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Padrões de distribuição de plantas ao longo de gradientes ambientais na Amazônia central: uma comparação entre duas paisagens

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Manaus, Amazonas

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P196

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Sinopse:

Foi estudada a distribuição de plantas ao longo de gradientes de fertilidade do solo, teor de argila e inclinação do terreno em duas paisagens em mesoescala. Discutiu se sobre o que pode determinar essas distribuições e como as variáveis medidas interagem entre si determinando subgrusição de espécies.

Palavras chave: Leguminosae – Pteridófitas – Florestas tropicais – Gradientes ambientais

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RESUMO

Embora exista uma extensa literatura sobre padrões de distribuição de plantas em florestas tropicais e suas relações com variáveis ambientais, tais estudos não levam em conta que seus resultados podem depender em grande parte da amplitude de variação ambiental presente nos sítios amostrados e que dentro da variável preditora principal, um ou mais gradientes podem também ser importantes em definir associações de espécies. Leguminosas arbóreas e pteridófitas terrestres foram amostradas em duas áreas, cada uma com cerca de 25 km^2 de tamanho e separadas por ~150 km. Ambas as áreas possuem características topográficas similares. Uma área possui apenas solos pouco férteis, enquanto a outra possui uma grande amplitude de fertilidade do solo, pois está localizada no contato entre dois substratos geológicos distintos. Análises de Coordenadas Principais (PCoA) foram utilizadas para ordenar as parcelas com relação as suas dissimilaridades e Árvores de Regressão Multivariada (ARM) para visualizar de maneira hierárquica os preditores ambientais definindo grupos composicionais. Na área com solos menos férteis, a textura do solo foi a variável ambiental mais importante para definir a composição de espécies enquanto que na área com maior amplitude de fertilidade, a soma de bases trocáveis foi o determinante principal das diferenças na composição de espécies dos dois grupos de plantas estudados na mesoescala. Para as árvores, dentro de certos valores das variáveis principais, a inclinação do terreno aparece como importante estruturadora da composição. Para as pteridófitas, importantes diferenças de composição foram encontradas dentro dos valores mais baixos da variável principal. Na escala regional, a fertilidade dos solos foi o gradiente principal para os dois grupos de plantas estudados, embora a textura do solo tenha sido um importante preditor para as pteridófitas. Neste estudo, fica claro que ao generalizar padrões de comunidades vegetais, devemos levar em conta que a heterogeneidade das paisagens pode mudar de maneira imprevista e que a importância de cada preditor estudado tende a ser condicionada à sua amplitude da variação.

ABSTRACT

Plant distribution patterns along environmental gradients in central Amazonia: a comparison between two landscapes.

Although an extensive literature deals with plant distribution patterns in tropical rainforests and their relation to environmental variables, these studies usually do not take in account that their results may be, at least in part, due to the amplitude of environmental variables present in the sampled sites and that within the main predictor variable one or more subordinate gradients may also be important in defining compositional groups. We sampled legume trees and terrestrial pteridophytes in two areas, each about ~25 km^2 in size and separated by ~150 km. Both sites have similar topographic characteristics. One site has only infertile soils, while the other has a broad range of soil fertility, as it is located at the contact between two distinct geological substrates. Principal Coordinates Analysis and similarity matrices were used to ordinate the plots. Multivariate Regression Trees were used to organize the environmental predictors in a hierarchy according to their importance in determining compositional groups. At the site with only infertile soils, clay content was the most important predictor of composition. At the site with a broad range of soil fertility, the sum of exchangeable bases was the most important determinant of compositional differences. This was true for both plant groups. For legume trees, within certain a range of values of the main predictive variable, terrain slope appeared as a subordinate predictor. For pteridophytes, the most important differences in composition were nested within the low end of the values of the main predictor, i.e. a nonlinear relationship. When all samples from both sites were pooled for an analysis at the regional scale, soil fertility was the main compositional predictor. Low fertility plots from the two different sites were more similar than low and high fertility plots within the same site. At this regional scale, clay content was an important subordinate predictor for pteridophytes. This study shows that, when generalizing plants community patterns, we must take into account that landscape heterogeneity can change in an unexpected way and that the importance of an environmental predictor tends to be constrained by its amplitude.

SUMÁRIO

Apresentação

A presente dissertação foi realizada como parte dos requisitos para a obtenção do título de Mestre em Biologia (Ecologia) pelo Instituto Nacional de Pesquisas da Amazônia – INPA. Neste trabalho, foram amostradas as árvores e samambaias presentes em, respectivamente, 57 e 51 parcelas distribuídas entre duas paisagens de florestas de terra firme na região central da Amazônia.

A dissertação é composta por um capítulo em forma de artigo, que obedece, quanto a sua formatação, as normas da revista *Biotropica*. O artigo estuda a distribuição das plantas e suas relações com a textura e fertilidade do solo e com a inclinação do terreno. Isto foi feito para verificar a existência de grupos de espécies que podem responder de maneira hierárquica às variáveis ambientais, evidenciando que alguns preditores podem ser importantes estruturadores das comunidades, mas apenas dentro de certos valores da variável principal, consideração ainda pouco explorada em trabalhos sobre a distribuição de plantas em florestas tropicais.

Objetivos

Objetivo geral: Estudar a distribuição de plantas ao longo de gradientes ambientais em duas áreas de mesmo tamanho, mas que diferem quanto a sua heterogeneidade ambiental.

Objetivos específicos:

1. Estudar quais são os principais fatores ambientais que determinam a estrutura de comunidades de samambaias e leguminosas arbóreas e como o comprimento dos gradientes afetam a relação comunidade-ambiente.

2. Verificar se existem evidências de uma estruturação hierárquica das comunidades vegetais, com algumas variáveis ambientais importando apenas dentro de certos valores de outras variáveis.

Capítulo 1

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Spatial scale or amplitude of predictors as determinants of the relative importance of environmental factors to plant community structure

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Abstract: The literature on tropical-rainforest plant-communities relationships with environment does not recognize the relative importance of environmental factors taking into account the amplitude of variation in those factors. Environmental effects may be hierarchically structured, with some factors being important within a certain range of another gradient. Ferns and trees of two mesoscale landscapes (each 25 km^2) with different soil fertility amplitudes but similar soil texture range, were sampled in central Amazonia. We found that major determinants of community structure were the same for both groups. In the site with homogeneous soil fertility, texture was the main predictor of community structure. On the other hand, exchangeable cations were the main predictor in the site that presented a wider fertility range. When both sites where analysed togheter, soil fertility was the main determinant of community structure. Therefore, soil texture segregated floristic subgroups withing certain ranges of soil fertility gradient. We conclude that the gradient's length is crucial in determining which factors will be recognized as most important in structuring plant communities, and the relative importance of predictors is not only a function of scale but also of the landscape's spatial structure.

Keywords: Legume trees – Terrestrial pteridophytes – Tropical rainforest – Abiotic variables – Ecology of plant communities

Escala espacial ou amplitude dos preditores como determinantes da importância relativa de fatores ambientais na estrutura de comunidades vegetais

Resumo: A literatura sobre as comunidades de plantas das florestas tropicais e suas relações com o ambiente leva em conta a importância relativa dos fatores ambientais, mas não considera a amplitude de variação nesses fatores. Os efeitos ambientais podem ser hierarquicamente estruturados, com algumas variaveis sendo importantes apenas em um determinado intervalo de outro gradiente. Samambaias e árvores de duas paisagens de meso-escala (25 km2 cada), com amplitudes diferentes de fertilidade dos solos, mas com similar variação de textura do solo, foram amostradas na Amazônia central. Descobrimos que os principais determinantes da estrutura da comunidade foram os mesmos para ambos os grupos. Na área com a fertilidade do solo mais homogênea, a textura foi o principal preditor da estrutura da comunidade. Por outro lado, a soma de bases trocáveis foi o preditor principal no local que apresentava uma gama mais ampla de fertilidade. Quando ambos os locais foram analisados conjuntamente, a fertilidade do solo foi o principal determinante da estrutura da comunidade. Portanto, a textura do solo segregou subgrupos florísticos dentro de determinadas faixas de gradiente de fertilidade do solo. Concluímos que o comprimento do gradiente é de crucial importância na determinação de quais fatores serão reconhecidos como mais importantes na estruturação das comunidades de plantas, e que a importância relativa de preditores é não apenas função de sua escala, mas também da estrutura espacial da paisagem.

Palavras chave: Leguminosas arbóreas – Pteridófitas terrestres – Florestas tropicais – Variáveis abióticas – Ecologia de comunidades vegetais

INTRODUCTION

The amplitude of environmental gradients varies among sites, and although heterogeneity tends to increase with area, sites of the same size do not necessarily harbor the same amount of heterogeneity (Rosenzweig 1995). The relative importance of environmental gradients in generating patterns of species distribution may depend only on the existence of enough variation to create distinct habitats. As heterogeneity may change with scale in an unpredictable manner, partitioning of niches may occur at very different scales between sites. While this may seem obvious, the literature is replete with a long debate about which factors are most relevant for determining the structure and composition of plant communities (Bohlman *et al*. 2008, Clark *et al*. 1998, 1999, Costa *et al*. 2005, Duivenvoorden *et al*. 2002, Normand *et al*. 2006, Paoli *et al*. 2006, Pitman *et al*. 2008, Svenning *et al*. 2004, Swaine 1996, ter Steege *et al*. 2006, Tuomisto *et al*. 1995, Valencia *et al*. 2004) that does not take into account that the results may depend, at least in part, of the length of gradients studied in each scale. There are suggestions that the relative importance of environmental and neutral factors are related to scale (Normand *et al*. 2006) but it is possible that this is also dependent on the internal heterogeneity in each area studied, which is not necessarily correlated with the extent of the area.

Studies of plant communities in central Amazonia have identified topography or some related variable (mostly soil texture) as a strong predictor of community structure (e.g. Costa *et al*. 2005, 2009, Kinupp & Magnusson 2005, Zuquim et al. 2009), in contrast to studies in the western Amazon, where soil fertility has generally been the most important predictor (e.g. Duivenvoorden 1995, Duque *et al*. 2002, Ruokolainen *et al*. 2007, Tuomisto *et al*. 1995, 2002). In regional and local contexts, topography may be associated with soil texture, due to the process of soil formation (Lucas & Chauvel 1992, Chauvel 1987 and Luizão et al. 2004 address specifically this relationship for the Manaus region) and, to some degree, to its fertility, but many other factors are correlated with topography, such as water availability (Daws *et al*. 2002) and litter deposition (Luizão *et al*. 2004). Some models suggest that light availability and canopy opening are associated with surface slope (Robert 2003). Therefore, disentangling the relative contribution of fertility and topography in structuring communities is not easy. The relative importance of these predictors may depend on the scale of analysis and the range of variation of each predictor included in the sample. Huge areas in central Amazonia are covered by poor soils, and vary little in soil fertility (Chauvel *et al*. 1987). However, there are some small, scattered patches of rich soils in upland forests (RADAMBRASIL 1978, Quesada *et al*. 2011). The occurrence of these fertile spots near the typically poor soils of the basin allows the relationship of fertility and topography, and its consequences in the structuring of plant communities to be examined.

The effects of abiotic factors may also differ among different taxonomic and/or functional groups. Ruokolainen *et al*. (2007) showed that the composition of ferns, trees and Melastomataceae vary similarly in relation to edaphic factors in the western Amazon. In central Amazonia, Costa *et al*. (2005) showed similar distribution patterns of Marantaceae and Poales, but the distribution of ferns differed. Costa *et al*. (2009) showed that understory palms have a narrow niche partition, while canopy palms did not. Environmental factors that are limiting to understory plants may not be for canopy trees (Wiens 1989), as trees may be able to access resources that are unavailable to understory plants. Therefore, differing access to limiting resources is expected to cause different patterns of distribution between understory and canopy plants. However, the evidence to date does not make clear if different taxonomic groups and life forms respond similarly to environmental characteristics or if these responses may be conditioned by the attributes of the studied landscape.

