

**Environmental variables and *Piper* assemblage composition:  
a mesoscale study in the Madeira-Purus interfluve, Central Amazonia**

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**Abstract:** This study aimed to determine the effects of canopy openness, litter depth, soil cation content and texture on *Piper* assemblage composition at a mesoscale. *Piper* assemblage composition and environmental variables were inventoried in 41 0.125 ha (250 × 5 m) plots placed in a terra firme forest located in the Madeira-Purus interfluve, Central Amazonia. Ordination of the 41 plots by Non-metric Multidimensional Scaling (NMDS) in one dimension captured 58% of the floristic variation and was used as the response variable in multiple regression models. Environmental variables explained 39% of the variation in *Piper* assemblage composition, which was significantly related to litter depth, soil texture and canopy openness, but not to the cation content. Effects of edaphic components on plant assemblage structure have been reported for different plant groups, however the strong effect of litter depth at a mesoscale had not yet been demonstrated. We suggest that litter depth variation not only influences the structure of *Piper* assemblages, but also of other plant groups at a mesoscale, as this environmental variable has a direct or indirect effect on species germination and establishment.

**Keywords:** Brazil, canopy openness, cation content, litter depth, multiple regression, soil, terra firme forest.

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**Resumo:** Este estudo visou determinar o efeito da abertura de dossel, profundidade da serapilheira, cátions e textura do solo sobre a composição da assembléia de *Piper* em mesoescala. A composição da assembléia de *Piper* e as variáveis ambientais foram amostradas em 41 parcelas de 0,125 ha (250 × 5 m) localizadas em áreas de floresta de terra firme no interflúvio Madeira-Purus, Amazônia Central. A ordenação das 41 parcelas por NMDS em uma dimensão capturou 58% da variação florística e foi usada com a variável resposta nos modelos de regressão múltipla. As variáveis ambientais explicaram 39% da variação na composição da assembléia de *Piper*, que esteve significativamente relacionada com profundidade da serapilheira, textura do solo e abertura de dossel. O efeito de fatores edáficos sobre a estrutura de comunidades vegetais foi reportado para diferentes grupos de plantas, entretanto o forte efeito da profundidade da serapilheira em mesoescala ainda não tinha sido demonstrado. Sugerimos que a variação da profundidade da serapilheira, por ter um efeito direto ou indireto na germinação e conseqüente estabelecimento dos indivíduos, influencia a distribuição das espécies de *Piper* e provavelmente de outros grupos de plantas em mesoescala espacial.

**Palavras-chave:** Brasil, abertura de dossel, conteúdo de cátions, profundidade da serapilheira, regressão múltipla, solo, floresta de terra firme.

## Introduction

A variety of empirical studies have proposed the role of environmental features, such as edaphic and topographic gradients, in determining changes in species composition throughout Neotropical forests, especially at local and large scales (Gentry 1988, Vormisto et al. 2000, Tuomisto & Ruokolainen 2002, Tuomisto et al. 2003, Poulsen et al. 2006). However, features or processes involved in the determination of understory assemblage composition at a mesoscale are less well documented (Duque et al. 2002, Svenning et al. 2004, Costa et al. 2005, Jones et al. 2006) and have mainly recorded the relative importance of edaphic and topographic gradients as environmental factors affecting community or assemblage composition. Though the importance of environmental factors is well documented, some of these studies have also highlighted the importance of stochastic and historical events in explaining community structure. Neutral models assume that species are competitively equivalent and that changes in community composition occur as a result of historical processes, including extinction, immigration and dispersal limitation. Although neutral models and environmental determinism explain part of the variation in community structure, a great part of it still remains unexplained (Duijvenvoort et al. 2002, Tuomisto et al. 2003, Vormisto et al. 2004, Normand et al. 2006, Réjou-Méchan et al. 2008).

Apart from edaphic features, other environmental factors such as leaf litter, light availability and vegetation structure (Denslow et al. 1990, Miyamoto et al. 2003, Xiong et al. 2003, Farris-Lopez et al. 2004, Harms et al. 2004) have also been reported to affect understory species densities and species composition.

