part of the compositional variation remains unexplained (Duivenvoorden et al. 2002; Tuomisto et al. 2003a; Jones et al. 2006) and part of it may be related to environmental variables that have not been measured in the field. Light availability is one of such commonly unmeasured variables. The inclusion of canopy openness increased the predictive power of our environmental model by 9% (quantitative data) to 27% (qualitative data), even under the narrow range of less than 5% in canopy openness registered in our plots. However, there is still a large amount of unexplained variance. The unexplained variance in models relating community composition has at least three possible technical sources—sampling errors, limited analytical tools and failure in the inclusion of relevant predictors. This single attempt to improve estimation of community composition suggests that, although important, the lack of a variable to represent light is not the main factor that limits the previous models.

The response of the community to the light gradient was hierarchical, meaning that most species were concentrated in low light plots and a few common and abundant spe-





**Fig. 2** Species abundances along the gradient of soil properties (partial from the multiple regression) on 37 plots of the reserves of BDFFP, Manaus, Brazil. The ordination of species was based on the partial gradient of (a) exchangeable bases on PCoA2 axis and (b) clay content on PCoA1, obtained from a multiple linear regression model including the effects of soil texture, base content, terrain slope and canopy openness on community composition axes



**Fig. 3** Species abundances along the gradient of canopy openness (partial from the multiple regression) on 37 plots of the reserves of BDFFP, Manaus, Brazil. The ordination of species was based on the partial of the gradient of canopy openness, obtained from a multiple linear regression model including the effects of soil texture, base content, slope and canopy openness on community composition represented by PCoA1

cies occurred across the entire gradient. Therefore, we could not see evidence of light partitioning along this range. Many authors showed that light availability in the understory can be limiting for plants. For example, low available light in the understory can reduce survival probability of some tree seedlings (Montgomery and Chazdon 2002). On the other hand, some understory plants can efficiently use the small light quantities that reach the forest floor (Chazdon et al. 1996). Understorey ferns have evolutionary adaptations for low levels of light (Page 2002) such as low light saturation of photosynthetic rates (Ayob et al. 1996). These may determine high sensibility to slight increases in the levels of light incidence.

These results can not be directly interpreted as an evidence of treefall gap influence on pteridophyte community structure. Montgomery and Chazdon (2002) found light gradient partitioning between seedlings of tropical tree species in Costa Rica in the absence of gaps. Hubbell et al. (1999) found that the composition of tree species in gaps was not predictable in a 13-years monitoring. The temporal and spatial ephemeral nature of gaps on improving light availability and influencing forest dynamics cannot be easily extrapolated to mesoscale studies probably due to the absence of spatial structure of gaps in tropical forests.

#### Pteridophyte community distribution along edaphic and topographic gradients

Soil texture was the main factor related to variations in the pteridophyte community in this study. The effect of soil fertility was weak, being associated to the second PCoA axis, which captured about 20% of pteridophyte community composition variation. Spatial segregation of pteridophyte species due to edaphic factors had been reported at different scales (Ranal 1995; Tuomisto and Poulsen 1996; Tuomisto et al. 2003a, b; Jones et al. 2006).

Description of patterns in gradients is recommended to be viewed as a mechanism of hypothesis generation rather than for inference and testing (MacKenzie et al. 2006). The causal factors of the relationship between soil and pteridophyte community composition were not addressed in this work, but correlations found do indicate some possible relevant causal effects. In Central Amazonia, clay content gradually increases from bottomlands (with sandy-podzolic soils) to uplands (with very clayey latosols) (Chauvel et al. 1987). Soil structure in catenas leads to an increase in clay content with increasing distance from streams, and it is possible that the response to clay reflects a gradient of tolerance to varying water availability in the soil, since pteridophytes are highly dependent on water for sexual reproduction and for gametophyte establishment (Page 2002). Soil pH was also correlated with soil texture and has been previously recognized as an important factor for sporophyte development (Ranal 1995), because it determines nutrient availability. Biotic interactions were not considered and play an important role in species distribution. The interaction of herbivore pressure and soil types may intensify the differences between sandy and clayey habitats and promote habitat specialization of some Peruvian Amazonian trees (Fine et al. 2004). Although we can not extrapolate these results to pteridophyte community, Mehltreter et al. (2003) found that leaf damage on fern leaves is similar to that on angiosperms. We are not aware of studies about the influence of herbivores on pteridophyte distribution patterns.