In the present study, we analyzed the community patterns of two functionally and phylogenetically distant plant groups - legume trees and terrestrial ferns - of two sites in central Amazonia that differ in soil heterogeneity. Sites are only ~100 km apart and within the same ecorregion (Dinerstein et al. 1995). Both areas have strong variation in soil texture on a small scale (25 km^2), but one of them has a variation in soil cation content of one order of magnitude higher than the other site. We address the following questions: (1) What are the major environmental factors determining the community structure of ferns and legumes and how grandient lengh affect this community-environment relationship? (2) Is there evidence for a hierarchical community organization, with some environmental factors being important only within some values of other factors?

METHODS

STUDY SITES

BIOLOGICAL RESERVE OF UATUMÃ (RBU) – The Uatumã Reserve is located about 120 km north of Manaus (1.80 º S - 59.25 º W), and covers 942,786 hectares of dense terra-firme forest (Fig.1). It lies on the geological contact between the sedimentary Paleozoic Trombetas formation, and the igneous/volcanic Pre-Cambrian Iricoumé formation (Irion 1978, RADAM 1978). Soils form a gradient from poor latosols (ferralsols in the World Reference Base classification) to richer soils derived from outcrops of igneous Precambrian rocks (c. 1,990 –

1,800 MY) of the Guiana Shield (RADAMBRASIL 1978). These two soil types combined make a wider range in fertility than that found commonly in central Amazonia. The average annual temperature is about 27 ºC and average annual rainfall is 2370 mm (Sombroek 2001). Altitude ranges between 57 and 195 meters above sea level. See Tables 1 and 2 for information on the plots.

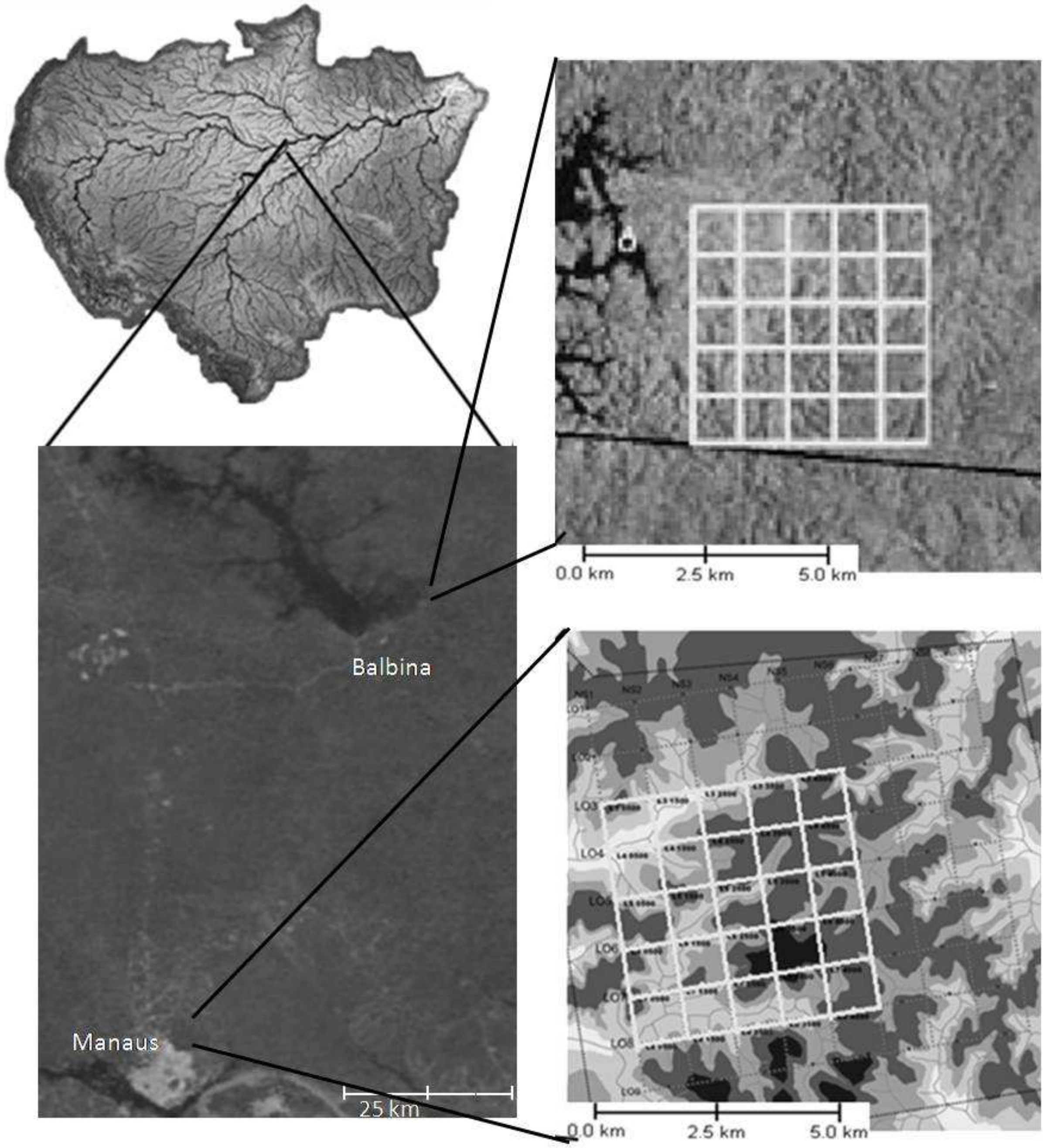

FIGURE 1: Geographic location of study sites: at the top right corner Biological Reserve Uatumã, at the bottom right corner Ducke Forest Reserve.

DUCKE FOREST RESERVE (RFD) – Located 26 km north of Manaus (2.90 º S - 59.90 º W), the reserve covers 10000 hectares of dense terra-firme forest (IBGE 2004) (Fig. 1). Soils are derived from Tertiary sediments of the Alter do Chão formation and represent a continuum from clayey latosols on the ridges to sandy podzols at valleys (Chauvel *et al.* 1987). The average annual temperature is around 26 ºC and average annual rainfall is around 2300 mm (Sombroek 2001). Altitude ranges between 39 and 110 m above sea level. See Tables 1 and 2 for information on the plots.

Table 1. *Range and mean values for the environmental factors in both study sites. Values concern the plots in which legume trees and ferns were sampled.*

Study Site	# plots (trees/ferns)		Clay content (%)	Bases (cmol/kg)	Slope (degrees)
RFAD	30/24	Min. – Max.	1 - 83.50	0.021 - 0.434	2 - 26.30
		Mean ± SD	39.05 ± 34.10	0.234 ± 0.116	4 ± 6.08
RBU	27/27	Min. – Max.	16.50 - 85.50	0.165 - 5.675	1 - 25.66
		Mean ± SD	47.50 ± 23.12	0.925 ± 1.302	10 ± 7.46

SAMPLING DESIGN – In both study areas, regular grids of 25 km^2 of trails, following the RAPELD (RAP + PELD, the Brazilian acronym for long-term ecological research- LTER) protocol (Costa & Magnusson 2010, Magnusson *et al.* 2005) are available. The grid at Ducke has 30 permanent plots, and the grid at Uatumã 27 plots. In both cases plots are regularly spaced by 1 km. Plots are 250 m long and follow the terrain altitude contour. As in central Amazonia soil type is correlated with altitude within a catena (Chauvel *et al*. 1987), plots that follow the altitudinal contour are more homogeneous in soil conditions along its length than they would be if they crossed along the catena.

DATA COLLECTION – Within the Uatumã grid the 27 plots were sampled for both legume trees and ferns, and at Ducke 30 plots were sampled for trees and 24 for ferns. Plots without fern sampling at Ducke were missing in the database obtained from the PPBio. The family Leguminosae was chosen as a model for trees since it has the highest importance value in the Amazon region and is the richest family (138 known species) in the Reserva Ducke (Ribeiro *et al*. 1999). In each plot, vouchers from all individuals of the family Leguminosae with DBH ≥ 30 cm were collected and identified to the lowest taxonomic level possible within an area of one hectare (250 x 40 m). Individuals with DBH ≥ 10 cm were collected and identified in a sub-sample of 0.5 hectare (250 x 20 m). Samples were identified to species or morphotypes in the INPA herbarium, with specialized literature (Ribeiro *et al*. 1999), and the help of a specialist (Dr Michael Hopkins) who identified *Parkia* and supervised the identification of the other genera. Vouchers from both sites were compared to assure that morphotypes were the same. Fertile vouchers were deposited at INPA Herbarium and unfertile specimens are stored at INPA Biodiversity Department for consultation. The abundance (number of individuals per plot) of plants from the 1ha plot (250 x 40 m) and from the sub-sample of 0.5 ha (250 x 20 m) for smaller plants was summed to provide an estimate of abundance for each species. The abundance of smaller plants in the 0.5 ha was not extrapolated to a 1 ha basis since this would require an uniform distribution over the plot to produce an unbiased estimate. Most species were present in both the 0.5 and the 1 ha sample.

Terrestrial ferns (not including fallen epiphytes and hemiepiphytes) were sampled in 0.1 ha of each plot in Uatumã (250 x 2 m) and 0.05 ha (250 x 1 m) in Ducke. In order to make the samples comparable between sites, only half of the sample made in Uatumã was used in the analyses. Since plants were mapped and sampled in subplots of 10 x 2 m, a sample of 125 x 2 m (0.05 ha) was built including interspaced 10 m segments for the Uatumã plots. Each individual rooted within the plot, with fronds larger than 5 cm in length was counted and identified. For the majority of species, it was possible to distinguish and count individuals. In clonal species, each clump of leaves arising at least 20 cm from another was counted as an individual. Identifications were based primarily on taxonomic treatments (Mori *et al*. 1997, Ribeiro *et al*. 1999) and were confirmed by Dr. Jefferson Prado. Material of all species was collected for confirmation in the Herbarium of the National Institute for Amazon Research (INPA).

Data on soil texture and chemistry was obtained from the PPBio database (http://ppbio.inpa.gov.br/). Soil samples were taken from 0 to 5 cm depth, after removal of the litter layer, at 6 points regularly spaced along the largest length of the plot. A composite soil sample was analyzed for each plot. Composite samples were made with 50 g of soil from each of the 6 points, mixed throughout and analyzed in the Laboratory of Soil and Plants at INPA. Exchangeable bases (Ca^{+2}, K^{+}, Mg^{+2} and Na+) were used to represent soil fertility. Ca^{+2} and Mg^{+2} were extracted by 1N KCl and determined by atomic absorption spectrometry. K^{+} was extracted with the Mehlich I solution. Na^{+} concentration was bellow spectrometer detection and therefore not included. Sodium pyrophosphate was used as a dispersant to determine soil texture. The soil collection and analysis protocol was the same for both areas. Slope of each plot was the average of six measurements spaced 50 m apart, taken with a clinometer facing perpendicular to the main axis of the plot.. All data and metadata referred to here is available at the PPBio database (http://ppbio.inpa.gov.br/Port/dadosinvent/).

DATA ANALYSIS – Principal Coordinates Analysis (PCoA, Legendre & Legendre 1998) was used to reduce the dimensionality of the communities studied. We ran PCoA's with quantitative (number of individuals per plot) and presence-absence data. Quantitative dissimilarity matrices were constructed with the Bray-Curtis index, based on the number of individuals per plot, and the Sorenson index was used in case of presence-absence data. Data was standardized by the total number of individuals in each plot. This will make two plots to be considered similar if they contain similar relative abundances of species, and not because they both contain high or low abundances of individuals, irrespective of the species. Since species turnover in Uatumã was large, resulting in plots with no shared species, we used extended dissimilarities over the Bray-Curtis measures (De'ath 1999). The first three PCoA axes were used as dependent variables in multiple regression models, to access the relative importance of soil texture (represented by the clay content), soil fertility (represented by the sum of exchangeable bases) and terrain slope for community structure.