Overstory structure and litter depth might create variation in light habitats at the ground level within tropical forests (Denslow et al. 1990, Vázquez-Yanes et al. 1990, Montgomery & Chazdon 2001, Harms et al. 2004). This variation in light conditions affects differently the germination of *Piper* species, which have particular responses to light quality and quantity (Denslow et al. 1990, Vázquez-Yanes et al. 1990, Daws et al. 2002). Hence, differential patterns of germination and establishment may be partly responsible for patterns of species distribution along the ground light availability gradient. Leaf litter not only influences the variation in light habitats in the ground-level, but it can also act as a physical barrier, as seedlings and sprouts may not be able to emerge from beneath a litter mat, due to energy shortage (Facelli & Pickett 1991, Molofsky & Augspurger 1992). Hence, understory variation in light availability and litter depth may create different niches, thus accounting for coexistence of *Piper* species (Denslow et al. 1990, Daws et al. 2002). Therefore, we can expect to explain floristic variation better if we include light and litter as environmental predictors.

*Piper* is a pantropical genus varying from shrubs to herbs and lianas, and is one of the most speciose genera in the Neotropics, represented by over 700 spp. (Jaramillo & Manos 2001). It is an abundant element of the understory in tropical forests and is widely distributed through a variety of environments in the understory (Fleming 1985, Greig 1993). *Piper* species are of great ecological importance, as they provide resources for many animals, especially bats, frugivore birds and insects (Fleming 1985), while pioneer species are involved in regeneration processes. Members of this genus are also economically important in different parts of the world, as food flavoring agents, in the cosmetic industry and in phytochemical research (Rahman et al. 1999, da Silva et al. 2002, Reddy et al. 2004).

Studies on the relationship of understory plant communities and environmental variables have shown that ferns, Melastomataceae, *Psychotria* and herb communities respond to soil texture and fertility (Tuomisto & Ruokolainen 2002, Costa et al. 2005, Kinupp &

Magnusson 2005, Costa 2006), however, there is no information on how *Piper* species respond to these gradients. This genus contributes largely to the biodiversity of the understory in neotropical forests and it has also large economical importance, hence an understanding of the distribution patterns of *Piper* and its relationship with the environmental variation provides key information for dissecting Amazonian biodiversity and gives information on the distribution patterns of potential economical valuable species. With this study we aim to understand more about the effects of environmental factors in *Piper* species distribution at the mesoscale, by addressing the following question: How does *Piper* assemblage composition respond to the selected environmental variables canopy openness, litter depth, soil fertility and texture?

## Material and Methods

**Study site.** – This study was conducted in the terra firme forest between the Purus and Madeira rivers, in the Central Amazon, Brazil, close to Km 158 of the BR- 319 highway, which links Manaus to Porto Velho (04° 07' 67" S and 60° 45' 14" W). According to RADAMBRASIL (1978), this area belongs to the Solimões formation, which is constituted by sediments from the Pleistocene. Rossetti et al. (2005), suggested that this area has deposits dating from 7,000 to 27,000 years old, and was subject to frequent environmental changes, probably as a result of climatic changes and tectonic factors. These historical changes modulated biodiversity throughout time and they might have been very important factors in determining current biodiversity. The terrain is characterized by plane topography and altitude ranges from 25 to 50 m. Canopy height is on average 40 m and palm trees are constant elements covering extensive areas in the region.

**Sampling design.** – Forty one 0.125 ha (250 × 5 m) plots were established at a minimum distance of 500 m from one another, along two pre-existing trails, with 5 and 16 km each, which were at least 1 km apart ( see Figure 1). The trails cover the main geomorphological features found in the area, tabular interfluves and mega-slopes. Tabular interfluves are the highest terrains between major rivers, are very flat and badly drained, forming many bogged areas during the rainy season. Mega-slopes follow the largest streams, being crossed by stream meanders which may flood during the rainy season. Plots were established using a clinometer, each following a topographic isocline, to minimize soil and drainage variation within each plot (Magnusson et al. 2005).

**Data sampling.** – All shrub *Piper* individuals higher than 10 cm were identified or morphotyped and counted within each plot, resulting in a total of 5.125 ha sampled. Many *Piper* species are known to develop clonal growth, therefore plants were considered as being one individual when they had no visual link with other, and were at least 20 cm apart. Species were identified by comparison with specimens from the Herbarium of the Instituto Nacional de Pesquisas da Amazonia (INPA), identification keys (Yuncker 1972) and mainly by the specialist Dr. Ricardo Callejas from the University of Antioquia, Colombia.