The absence of a relationship between slope and the quantitative community composition is inconsistent with the findings of Costa et al. (2005) within the same biogeographical area. This lack of consistency leads to a conclusion that topographic patterns are site-specific (Vormisto et al. 2004), or that other relief features are necessary to predict community structure. The effect of slope is probably a synergistic response of the community to differences on soil moisture, drainage, litter deposition and other factors. Therefore, slope is a poor surrogate for these features, because the same flat slope can be found on two very different habitats: at dry and clayey hilltops and at humid and sandy bottomlands near streams.

Geographic distance plays minor role on pteridophyte community turnover at 90 km<sup>2</sup>

Our results do not support the occurrence of dispersal limitation for pteridophytes at the scale of 1–21 km. Floristic similarity did not decrease with increasing geographic distance

and environment was a better predictor of community composition. Therefore, although environmental variation determines high turnover of species locally, mesoscale turnover is low. Ferns are wind-dispersed and produce large amounts of spores (Kramer et al. 1995 *apud* Ponce 2002) that can travel thousands of kilometers (Wolf et al. 2001). Turbulent winds are not common above rain forest canopies (Kruijt et al. 2000), but unpredictable but frequent wind storms and gap openings may provide opportunities for long dispersal events. Jones et al. (2006) tested whether the effects of spatial processes would be stronger at smaller scales, since most pteridophyte spores fall close to the mother plant (Wolf et al. 2001). However, they found no evidence for this, and concluded that environment played a major role in determining pteridophyte community composition.

#### The need for inventories to supply conservation demands

Ideally, complementarity of species composition between the already protected and planned protected areas network should be the main criteria to be used for creation of new conservation units (Margules et al. 2002), but data on spatial patterns of Amazonian plant biodiversity are scattered and scarce. Low and clumped density of botanical collections is a constraint for biodiversity mapping in Amazonia (Nelson et al. 1990; Hopkins 2007) and consequently, biodiversity surrogates such as vegetation physiognomies are used as predictors of species distribution. Nevertheless, studies comparing floristic differences between Amazonian physiognomies like savannah, white-sand, and terra firme forests will not surprisingly find higher beta-diversity than studies focusing on the floristic turnover within a single forest physiognomy. But these coarse comparisons can not reveal more subtle patterns that are relevant for biodiversity conservation planning.

This study found some important changes in fern communities in the same type of forest that are mainly related to environmental heterogeneity, even in narrow ranges of variation like that of canopy openness. Inventories need to be conducted at multiple sites and different scales to allow deeper comprehension on the biodiversity-environment relationship. This information is essential to improve the capacity to predict patterns of biodiversity. Moreover, since composition does not change with geographic distance at this scale, but soils may form patches that have different species composition, protected areas should be planned as a network including the whole range of variation on these features.

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**Appendix: Pteridophyte species abundance and frequency**

**Appendix 1** List of all pteridophyte species found in 38 plots of the reserves of BDFFP, Manaus, Brazil

Family	Species	Author	Habit	Number of individuals	Frequency
Aspleniaceae	<i>Asplenium angustum</i>	Sw.	Epiphyte	2	2
	<i>Asplenium serratum</i>	L.	Epiphyte	60	18
Blechnaceae	<i>Salpichlaena hookeriana</i>	(Kunze) Alston	Hemiepiphyte	21	1
	<i>Cyathea microdonta</i>	(Desv.) Domin	Terrestrial	101	6
Davalliaceae	<i>Cyathea surinamensis</i>	(Miq.) Domin	Terrestrial	1	1
	<i>Oleandra articulata</i>	(Sw.) C. Presl	Epiphyte	2	1
	<i>Nephrolepis rivularis</i>	(Vahl) Mett. ex Krug	Epiphyte	1	1
	<i>Nephrolepis</i> sp. 1		Epiphyte	3	2
	<i>Saccoloma inaequale</i>	(Kunze) Mett.	Hemiepiphyte	20	4
Demnstaedtiaceae	<i>Lindsaea guianensis</i>	(Aubl.) Dryand.	Terrestrial	15	6
	<i>Lindsaea lancea</i>	(L.) Bedd.	Terrestrial	547	38
	<i>Polybotrya osmundaceae</i>	Willd.	Hemiepiphyte	119	19
Dryopteridaceae	<i>Cyclodium meniscioides</i>	(Willd.) C. Presl	Hemiepiphyte	124	9
	<i>Cochlidium serrulatum</i>	(Sw.) L.E. Bishop	Epiphyte	4	4
Grammitidaceae	<i>Trichomanes ankersii</i>	Parker ex Hook. & Grev.	Epiphyte	357	38
	<i>Trichomanes arbuscula</i>	Desv.	Terrestrial	2	1
Hymenophyllaceae	<i>Trichomanes cellululosum</i>	Klotzsch	Terrestrial	51	5
	<i>Trichomanes cristatum</i>	Kaulf.	Terrestrial	1	1
	<i>Trichomanes elegans</i>	Rich.	Terrestrial	58	3
	<i>Trichomanes kappleurianum</i>	J.W. Sturm	Epiphyte	2	1
	<i>Trichomanes martusii</i>	C. Presl	Terrestrial	3	1
	<i>Trichomanes pinnatum</i>	Hedw.	Terrestrial	5,035	38
	<i>Trichomanes</i> sp. 1		Epiphyte	3	3
	<i>Trichomanes trollii</i>	Bergdolt	Terrestrial	151	3
	<i>Trichomanes tuerckheimii</i>	Christ	Epiphyte	68	21
	<i>Hymenophyllum polyanthos</i>	(Sw.) Sw.	Epiphyte	3	3
Lomariopsidaceae	<i>Lomariopsis prairieana</i>	Fée	Hemiepiphyte	724	26
	<i>Elaphoglossum flaccidum</i>	(Fée) T.M. Moore	Epiphyte	18	4
	<i>Elaphoglossum glabellum</i>	J. Sm.	Epiphyte	2	1
	<i>Elaphoglossum luridum</i>	(Fée) H. Christ	Epiphyte	4	4