Because spatial autocorrelation may be a problem in observational studies (Legendre 1993), we evaluated model residuals (Dormann *et al.* 2007). If residuals are autocorrelated, the autocorrelation is a problem when both response and predictor variables are autocorrelated (Peres-Neto & Legendre 2010, Landeiro & Magnusson 2011) at the same spatial scale (de Knegt *et al.* 2010). The existence of spatial structure in the original data and in the residuals of regressions was checked by correlograms using the Moran's I statistic. The number of distance classes in the correlograms was adjusted to represent intervals of around 1km, which is the minimum distance between plots.

To evaluate the hierarchy of importance of environmental predictors in determining the community structure we generated multivariate regression trees - MRT (De'ath 2002) for each plant group in each site (here considered as mesoscales) and for both sites taken together in a group (regional scale). The regional scale MRT for ferns was based on a data table standardized to make the sampling area equal for both areas (250 x 1 m). MRT was run over the set of quantitative PCoA axes that captured ~70% of the total community variation. This was decided in order to compare sites and groups based on the same amount of original variance. The sizes of MRTs were determined by cross validation (De'ath 2002, Larsen & Speckman 2004).

To enable visualization of community patterns and the limits of species distributions we performed direct ordinations of species along the main gradients studied. All analyses were done in the R statistical environment, version 2.12.1.

RESULTS

ENVIRONMENTAL VARIATION – The range and means of the soil clay content and slope were similar in Ducke and Uatumã, although Ducke had more very sandy plots (< 10 % clay). However, the variation in fertility, represented by the sum of bases, is 13 times higher in Uatumã (Table 1). Fertility was related to texture in Ducke (r = 0.53) and to inclination in Uatumã (r = 0.55). However, the tolerance (which is the inverse of the multiple correlation) between soil texture, cation content and inclination in the multiple regressions conducted to evalute their effect on composition was high, indicating that their behaviour in these models is independent of each other.

LEGUME TREE SPECIES COMPOSITION AND COMMUNITY STRUCTURE – We found 1276 trees in Ducke and 630 in Uatumã, distributed in 136 species and 60 morphotypes (Apêndices). Mimosoideae was the richest subfamily and *Inga* the richest genus. In Ducke we found 118 species and 13 morphotypes and in Uatumã 92 species and 47 morphotypes. *Eperua glabriflora* (Ducke) R.S.Cowan was the most abundant and frequent species at Ducke (13.94% of all individuals, 100% frequency), but did not occur in Uatumã plots. *Pterocarpus officinalis* Jacq. was the mos abundant species at Uatumã (5.5% of the individuals).

At Ducke, for both the quantitative and qualitative data sets, the effect of clay was greater than the effect of terrain slope, and there was no significant effect of soil fertility

(Table 2). Although most tree species were widely distributed over all gradients studied (Fig. 2a), 17 species in the reserve Ducke occurred only in bottomlands (clay content <13.5%) and about ten species only in the clayey and relatively flat areas (Fig. 2b). From these, 6 species in sandy plots and 9 species in clayey plots had only 3 or less individuals, and their patterns may have been due to chance, while the others had 4 to more than 50 individuals consistently restricted to high sand or high clay plots. In Uatumã, soil fertility, followed by the clay content, were the factors most strongly associated with the first quantitative ordination axis (Table 2).

Table 2. *Standard partial regression coefficients (b_{std}) for each predictor included in the multiple linear regressions models and their associated probabilities (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). The probability associated with the Pillai-trace statistic, which represents the summed effect of each predictor over the three ordination axes is given. PA – presence/absence data, QA – quantitative data.*

Plant Group	Site	Data type	Ordination axis	Explained variance	Clay content	Bases	Slope	R^2
Legume trees	Ducke	QA data	PCoA 1	0.26	0.27 ***	-0.08	0.08 **	0.75
			PCoA 2	0.09	-0.01	-0.02	0.07 *	0.24
			PCoA 3	0.07	0.01	-0.02	-0.03	0.03
			Pillai-trace		0	0.283	0.002	
		PA data	PCoA 1	0.23	-0.26 ***	0.07	-0.06 *	0.77
			PCoA 2	0.08	0.03	-0.07	0	0.12
			PCoA 3	0.08	-0.01	0	-0.03	0.03
			Pillai-trace		0	0.108	0.02	
	Uatumã	QA data	PCoA 1	0.22	0.43 **	-0.56 ***	-0.1	0.69
			PCoA 2	0.15	0.25	-0.33	0.07	0.15
			PCoA 3	0.08	-0.31	-0.45 *	0.3	0.41
			Pillai-trace		0	0	0.062	
		PA data	PCoA 1	0.21	0.51 ***	-0.54***	-0.04	0.74
			PCoA 2	0.12	0.26	0.39	0.02	0.15
			PCoA 3	0.08	0.06	-0.09	-0.1	0.03
			Pillai-trace		0	0	0.122	
Ferns	Ducke	QA data	PCoA 1	0.52	-0.38***	0.18 **	-0.05	0.71
			PCoA 2	0.11	-0.02	0.07	0.06	0.18
			PCoA 3	0.11	-0.01	-0.02	0	0.02
			Pillai-trace		0	-0.031	-0.17	
		PA data	PCoA 1	0.59	0.31 ***	-0.14 *	0	0.57

table 2 continued.

Plant Group	Site	Data type	Ordination axis	Explained variance	Clay content	Bases	Slope	R^2
Ferns		PA data	PCoA 2	0.15	-0.05	-0.01	-0.06	0.19
			PCoA 3	0.07	0.01	0.02	0.08 **	0.42
			Pillai-trace		0	-0.217	-0.001	
	Uatumã	QA data	PCoA 1	0.42	-0.21	-0.27 **	-0.03	0.3
			PCoA 2	0.21	0.08	-0.27 ***	-0.05	0.76
			PCoA 3	0.09	-0.07	-0.1	0.10 *	0.38
			Pillai-trace		0	0	-0.041	
		PA data	PCoA 1	0.35	-0.16	-0.24 **	-0.08	0.34
			PCoA 2	0.18	-0.02	0.20 ***	-0.03	0.62
			PCoA 3	0.12	0.11	-0.05	-0.07	0.5
			Pillai-trace		0	0	-0.043	

The third axis was also significantly related to cation centent. Many species did not occur in the more fertile plots, while most species occurring in these plots also occurred in other values of the gradient, although with lower abundances (Fig. 2d). A group of 48 species of legume trees (56.4% of all species with more than one individual) occurred only in plots where clay content is below 80%, being absent in plateaus (Fig. 2c). Over both sites, legume trees had a wider distribution range over all gradients than ferns.

TERRESTRIAL FERNS COMPOSITION AND COMMUNITY STRUCTURE – We found 2401 fern individuals in Ducke and 708 in Uatumã. Twenty one species were found in Ducke, and *Trichomanes pinnatum* Hedw. was the most abundant (48% of all individuals). In Uatumã we found 41 species and three morphotypes, and *Selaginella pedata* Klotzsch accounted for 13.84% of the total individuals in this site (Apêndice).

For the fern community in Ducke, both the quantitative and qualitative data sets had the first ordination axis significantly related with the clay content, followed by soil fertility (Table 2). Several species were restricted to very sandy plots and the three most abundant species are distributed over almost the entire gradient of clay content, but with higher abundances in clayey plots (Fig. 3a-b). In Uatumã, soil fertility was the only environmental factor significantly related to the first two axes of community structure (Table 2). About 16 species were restricted to six plots with the highest soil fertility (Fig. 3c). Most species of Rebio Uatumã did not occur in high clay content plots, which housed about 11 species (Fig. 3d).

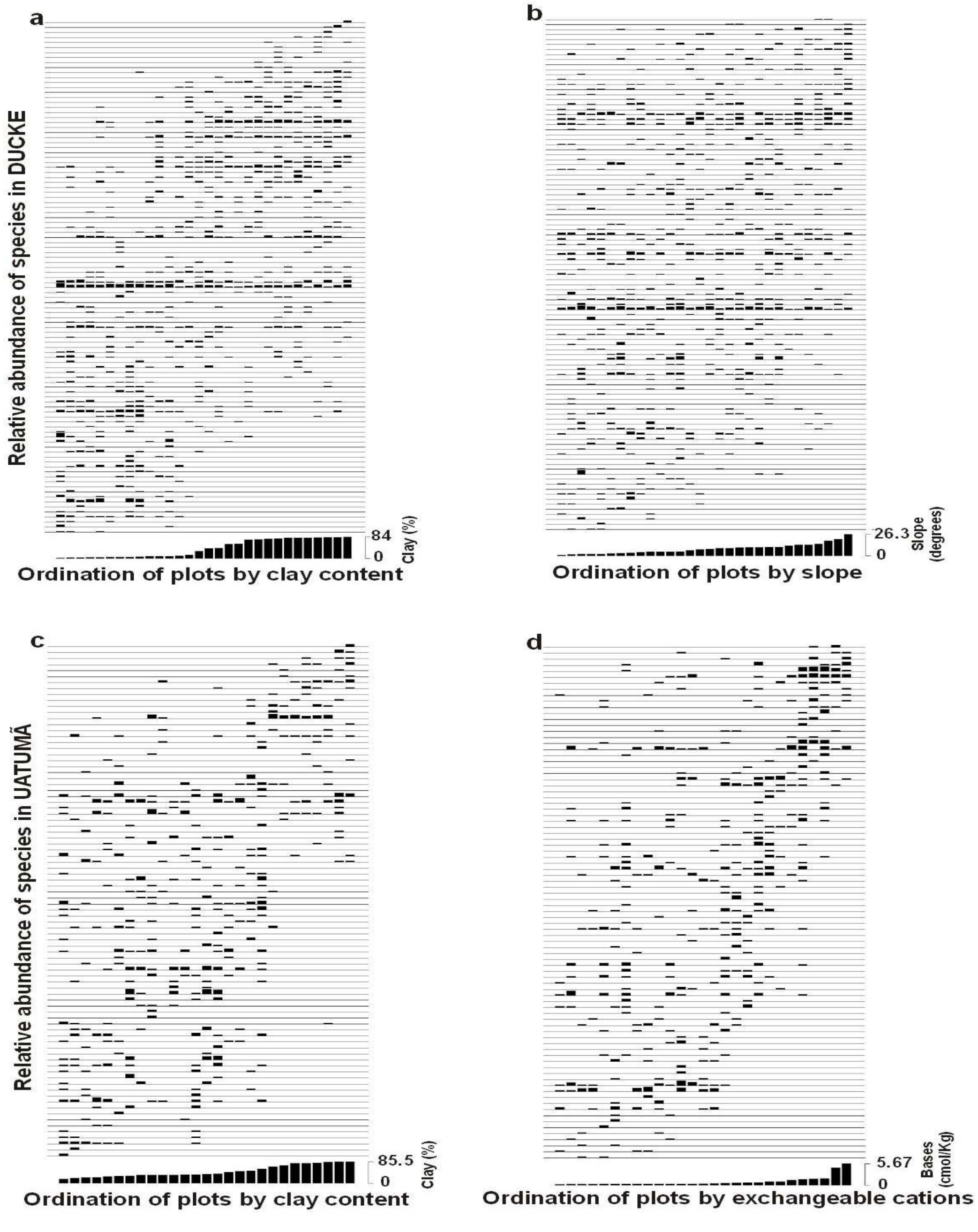

FIGURE 2: Distribution of legume tree species with more than one individual sampled in Ducke (a - b) and Uatumã (c – d) along the most important environmental predictors for their distributions. The relative abundances were standardized in log-scale, and names were supressed for better visualization.