Hemispherical photographs were taken as an indirect measure of light availability, at six stands along each transect, distant 50 m of each other. Photographs were taken with a Nikon Coolpix 4500 digital camera with a FC-E8 fish-eye lens, mounted on a leveled tripod at a height of 1 m. Measurements were taken in the same season and were restricted to periods just after sunrise and just before sunset, to avoid direct sun. Each photograph was transformed into a black and white image and analyzed for the percentage of canopy openness based on the proportion of white pixels, representing sky, and black pixels, representing any other object different to sky. These analyses

were performed with the Gap Light Analyzer software (Frazer et al. 1999). Percentage of canopy openness for each plot was summarized as the mean of the six hemispherical photographs analyzed per plot.

Soil was sampled in each plot from a depth of 0-10 cm at six stands distant 50 m of each other. The six samples were then mixed resulting in a composite soil sample for each plot, and were analyzed for  $K^+$ ,  $Mg^{+2}$ ,  $Ca^{+2}$  and texture (silt, clay and sand percentages) at the soil laboratory of the Agronomy Department at INPA. The cation content (sum of bases  $K^+$ ,  $Mg^{+2}$ ,  $Ca^{+2}$ ) was used to represent soil fertility.  $Na^+$  was below the spectrometer detection level, and was therefore not included. As there was correlation among soil texture fractions (sand, clay, and silt percentages), we chose silt to represent soil structure as it represents the largest variation of soil structure among plots. Silt is a soil fraction responsible for soil's unstable structure, which results, at our study area, in badly drained soils with high water retention. (Juo & Franzluebbers, 2003).

Litter depth was measured by forcing a cylindrical iron stick through the litter layer until it reached the soil. The part of the stick introduced in the soil was then measured in centimeters with a measuring tape. Measurements were made at every 2 m, along the major axis of each plot (250 m), and summarized as the mean of the 126 measurements per plot. Leaf litter depth was measured during the dry season, so that there would be minimum variation in litter depth as a result of seasonality.

Numerical analysis. – The floristic pattern of the 41 plots was described using Non-Metric Multidimensional Scaling (NMDS), based on matrices constructed with the Bray-Curtis dissimilarity index, which was applied over site-standardized quantitative plant data. NMDS is the most robust ordination technique available, since it can accommodate any similarity measure, and has the best performance in recovering known structures when compared to other methods by simulation (Minchin 1987). Standardization involved

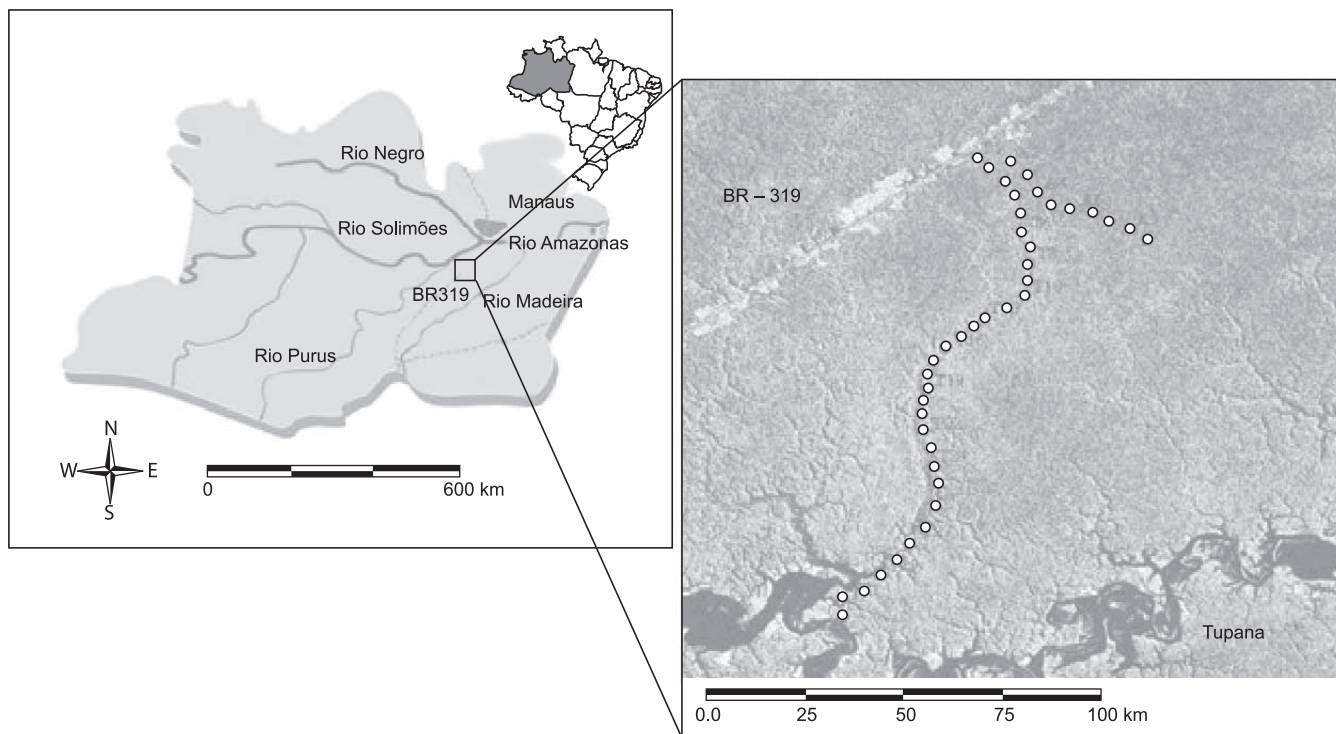
a transformation of each species' total abundance to their relative abundance in the plot. To decide which dimensionality of the NMDS solution to represent assemblage composition, NMDS was done in one, two and three dimensions, calculating the percentage of variance captured by each solution. Since the NMDS solution in one dimension described 58% of the variance in species composition, it was used to represent *Piper* assemblage composition in a multiple regression model. However, an ordination in two dimensions was also run, and a multivariate multiple regression model was applied to both the one-dimensional and two-dimensional NMDS axis, to check for consistency of the effects.