## Appendix 1 continued

Family	Species	Author	Habit	Number of individuals	Frequency
Marattiaceae	<i>Elaphoglossum obovatum</i>	Mickel	Epiphyte	3	2
	<i>Elaphoglossum styriacum</i>	Mickel	Epiphyte	40	12
	<i>Danaea elliptica</i>	Sm.	Terrestrial	120	3
	<i>Danaea simplicifolia</i>	Rudge	Terrestrial	52	8
	<i>Danaea trifoliata</i>	Kunze	Terrestrial	30	6
	<i>Metaxya rostrata</i>	(Kunth) C. Presl	Terrestrial	53	7
	<i>Polypodium bombycinum</i>	Maxon	Epiphyte	2	2
	<i>Microgramma baldwinii</i>	Brade	Epiphyte	5	4
	<i>Microgramma megalophylla</i>	(Desv.) de la Sota	Epiphyte	5	4
	<i>Microgramma thurnii</i>	(Baker) R. M. Tryon	Epiphyte	4	3
Pteridaceae	<i>Dicranoglossum desvauxii</i>	(Klotzsch) Proctor	Epiphyte	1	1
	<i>Adiantum cajennense</i>	Willd.	Terrestrial	101	30
	<i>Adiantum cinnamomeum</i>	Lellinger & J. Prado	Terrestrial	88	4
	<i>Adiantum multisorum</i>	Sampaio	Terrestrial	17	2
	<i>Adiantum obliquum</i>	Willd.	Terrestrial	1	1
	<i>Adiantum paraense</i>	Hieron.	Terrestrial	147	22
	<i>Adiantum tomentosum</i>	Klotzsch	Terrestrial	52	9
	<i>Schizaea elegans</i>	(Vahl) Sw.	Terrestrial	2	2
	<i>Schizaea fluminensis</i>	Miers ex J.W. Sturm	Terrestrial	12	6
	<i>Schizaea stricta</i>	Lellinger	Terrestrial	2	1
Selaginellaceae	<i>Selaginella asperula</i>	Spring	Terrestrial	121 <sup>a</sup>	2
	<i>Selaginella breynii</i>	Spring	Terrestrial	281 <sup>a</sup>	1
	<i>Selaginella palmiformis</i>	Alston ex Crabbe & Jermy	Terrestrial	369 <sup>a</sup>	1
	<i>Selaginella parkeri</i>	(Hook. & Grev.) Spring	Terrestrial	2,717 <sup>a</sup>	8
	<i>Selaginella pedata</i>	Klotzsch	Terrestrial	8,460 <sup>a</sup>	23
Tectariaceae	<i>Triplophyllum dicksonioides</i>	(Fée) Holttum	Terrestrial	385	25
	<i>Triplophyllum fanestum</i>	(Kunze) Holttum	Terrestrial	125	18
Vittariaceae	<i>Polytaenium guayanense</i>	(Hieron.) Alston	Epiphyte	4	4
	<i>Hecistopteris pumila</i>	(Spreng.) J. Sm.	Epiphyte	281	31

The list includes epiphytes which were not included in the complete analysis

<sup>a</sup> Number of stems



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