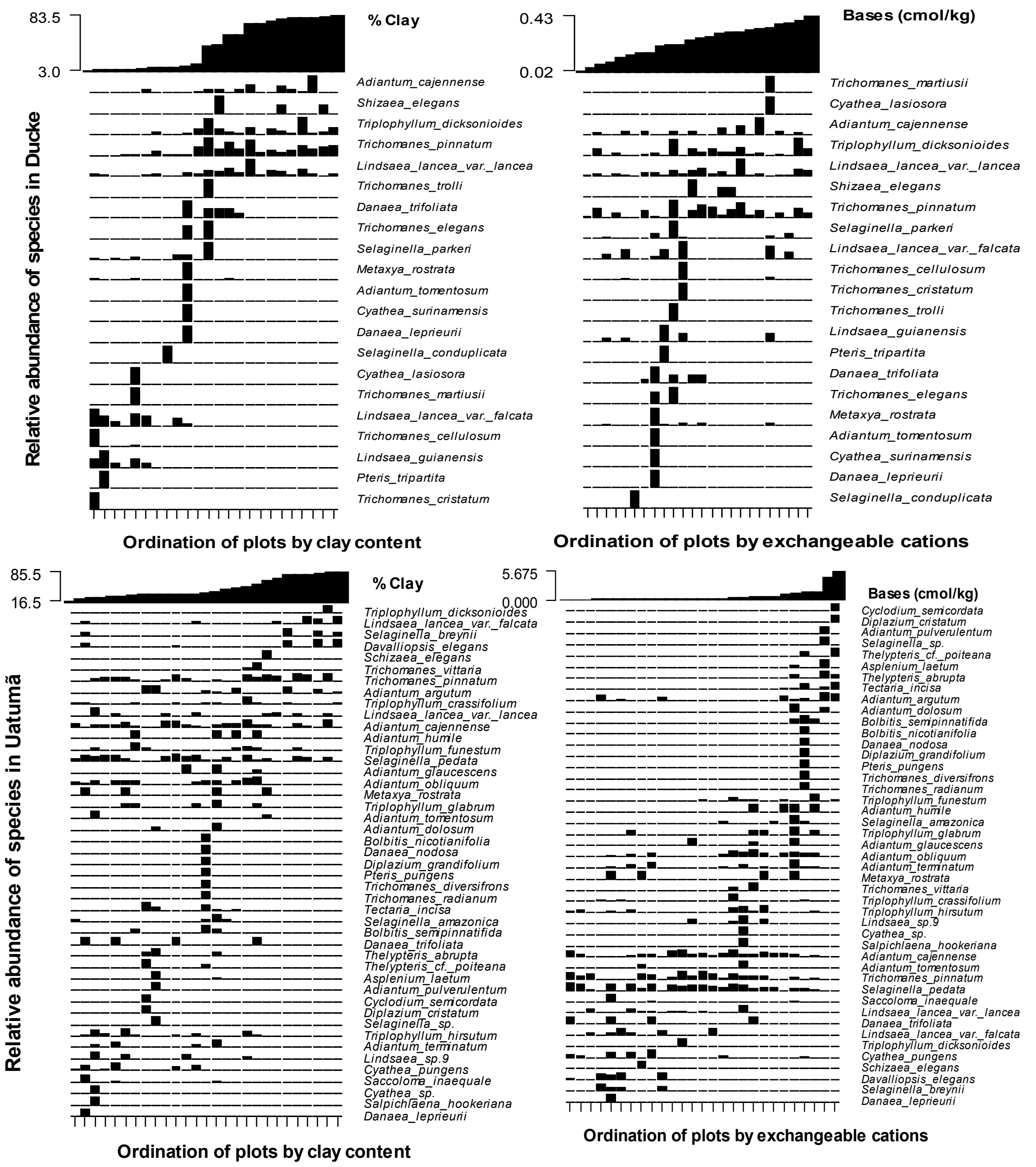

FIGURE 3: Distribution of terrestrial ferns sampled in Ducke (a - b) and Uatumã (c – d) along the most important environmental predictors for their distributions.

AUTOCORRELATION – There was no significant autocorrelation in the residuals of the models for trees, both in Ducke and Uatumã, and for ferns in Ducke. Residuals were autocorrelated in the first distance class for ferns in Uatumã (Moran I = 0.21, p= 0.003). This autocorrelation was also present in the same distance class for both the response (compositional NMDS axis) and the predictor variables ($p < 0.01$ in all cases).

HIERARCHY OF FACTORS AT THE MESOSCALE FOR LEGUME TREES – In the Ducke Reserve, the first division of the regression tree was produced by the clay content (Fig. 4a). A second branch of the tree within the clayey plots segregated the more inclined (slope > 11.5º) from less inclined plots. The MRT was based on nine ordination axes, which totaled 72% of explained variance. In Uatumã, the sum of exchangeable bases was responsible for the first division of the tree (Fig. 4c). The second branch was also given by bases and only within the group of less fertile plots slope segregated more inclined (>15º) from less inclined plots. In this MRT eight ordination axes were used, which totaled 72% of variance explained.

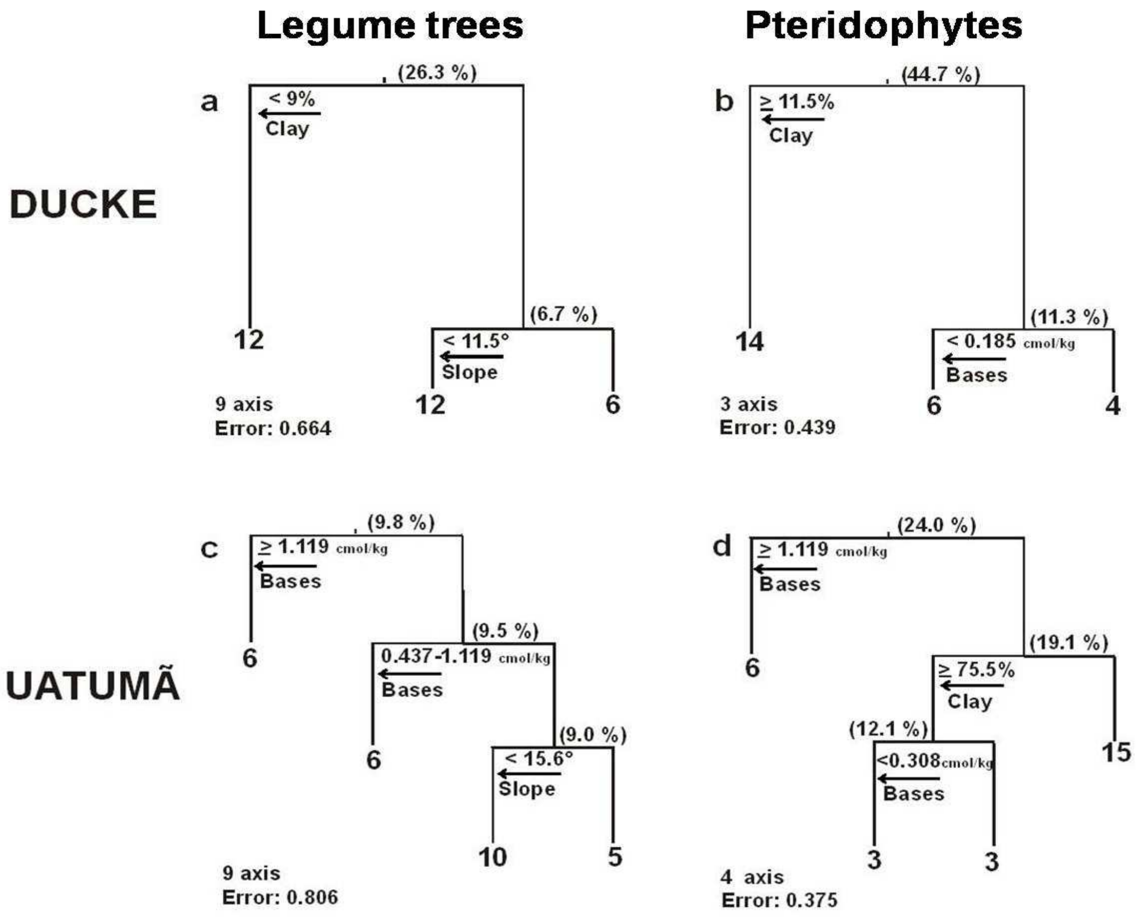

FIGURE 4: Multivariate Regression Trees (MRT) for the four plant communities studied. (a) Ducke legume trees, (b) Ducke terrestrial ferns, (c) Uatumã legume trees and (d) Uatumã terrestrial ferns. Values at the end of the branches are the number of plots in that branch. Values in parentheses are the percentage of improvement given by each bifurcation. The bottom of the tree shows the number of PCoA axis necessary to achieve at least 70 % of variance explained, which were used as response variables, and the error, which is the variance not explained by the tree.

HIERARCHY OF FACTORS AT THE MESOSCALE FOR TERRESTRIAL FERNS AND LYCOPHYTES – The first division of the regression tree for ferns at Ducke was determined by clay content, followed by soil fertility (Fig. 4b). Three axes of ordination that together explained 74% of the variance in species composition were used. In Uatumã, the sum of exchangeable bases was responsible for the first division of the regression tree (Fig. 4d). The second division was generated by the clay content in the soil and within high clay plots (≥ 75.5%) a third branch distinguished again plots by soil fertility. This MRT used four ordination axes that together explained 71% of variance in community structure.

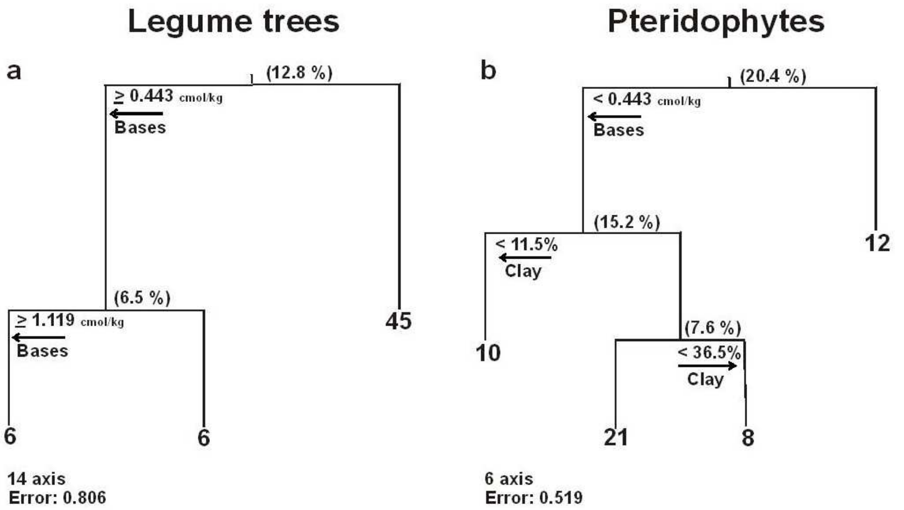

FIGURE 5: Multivariate Regression Trees (MRT) for both taxonomic plant groups at the regional scale. (a) legume trees and (b) terrestrial ferns. All additional information is the same as in Figure 4.

HIERARCHY OF FACTORS AT THE REGIONAL SCALE – The regional legume tree MRT had its first bifurcation determined by the sum of exchangeable bases (Fig. 5a), and the second bifurcation was also determined by soil fertility. Fourteen ordination axes, which totaled 71% of explained variance, were used to construct the tree. The regional fern MRT had its first division also determined by the sum of bases (Fig. 5b). Clay content was responsible for another branch within less fertile plots, separating very sandy (<11.5% clay) from more clayey plots, and a third bifurcation was also determined by clay content. This regression tree used six axes of ordination, which explained 73% of variance in community structure.