The Regression models included silt content (to represent soil texture), cation content (to represent soil fertility), litter depth and the percentage of canopy openness as explanatory variables, whereas the one or two-dimensional NMDS axes represented the response variables. Estimates of relative importance of predictors were calculated using the LMG method (Lindemann et al. 1980), as implemented by Grömping (2009) in the R *relaimpo* package. All analyses were performed in R 2.9.1 (R Development Core Team 2008) and ordinations were done in the *Vegan* package (Oksanen et al., 2009).

## Results

A total of 1952 individuals of 25 *Piper* species or morphotypes were recorded in the 41 plots. *P. bartlingianum* (Miq) C. DC., *P. cililimum* Yunk. and *P. carnioconnectivum* C. DC. were the most abundant species, representing 48% of all individuals. These were also the most frequent species, found in more than 75% of the 41 plots (Table 1).

Soil texture, represented by silt percentage, ranged from 38 to 75. Soil fertility, represented by cation content ranged from 0.15



**Figure 1.** Location of the 41 0.125 ha plots installed, near Km 158 of the BR-319 highway in the Madeira-Purus interfluvium, Central Amazonia (Landsat image from 2000 provided by NASA).

**Figura 1.** Localização das 41 0,125 ha parcelas instaladas, próximas ao Km 158 da rodovia BR- 319 no interflúvio Madeira- Purus, Amazônia Central (Imagem Landsat 2000 fornecida pela NASA).

to 0.78 (cmol.kg<sup>-1</sup>). Most plots were closed understory areas and there was little variation of canopy openness values among plots, considering that this environmental variable can range from 0 to 100%. Cation content was the variable with the widest range of values distributed, whereas the percentage of silt had the narrowest range (Table 2). There was no linear correlation between soil texture and litter depth ( $r = 0.094$ ).

Ordination of the 41 plots by NMDS in one dimension captured 58% and the ordination in two dimensions captured 75% of the floristic variation. The multiple regression relating assemblage composition to the environmental predictors was significant ( $P < 0.001$ ) and explained 39% of *Piper* assemblage composition. *Piper* assemblage composition was significantly associated with litter depth ( $b = 0.41$ ,

$P = 0.009$ ), soil texture ( $b = -0.41$ ,  $P = 0.004$ ) and canopy openness ( $b = 0.37$ ,  $P = 0.024$ ), (Figure 2). Cation content ( $b = -0.10$ ,  $P = 0.497$ ) had no significant effect on *Piper* assemblage composition. A partition of the relative importance of predictors showed that soil silt content was the most important predictor of *Piper* assemblage composition, accounting for 37.6% of the variance explained by the model. Litter depth was the second most important predictor (26.5%) and canopy openness was the third (22.2%). The results with the two dimensional NMDS solution were similar, indicating the same hierarchy of effects.

Relative species abundances distributions along the litter gradient (Figure 3a) showed that around a third of the species occurred along most of the gradient. Contrary to the expected, only a few species were consistently restricted to shallow litter depths. Four of the seven

**Table 1.** Abundance (number of individuals), percent of total abundance and frequency of occurrence of shrub *Piper* species or morphotypes recorded in the 41 plots, (5,125 ha) near Km 158 of the BR-319 highway, Central Amazonia.

**Tabela 1.** Abundância (número de indivíduos), porcentagem de abundância e frequência de ocorrência de espécies arbustivas de *Piper* ou morfotipos registrados nas 41 parcelas, (5,125 ha) próximas ao Km 158 da rodovia BR-319, Amazônia Central.

Species or morphotypes	Abundance (5,125 ha)	Abundance (%)	Frequency (%)
<i>P. bartlingianum</i> (Miq.) C.DC.	472	24	80
<i>P. cililimum</i> Yunk.	278	14	78
<i>P. carniconnectivum</i> C.DC.	190	10	76
<i>P. liesneri</i> Steyerem.	162	8	63
<i>P. cyrtopodum</i> (Miq.) C.DC.	130	7	80
<i>P. sp 26</i>	110	6	66
<i>P. gurupanum</i> Yunk.	99	5	37
<i>P. subglabrifolium</i> C.DC.	93	5	56
<i>P. piresii</i> Yunk.	80	4	27
<i>P. krukoffii</i> Yunk.	75	4	22
<i>P. consanguineum</i> Kunth.	66	3	37
<i>P. sp 27</i>	61	3	27
<i>P. gentryi</i> Steyerem.	31	2	20
<i>P. sp 8</i>	16	1	22
<i>P. sp 12</i>	15	1	5
<i>P. sp 24</i>	15	1	12
<i>P. chumboense</i> Yunck.	14	1	20
<i>P. sp 10</i>	14	1	17
<i>P. madeiranum</i> Yunck.	12	1	15
<i>P. aulacospermum</i> Callejas	6	0,3	7
<i>P. hostmannianum</i> (Miq.) C.DC.	4	0,2	2
<i>P. sp 23</i>	3	0,2	2
<i>P. tortivenulosum</i> Yunck.	3	0,2	5
<i>P. retropilosum</i> (Miq.) C.DC.	2	0,1	2
<i>P. japurense</i> (Miq.) C.DC.	1	0,1	2
Total	1952	100	100

**Table 2.** Selected environmental variation in the 41 0.125 ha (250 × 5 m) plots near Km 158 of the BR-319 highway in the Madeira-Purus interfluvium, Central Amazonia.

**Tabela 2.** Variação ambiental de variáveis selecionadas nas 41 parcelas 0.125 ha (250 × 5 m) próximas ao Km 158 da rodovia BR-319, Amazônia Central.

Environmental variables	Mean	SD	Range
Cation content (cmol.kg <sup>-1</sup> )	0.3	0.12	0.15 - 0.78
Silt (%)	57.1	10.31	38.2 - 75.9
Litter depth (cm)	11.8	4.0	3.2 - 19.4
Canopy openness (%)	7.7	1.9	3.2 - 10.7