DISCUSSION

FLORISTIC VARIATION DEPENDS ON THE LENGTH OF GRADIENT, MORE THAN ON GEOGRAPHICAL SCALE – The influence of environmental predictors varied considerably between study areas and the main predictors of composition in each area were those with the longest gradients. In the Ducke Reserve, both ferns and legume trees responded more strongly to the soil texture gradient, represented by the percentage of clay. These results are consistent with previous studies, both for the composition of herbs (Costa *et al*. 2005, Drucker *et al*. 2005, Zuquim *et al*. 2009), palms (Costa *et al*. 2009) and shrubs (Bernardes & Costa 2011, Kinnup & Magnusson 2005) and the woody vegetation structure (de Castilho *et al*. 2006), where soil texture or a related variable (altitude) was the factor that best explained community patterns. The soil fertility had little or no influence on patterns found in these studies. The diversity of soils in the Amazon are mainly related to differences in geology and geomorphology (Quesada *et al*. 2009). However, most of the central Amazonia is derived from old to very old geological formations, and so are dominated by sandy to clayey ferrassols which had underwent long periods of leaching and are generally low in nutrients (Chauvel *et al.* 1987, Quesada *et al*. 2011). The range of variation of soil fertility in most of the central Amazon is low when the high fertility spots associated with special geological formations are not included.

In Uatumã, terrestrial ferns and legume trees responded more strongly to the gradient of soil fertility, represented by the sum of exchangeable bases. The distribution patterns of plant communities in Uatumã were more similar to those found in the western Amazon, where fertile soils are more common (Duivenvoorden 1995, Duque *et al*. 2002, Ruokolainen *et al.*

2007, Tuomisto *et al*. 1995, 2002). Tuomisto & Poulsen (1996) classified several fern species of this region as fertile soils specialists. However, although predominantly fertile, the sites studied in western Amazonia had also a large amplitude of variation in the amount of exchangeable bases, e.g from 1.16 to 27.3 cmol/kg in some areas of the Ecuadorian Amazon studied by Tuomisto *et al*. (2002).

Although the main determinants in the mesoscale differed between sites, at the regional scale, soil fertility was the main predictor for both groups of plants studied. The floristic separation caused by high fertility plots was stronger than the effect of the 120 km distance separating the two study sites. Our results, as well as possibly those of several studies in western Amazonia, are consistent with the hypothesis that the length of the gradient analyzed is crucial in determining which factors will be recognized as most important in structuring plant communities, as suggested by Vormisto *et al*. (2000) and Costa *et al*. (2009). Furthermore, although it is expected that an increase in the size of the area will increase environmental heterogeneity, this relationship is not always linear and this study makes it clear, since both areas studied had the same size (25 km^2) and the same spatial distribution of plots, but the heterogeneity of the soil varied greatly between them. Thus, the simple control of the experimental design in terms of the extent of the study area, number and spatial distribution of samples is not enough to ensure that the "true" determinants of community structure will be detected, since these depend intrinsically on the spatial structure of the environmental variation in the landscape.

FLORISTIC PATTERNS FOR TREES AND FERNS ARE CONGRUENT.– The main factors determining community composition were the same for ferns and legume trees, irrespective of the spatial scale. This is in accordance with results from studies in western Amazonia (Ruokolainen *et al.* 2007). Therefore, these disparate plant groups have congruent responses to the main gradients, but the main predictors of their floristic patterns differ depending on the landscape context, as discussed in the previous sections. It is not possible to directly generalize this congruence to other plant groups, since some gradients may not be relevant to them. Ephiphytes, for example, are largely independent of the soil, and therefore not expected to vary according to soil gradients. However, a mesoscale study has shown a high congruence of floristic patterns between 15 taxonomic plant groups in central Amazonia, including herbs, shrubs, trees and lianas (Landeiro *et al. in press*), suggesting that terrestrial tropical plants are controlled by the same main gradients in each landscape. This does not implies that their response to the secondary gradients are also similar, and this variation seem to be linked to their particular evolutionary strategies.

COMMUNITIES ARE STRUCTURED HIERARCHICALY – Multivariate regression trees revealed that the studied environmental variables interact, creating a hierarchical organization of communities. In the mesoscale, when the soils are relatively nutrient-poor, soil texture is the most important predictor, determining a group of species associated with very sandy bottomlands and another with clayey soils. Slope was important for trees within sandier areas. It seems that after the restriction imposed by the most important soil characteristics, possibly linked to the physiological requirements of species, there is a restriction on the ability of trees to attach to the soil. Several bottomland tree species have adaptations that optimize attachment to the soil, which is less consolidated, such as buttresses and anchoring roots (Ribeiro *et al.* 1999) and this can be a selective pressure for the occupation of such environments. The MRTs of legume trees at Ducke segregated the typical topographic classes recognized in central Amazonian landscapes, the plateaus, slopes and bottomlands, and in some other amazonian sites (Valencia *et al.* 2004). Although Jones *et al.* (2008) in Costa Rica have shown that ferns associated with bottomlands respond mainly to drainage conditions or humid air, an important division in the fern composition at Ducke occured within sandier areas, according to fertility. This suggests that there is still a finer niche segregation within this environment. Additionally, as in the present study, Jones *et al*. (2006) found little variation in the composition of ferns in plateau areas in Costa Rica.

If the amplitude of variation in soil fertility is high, the sum of exchangeable bases becomes the most important predictor in the mesoscale, as it determines compositional groups associated with more fertile or low fertility soils. This is reinforced by the fact that regression trees have separated in their first division, for both trees and ferns, the same group of the six most fertile Uatumã plots. When soil fertility is high, a group of species of ferns is separated clearly from the others. On the other hand, within low fertility plots, the clay content becomes a determinant of compositional differences.

Our results for meso and regional scales show that the importance of soil texture and slope is nested within soil fertility gradient: when fertility is high, other soil aspects are less relevant for community structuring, but when soil fertility is low, soil texture and terrain slope will be the largest determinants of plant community structure. Moreover, ferns and trees had similar responses to environmental heterogeneity, indicating that our results can be extrapolated for many others biological or functional groups.

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CONCLUSÕES

Nós vimos que a distribuição das espécies ocorre de maneira não linear ao longo dos gradientes ambientais estudados e que existem grupos de espécies que aparentam alguma preferência por valores extremos dentro da amplitude de variação ambiental. Além disso, os efeitos da fertilidade do solo e topografia ou textura do solo são hierarquicamente estruturados. Quando a fertilidade possui uma amplitude maior, ela terá um maior efeito sobre a estrutura da comunidade, caso contrário, ela pode ser subordinada à topografia. Quando a fertilidade do solo é alta, a composição é diferente devido a um grupo de espécies que é restrita a tais condições e mostramos que dentro dessa condição nenhum outro fator considerado no presente estudo afeta a composição. Por outro lado, quando a fertilidade é baixa, outros fatores ambientais entram em cena e causam o surgimento de outros grupos composicionais. Isso demonstra que é possível que além de algumas variáveis serem importantes apenas dentro de certos valores da variável principal, estas podem ser a causa de diversos padrões composicionais observados, que não o principal. Neste estudo, fica claro que se deve ter muita precaução ao generalizar tais padrões sem levar em conta que a heterogeneidade das paisagens pode mudar de maneira imprevista e que mudanças abruptas na composição florística de diversos grupos de plantas não podem ser detectadas com confiabilidade sem dados finos que podem apenas ser coletados *in situ,* a fim de se obter uma melhor resolução da heterogeneidade ambiental.

APÊNDICES

Apêndice A - Lista das espécies de leguminosas arbóreas e suas abundâncias em cada área de estudo.

Espécie	Autor	Ocorrência	Abundância
Abarema adenophora	(Ducke) Barneby & J.W. Grimes	RFAD	13
Abarema cochleata	(Willd.) Barneby & J.W. Grimes	RFAD	1
Abarema curvicarpa var. rodriguesii	Barneby & J.W. Grimes	RBU	1
Abarema floribunda	(Spruce ex Benth.) Barneby & J.W. Grimes	RFAD / RBU	1 / 1
Abarema jupunba	(Willd.) Urb.	RFAD / RBU	7 / 4
Abarema mataybifolia	(Sandwith) Barneby & J.W. Grimes	RFAD / RBU	1 / 3
Abarema piresii	Barneby & J.W.Grimes	RFAD / RBU	3 / 2
Albizia duckeana	L. Rico	RFAD	2
Albizia pedicellaris	(DC.) L. Rico	RFAD	1
Andira micrantha	Ducke	RFAD / RBU	59 / 5
Andira parviflora	Ducke	RFAD / RBU	6 / 1
Andira surinamensis	(Bondt) Splitg. ex Pulle	RBU	3
Andira unifoliolata	Ducke	RFAD / RBU	16 / 5
Batesia floribunda	Spruce ex Benth.	RFAD / RBU	1 / 2
Bocoa viridiflora	(Ducke) R.S. Cowan	RFAD / RBU	42 / 25
Calliandra surinamensis	Benth.	RFAD	3
Cassia fastuosa	Willd. ex Benth.	RBU	1
Cassia rubriflora	Ducke	RFAD	9
Cedrelinga cateniformis	Ducke (Ducke)	RFAD / RBU	7 / 10
Chamaecrista adiantifolia	(Spruce ex Benth.) H.S. Irwin & Barneby	RFAD	4
Chamaecrista negrensis	(H.S. Irwin) H.S. Irwin & Barneby	RFAD	1
Clitoria amazonum	Mart. ex Benth.	RBU	3
Copaifera multijuga	Hayne	RFAD	11
Dipterix magnífica	Ducke	RFAD / RBU	9 / 3
Dipterix odorata	(Aubl.) Willd.	RFAD / RBU	16 / 5
Dipterix polyphylla	Huber	RFAD	2
Dipterix punctata	Frag. & Cif.	RFAD / RBU	13 / 1
Cynometra marginata	Benth.	RBU	4
Dialium guianense	(Aubl.) Sandwith	RFAD / RBU	15 / 5
Dicorynia paraensis	(Ducke) R. Koeppen	RBU	1
Dimophandra parviflora	Spruce ex Benth.	RFAD / RBU	5 / 1
Dimorphandra pennigera	Tul.	RFAD	5
Dinizia excelsa	Ducke	RFAD / RBU	6 / 1
Diplotropis martiusii	Benth.	RFAD	1
Diplotropis triloba	Gleason	RFAD / RBU	6 / 1
Elizabetha speciosa	Ducke	RFAD	6
Enterolobium schomburgkii	(Benth.) Benth.	RFAD / RBU	6 / 3
Eperua duckeana	R.S. Cowan	RFAD	54
Eperua glabriflora	(Ducke) R.S. Cowan	RFAD	178
Hymenaea courbaril	L.	RBU	2
Hymenaea intermedia	Ducke	RFAD / RBU	5 / 1
Hymenaea oblingifolia	Huber	RBU	1
Hymenaea parvifolia	Huber	RFAD / RBU	3 / 1
Hymenaea reticulata	Ducke	RFAD / RBU	4 / 1
Hymenolobium excelsum	Ducke	RFAD	1
Hymenolobium heterocarpum	Ducke	RFAD	2
Hymenolobium modestum	Ducke	RFAD	6
Hymenolobium pulcherrimum	Ducke	RBU	1
Hymenolobium sericeum	Ducke	RFAD / RBU	3 / 1
Inga alba	(Sw.) Willd.	RFAD / RBU	3 / 25