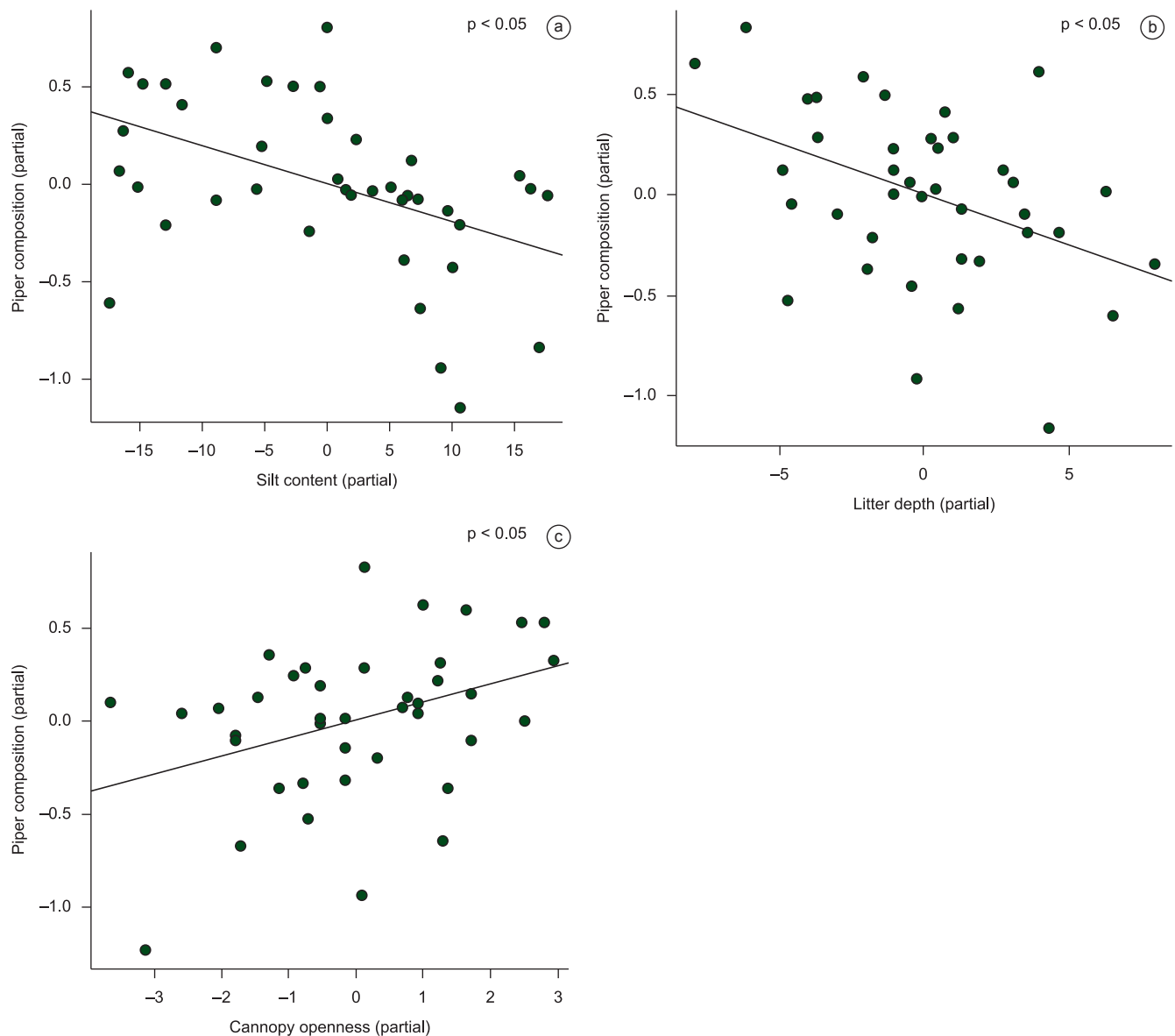


most abundant and frequent species (frequency > 50%, and summing 74% of the individuals) had distributions biased towards one of the ends of the litter gradient. *Piper bartlingianum* was present over the entire gradient, but was more abundant and frequent in shallower litter areas. Overall, we observed a change in composition along this gradient, and some species (*P. kruckofii*, *P. sp26* and *P. cilimum*) were clearly restricted to some regions of it, indicating that the litter gradient can be important for their niche definition. However, the pattern is not compatible to a hypothesis of a fine niche partition along the litter gradient.

No species were restricted along the soil texture gradient, although the most abundant species had clear changes in abundance along this gradient. *P. bartlingianum* was more abundant in less silty areas, whereas *P. carniconectivum* was more abundant in the middle of the gradient and *P. cyrtopodon* in siltier areas.