Apêndice A – continuação

Espécie	**Autor**	**Ocorrência**	**Abundância**
Inga auristellae	Harms	RBU	12
Inga bicoloriflora	Ducke	RFAD	18
Inga capitata	Desv.	RFAD / RBU	2 / 4
Inga cayennensis	Sagot ex Benth.	RFAD	1
Inga chrysantha	Ducke	RFAD	3
Inga cordatoalata	Ducke	RFAD / RBU	1 / 4
Inga edulis	Mart.	RBU	28
Inga fagifolia	(L.) Willd. ex Benth.	RFAD / RBU	13 / 7
Inga glomeriflora	Ducke	RFAD	1
Inga gracilifolia	Ducke	RFAD	22
Inga grandiflora	Wall.	RFAD / RBU	2 / 2
Inga huberi	Ducke	RBU	12
Inga lateriflora	Miq.	RFAD / RBU	7 / 21
Inga leiocalycina	Benth.	RFAD / RBU	6 / 7
Inga longiflora	Benth.	RBU	2
Inga macrophylla	Humb. & Bonpl. Ex Willd.	RFAD / RBU	1 / 5
Inga marginata	Kunth	RFAD / RBU	1 / 5
Inga melinonis	Sagot	RFAD / RBU	2 / 15
Inga obidensis	Ducke	RFAD / RBU	1 / 1
Inga oerstediana	Benth. Ex Seem.	RFAD	10
Inga pezizifera	Benth.	RFAD / RBU	2 / 5
Inga rhynchocalyx	Sandwith	RFAD / RBU	2 / 7
Inga rubiginosa	(Rich.) DC.	RFAD / RBU	1 / 10
Inga splendens	Willd.	RBU	2
Inga stipularis	DC.	RBU	3
Inga suberosa	T.D. Penn.	RFAD / RBU	1 / 3
Inga thibaudiana	DC.	RFAD / RBU	4 / 11
Inga umbellifera	(Vahl) Steud.	RFAD / RBU	4 / 7
Macrolobium angustifolium	(Benth.) R.S. Cowan	RBU	3
Macrolobium arenarium	Ducke	RFAD	3
Macrolobium limbatum	Spruce ex Benth.	RFAD / RBU	35 / 8
Macrolobium microcalyx	Ducke	RFAD	2
Macrolobium multijugum	(DC.) Benth.	RFAD	3
Macrolobium suaveolens	Spruce ex Benth.	RFAD / RBU	9 / 5
Monopteryx inpae	W.A. Rodrigues	RFAD	5
Ormosia grandiflora	(Tul.) Rudd	RFAD / RBU	3 / 2
Ormosia grossa	Rudd	RFAD	6
Ormosia paraensis	Ducke	RFAD / RBU	4 / 1
Parkia decussata	Ducke	RBU	2
Parkia igneiflora	Ducke	RFAD	3
Parkia multijuga	Benth.	RFAD / RBU	2 / 5
Parkia nítida	Miq.	RFAD / RBU	4 / 4
Parkia panurensis	Benth. ex H.C. Hopkins	RFAD	7
Parkia pendula	(Willd.) Benth. ex Walp.	RFAD / RBU	4 / 2
Parkia velutina	Benoist	RFAD / RBU	9 / 5
Peltogyne catingae	Ducke	RFAD	3
Peltogyne excelsa	Ducke	RFAD	6
Peltogyne paniculata	Benth	RFAD / RBU	6 / 2
Platymiscium trinitatis	Benth.	RBU	8
Pseudopiptadenia psilostachya	(DC.) G. P. Lewis & M. P. Lima	RFAD / RBU	11 / 17
Pterocarpus officinalis	Jacq.	RFAD / RBU	11 / 35
Pterocarpus rohrii	Vahl	RFAD / RBU	9 / 2
Pterocarpus santalinoides	L'HÃ©r. ex DC.	RBU	1
Sclerolobium melanocarpum	Ducke	RFAD / RBU	13 / 12
Stryphnodendron guianense	(Aubl.) Benth.	RFAD / RBU	10 / 5
Stryphnodendron paniculatum	Poepp.	RFAD / RBU	3 / 2

Apêndice A – continuação

Espécie	Autor	Ocorrência	Abundância
Stryphnodendron pulcherrimum	(Willd.) Hochr.	RFAD	1
Stryphnodendron racemiferum	(Ducke) W.A. Rodrigues	RFAD / RBU	13 / 2
Swartzia arborescens	(Aubl.) Pittier	RFAD / RBU	5 / 1
Swartzia brachyrachis	Harms	RFAD	1
Swartzia corrugata	Benth.	RFAD / RBU	8 / 4
Swartzia cuspidata	Spruce ex Benth.	RFAD	4
Swartzia ingifolia	Ducke	RFAD / RBU	15 / 1
Swartzia lamellata	Ducke	RFAD	26
Swartzia longistipitata	Ducke	RFAD	5
Swartzia oblanceolata	Sandwith	RFAD / RBU	7 / 2
Swartzia panacoco	(Aubl.) R.S. Cowan	RFAD / RBU	6 / 2
Swartzia polyphylla	DC.	RFAD	20
Swartzia recurva	Poepp.	RFAD / RBU	45 / 1
Swartzia reticulata	Ducke	RFAD	37
Swartzia schomburgkii	Benth.	RFAD / RBU	31 / 11
Swartzia tessmannii	Harms	RFAD	2
Swartzia tomentifera	(Ducke) Ducke	RFAD / RBU	10 / 14
Swartzia ulei	Harms	RFAD	15
Tachigali cf. myrmecophila	(Ducke) Ducke	RFAD / RBU	1 / 5
Tachigali chrysophylla	(Poepp.) Zarucchi & Herend.	RFAD / RBU	4 / 2
Tachigali plumbea	Ducke	RBU	20
Tachigali micropetala	(Ducke) Zarucchi & Pipoly	RFAD / RBU	7 / 9
Tachigali setifera	(Ducke) Zarucchi & Herend.	RFAD	14
Tachigali venusta	Dwyer	RFAD	11
Taralea oppositifolia	Aubl.	RFAD / RBU	23 / 3
Vatairea paraensis	Ducke	RFAD	14
Vatairea sericea	(Ducke) Ducke	RFAD / RBU	12 / 1
Vouacapoua pallidior	Ducke	RFAD	9
Zygia racemosa	(Ducke) Barneby & J.W. Grimes	RFAD / RBU	70 / 30
Zygia ramiflora	(F. Muell.) Kosterm.	RFAD / RBU	13 / 12

Apêndice B - Lista das espécies de pteridófitas terrestres e suas abundâncias em cada área de estudo.

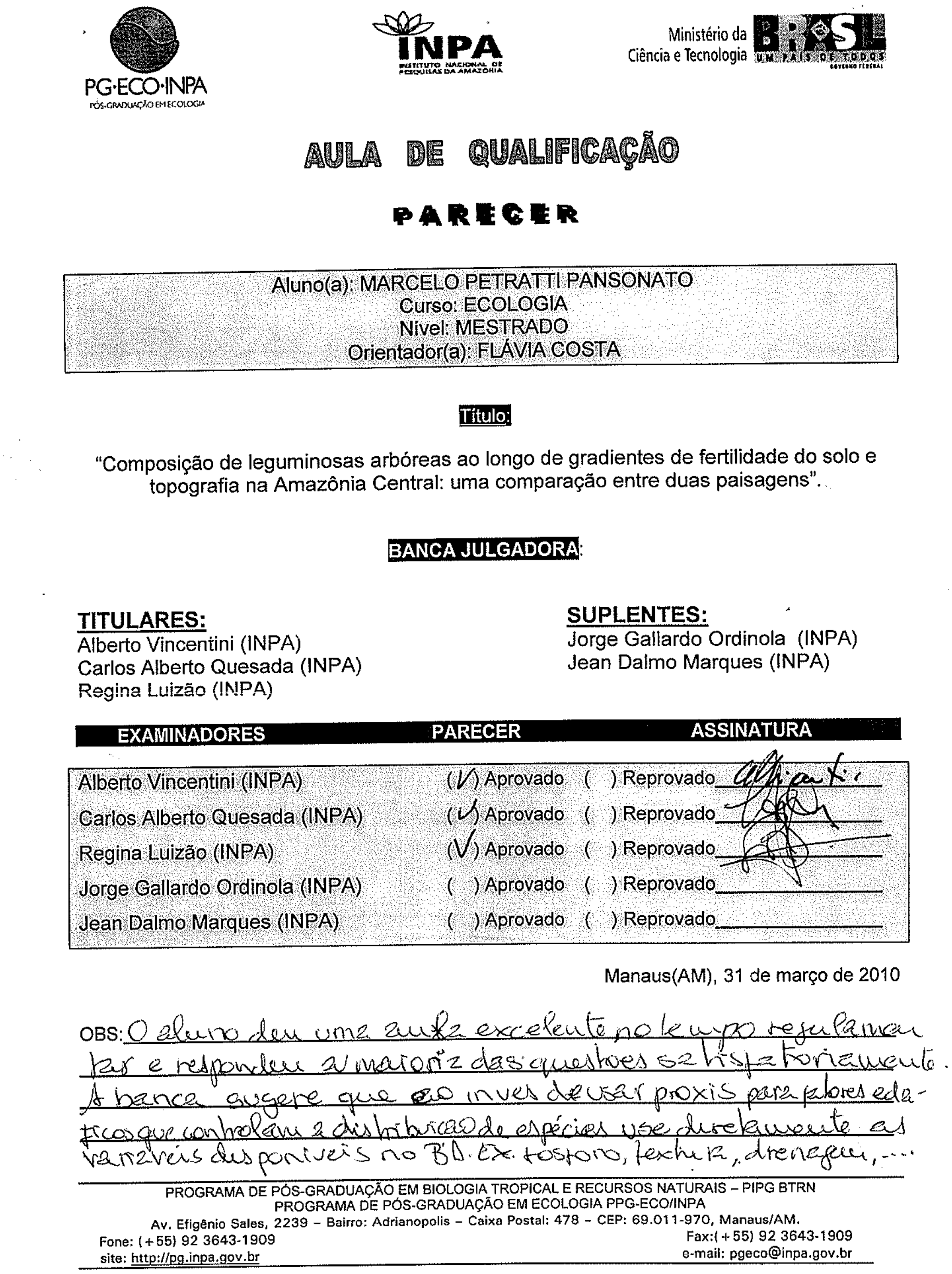
Espécie	Autor	Ocorrência	Abundância
Adiantum argutum	Splitg.	RBU	29
Adiantum cajennense	Willd.	RFAD / RBU	31 / 55
Adiantum dolosum	Kunze	RBU	3
Adiantum glaucescens	Klotzsch	RBU	5
Adiantum humile	Kunze	RBU	4
Adiantum obliquum	Willd.	RBU	41
Adiantum pulverulentum	L.	RBU	3
Adiantum terminatum	Kunze ex Miq.	RBU	23
Adiantum tomentosum	Klotzsch	RFAD / RBU	1 / 3
Asplenium laetum	Sw.	RBU	7
Bolbitis nicotianifolia	(Sw.) Alston	RBU	3
Bolbitis semipinnatifida	(Fée) Alston	RBU	4
Cyathea lasiosora	(Kuhn) Domin	RFAD	3
Cyathea pungens	(Willd.) Domin	RBU	37

Apêndice B - continuação

Espécie	**Autor**	**Ocorrência**	**Abundância**
Cyathea surinamensis	(Miq.) Domin	RFAD	3
Cyclodium semicordata	(Sw.) J. Sm.	RBU	6
Danaea leprieurii	(L.) Sm.	RFAD / RBU	1 / 3
Danaea nodosa	(L.) Sm.	RBU	1
Danaea trifoliata	Reichenb.	RFAD / RBU	11 / 4
Davalliopsis elegans	(Rich.) Copel.	RBU	44
Diplazium cristatum	(Desr.) Alston	RBU	2
Diplazium grandifolium	Sw.	RBU	2
Lindsaea guianensis	(Aubl.) Dryand.	RFAD	10
Lindsaea lancea var. falcata	(Dryand.) Hieron.	RFAD / RBU	26 / 11
Lindsaea lancea var. lancea	(L.) Bedd.	RFAD / RBU	168 / 13
Metaxya rostrata	(Kunth) C. Presl.	RFAD / RBU	33 / 4
Pteris pungens	Willd.	RBU	2
Pteris tripartita	Sw.	RFAD	1
Saccoloma inequale	(Kunze) Mett.	RBU	9
Salpichlaena hookeriana	(Kuntze) Alston	RBU	1
Schizaea elegans	(Vahl) Sw.	RFAD / RBU	4 / 2
Selaginella amazonica	Spring	RBU	6
Selaginella breynii	Spring	RBU	30
Selaginella conduplicata	Spring	RFAD	8
Selaginella parkeri	(Hook. & Grey.) Spring	RFAD	89
Selaginella pedata	Klotzsch	RBU	142
Tectaria incisa	Cav.	RBU	19
Thelypteris abrupta	(Desv.) Proctor	RBU	4
Thelypteris cf. poiteana	(Bory) Proctor	RBU	3
Trichomanes cellulosum	Klotszch	RFAD	46
Trichomanes cristatum	Kaulf.	RFAD	3
Trichomanes diversifrons	(Bory) Mett. ex Sadeb.	RBU	3
Trichomanes elegans	Rich.	RFAD	19
Trichomanes martiusii	C. Presl.	RFAD	2
Trichomanes pinnatum	Hedw.	RFAD / RBU	1153 / 98
Trichomanes radianum	Presl	RBU	7
Trichomanes trolli	Bergdolt	RFAD	3 / 2
Trichomanes vittaria	DC. ex Poir.	RBU	4
Triplophyllum crassifolium	Holttum	RBU	20
Triplophyllum dicksonioides	(Fée) Holttum	RFAD / RBU	786 / 1
Triplophyllum funestum	Kunze) Holttum	RBU	11
Triplophyllum glabrum	J. Prado & R. C. Moran	RBU	6
Triplophyllum hirsutum	(Holttum) J. Prado & R. C. Moran	RBU	20

ANEXOS:

Anexo A - Ata da Aula de Qualificação



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AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): MARCELO PETRATTI PANSONATO
Curso: ECOLOGIA
Nível: MESTRADO
Orientador(a): FLÁVIA COSTA

Título:

"Composição de leguminosas arbóreas ao longo de gradientes de fertilidade do solo e topografia na Amazônia Central: uma comparação entre duas paisagens".

BANCA JULGADORA:

TITULARES:
Alberto Vincentini (INPA)
Carlos Alberto Quesada (INPA)
Regina Luizão (INPA)

SUPLENTES:
Jorge Gallardo Ordinola (INPA)
Jean Dalmo Marques (INPA)

EXAMINADORES	PARECER		ASSINATURA
Alberto Vincentini (INPA)	(✓) Aprovado	( ) Reprovado	
Carlos Alberto Quesada (INPA)	(✓) Aprovado	( ) Reprovado	
Regina Luizão (INPA)	(✓) Aprovado	( ) Reprovado	
Jorge Gallardo Ordinola (INPA)	( ) Aprovado	( ) Reprovado	
Jean Dalmo Marques (INPA)	( ) Aprovado	( ) Reprovado	

Manaus(AM), 31 de março de 2010

OBS: O aluno deu uma aula excelente no tempo regulamentar e respondeu a maioria das questões satisfatoriamente. A banca sugere que ao invés de usar proxis para fatores edáficos que controlam a distribuição de espécies use diretamente as variáveis disponíveis no BD. Ex. fósforo, textura, drenagem, ...

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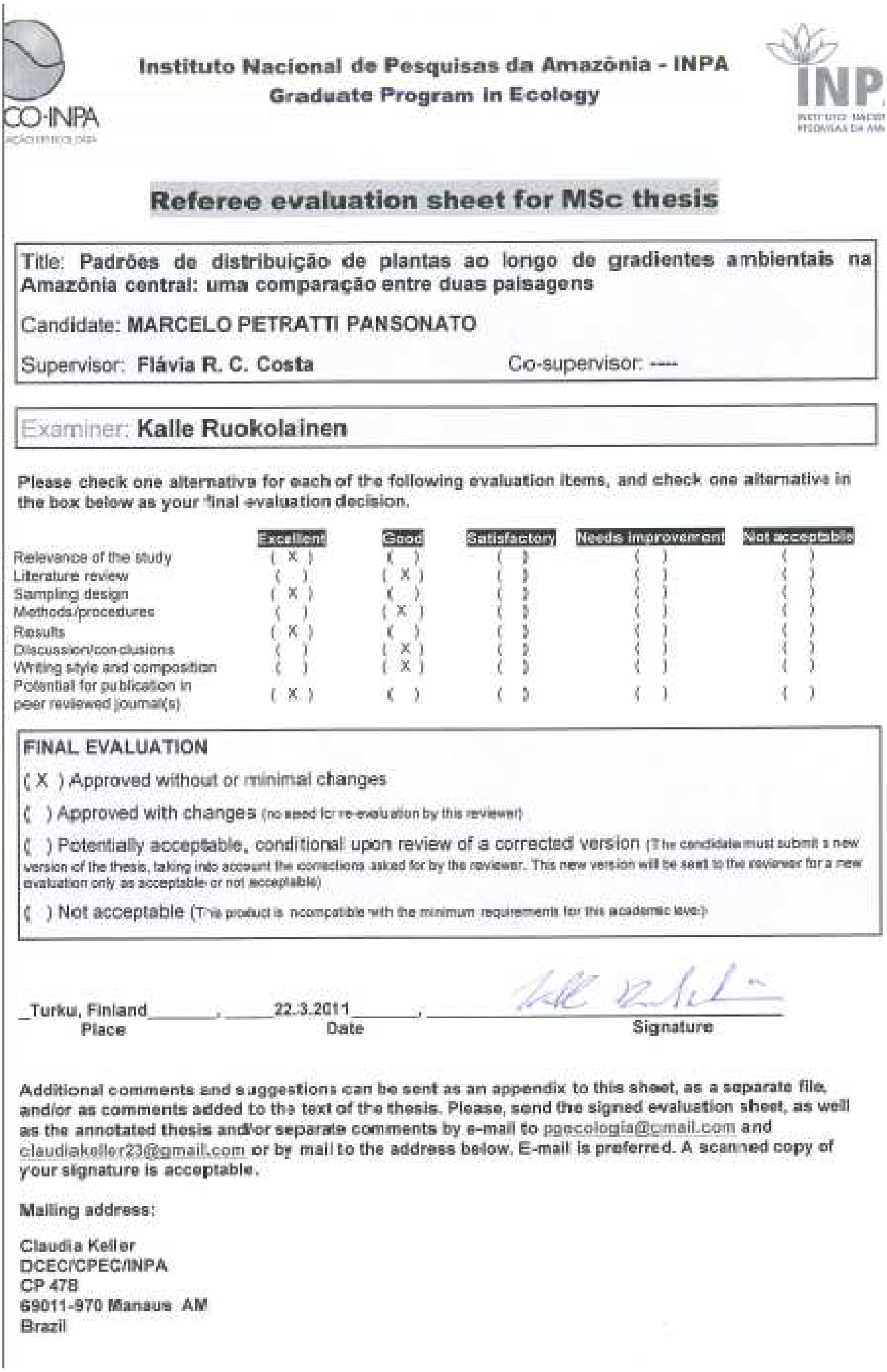
Anexo B - Parecer do avaliador do trabalho de conclusão Kalle Ruokolainen (Universidade de Turku – Finlândia)



Instituto Nacional de Pesquisas da Amazônia - INPA
Graduate Program in Ecology

Referee evaluation sheet for MSc thesis

Title: **Padrões de distribuição de plantas ao longo de gradientes ambientais na Amazônia central: uma comparação entre duas paisagens**

Candidate: **MARCELO PETRATTI PANSONATO**

Supervisor: **Flávia R. C. Costa** Co-supervisor: ----

Examiner: **Kalle Ruokolainen**

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Good	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	(X)	( )	( )	( )	( )
Literature review	( )	(X)	( )	( )	( )
Sampling design	(X)	( )	( )	( )	( )
Methods/procedures	( )	(X)	( )	( )	( )
Results	(X)	( )	( )	( )	( )
Discussion/conclusions	( )	(X)	( )	( )	( )
Writing style and composition	( )	(X)	( )	( )	( )
Potential for publication in peer reviewed journal(s)	(X)	( )	( )	( )	( )

FINAL EVALUATION

(X) Approved without or minimal changes

( ) Approved with changes (no need for re-evaluation by this reviewer)

( ) Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

( ) Not acceptable (This product is incompatible with the minimum requirements for this academic level)

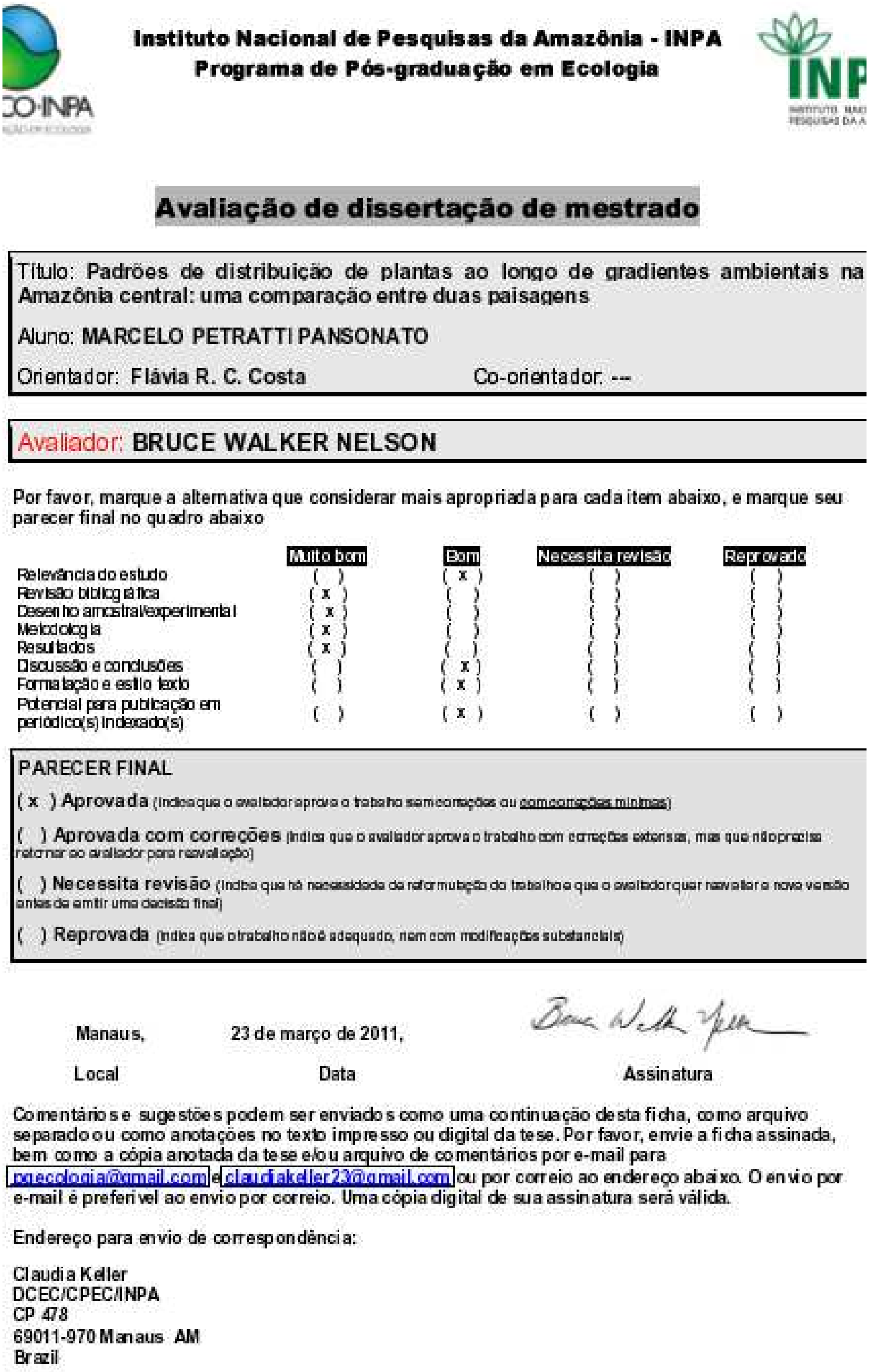
_Turku, Finland_______, _____22.3.2011_______, ______________________
Place Date Signature

Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to pgecologia@gmail.com and claudiakeller23@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.

Mailing address:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil

Anexo C- Parecer do avaliador do trabalho de conclusão Bruce Nelson (INPA)



Instituto Nacional de Pesquisas da Amazônia - INPA
Programa de Pós-graduação em Ecologia

Avaliação de dissertação de mestrado

Título: **Padrões de distribuição de plantas ao longo de gradientes ambientais na Amazônia central: uma comparação entre duas paisagens**

Aluno: **MARCELO PETRATTI PANSONATO**

Orientador: **Flávia R. C. Costa** Co-orientador: ---

Avaliador: **BRUCE WALKER NELSON**

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	( )	(x)	( )	( )
Revisão bibliográfica	(x)	( )	( )	( )
Desenho amostral/experimental	(x)	( )	( )	( )
Metodologia	(x)	( )	( )	( )
Resultados	(x)	( )	( )	( )
Discussão e conclusões	( )	(x)	( )	( )
Formatação e estilo texto	( )	(x)	( )	( )
Potencial para publicação em periódico(s) indexado(s)	( )	(x)	( )	( )

PARECER FINAL

(x) Aprovada (indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)

( ) Aprovada com correções (indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)

( ) Necessita revisão (indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)

( ) Reprovada (indica que o trabalho não é adequado, nem com modificações substanciais)

Manaus,	23 de março de 2011,	Bruce Walker Nelson
Local	Data	Assinatura

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

Claudia Keller
DCEC/CPEC/INPA
CP 478
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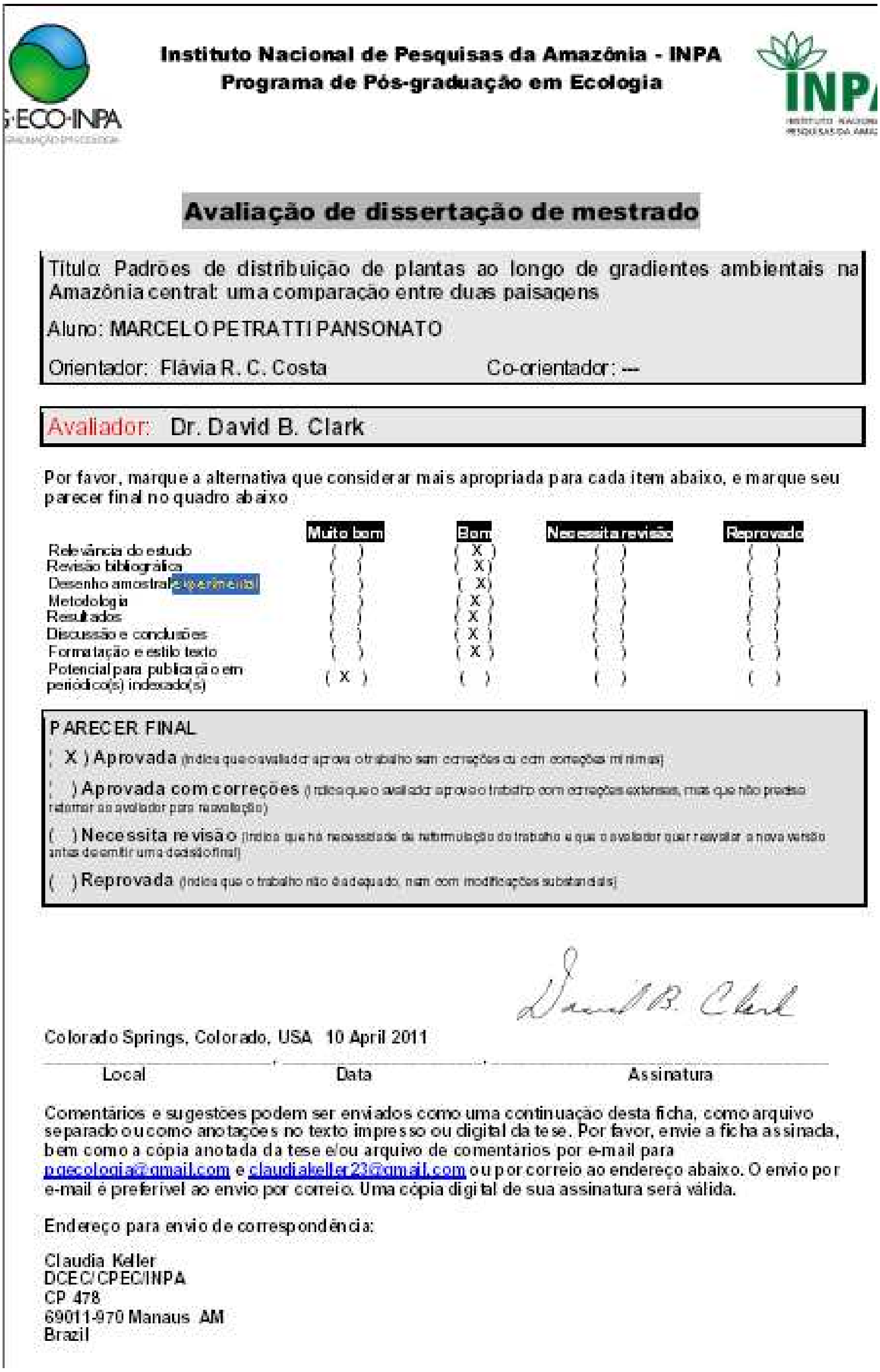
Brazil

Anexo D - Parecer do avaliador do trabalho de conclusão David Clark (Universidade do Missouri – EUA)



Instituto Nacional de Pesquisas da Amazônia - INPA
Programa de Pós-graduação em Ecologia

Avaliação de dissertação de mestrado

Título: Padrões de distribuição de plantas ao longo de gradientes ambientais na Amazônia central: uma comparação entre duas paisagens

Aluno: MARCELO PETRATTI PANSONATO

Orientador: Flávia R. C. Costa Co-orientador: ---

Avaliador: Dr. David B. Clark

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	( )	(X)	( )	( )
Revisão bibliográfica	( )	(X)	( )	( )
Desenho amostral/experimental	( )	(X)	( )	( )
Metodologia	( )	(X)	( )	( )
Resultados	( )	(X)	( )	( )
Discussão e conclusões	( )	(X)	( )	( )
Formatação e estilo texto	( )	(X)	( )	( )
Potencial para publicação em periódico(s) indexado(s)	(X)	( )	( )	( )

PARECER FINAL

(X) Aprovada (indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)

( ) Aprovada com correções (indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)

( ) Necessita revisão (indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)

( ) Reprovada (indica que o trabalho não é adequado, nem com modificações substanciais)

Colorado Springs, Colorado, USA 10 April 2011 David B. Clark

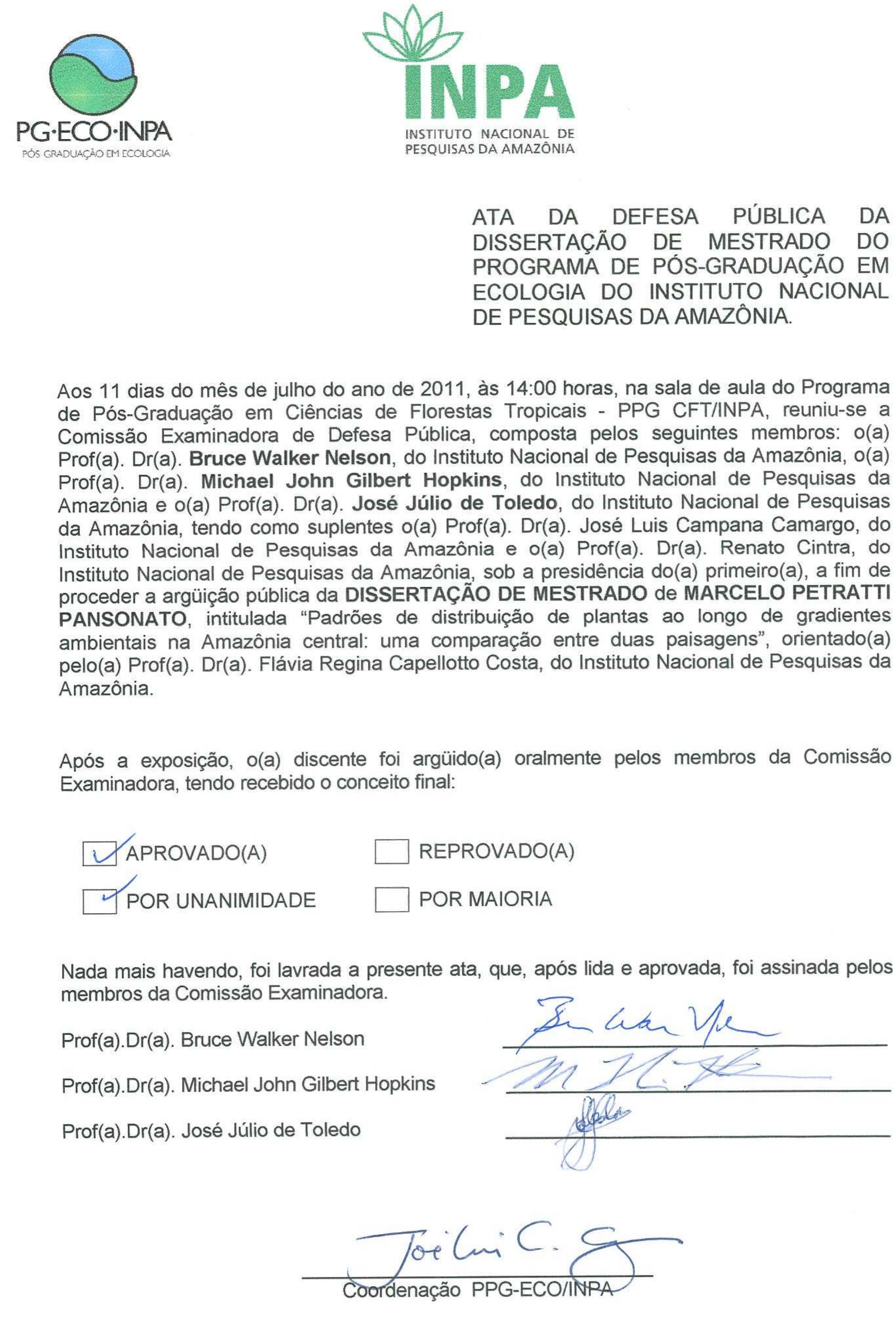
Local Data Assinatura

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil

Anexo E - Ata da Defesa Oral Pública



PG·ECO·INPA
PÓS GRADUAÇÃO EM ECOLOGIA

INPA
INSTITUTO NACIONAL DE
PESQUISAS DA AMAZÔNIA

ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 11 dias do mês de julho do ano de 2011, às 14:00 horas, na sala de aula do Programa de Pós-Graduação em Ciências de Florestas Tropicais - PPG CFT/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Bruce Walker Nelson**, do Instituto Nacional de Pesquisas da Amazônia, o(a) Prof(a). Dr(a). **Michael John Gilbert Hopkins**, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). **José Júlio de Toledo**, do Instituto Nacional de Pesquisas da Amazônia, tendo como suplentes o(a) Prof(a). Dr(a). José Luis Campana Camargo, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). Renato Cintra, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública da **DISSERTAÇÃO DE MESTRADO** de **MARCELO PETRATTI PANSONATO**, intitulada "Padrões de distribuição de plantas ao longo de gradientes ambientais na Amazônia central: uma comparação entre duas paisagens", orientado(a) pelo(a) Prof(a). Dr(a). Flávia Regina Capellotto Costa, do Instituto Nacional de Pesquisas da Amazônia.

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☑ APROVADO(A) ☐ REPROVADO(A)
☑ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Bruce Walker Nelson ____________________

Prof(a).Dr(a). Michael John Gilbert Hopkins ____________________

Prof(a).Dr(a). José Júlio de Toledo ____________________

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Coordenação PPG-ECO/INPA