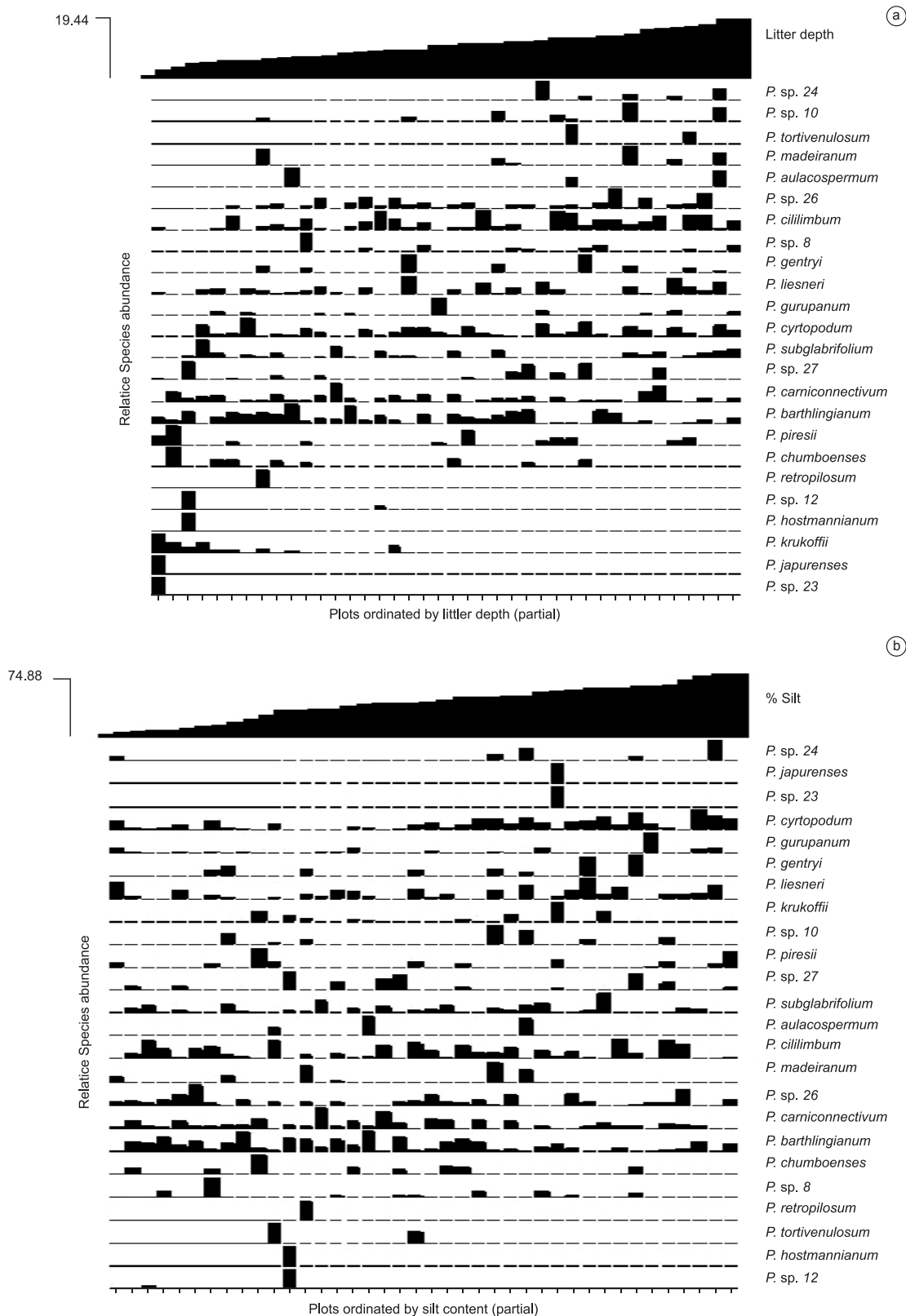
## Discussion

*Piper* assemblage composition was strongly related to soil texture and litter depth, and the importance of litter as predictor was almost as strong as soil texture. Recent studies have highlighted the important influence of edaphic components on tropical plant communities (Tuomisto et al. 2003, Costa et al. 2005, Poulsen et al. 2006), however the strong effect of litter variation on plant assemblage structure at a mesoscale has not yet been demonstrated, despite its known influence on assemblage structure at a local scale (Vázquez-Yanes et al. 1990, Facelli & Pickett 1991, Miyamoto et al. 2003). Leaf litter characteristics strongly affect plant species germination and growth as they control light quality, temperature and water availability (Vázquez-Yanes et al. 1990, Facelli & Pickett 1991), as well as morphological and chemical properties of topsoil profiles, altering pH, N and cation content (Ponge et al. 2002). Leaf litter can also affect plant species germination and growth by creating a physical



**Figure 2.** Relationship between the partials of assemblage composition, represented by the one-dimensional NMDS and partials of a) silt content; b) litter depth (cm); and c) percentage of canopy openness.

**Figura 2.** Relação entre os parciais da composição da assembléia, representado pelo NMDS unidimensional e os parciais de a) conteúdo de silte; b) profundidade de serapilheira; e c) porcentagem de abertura do dossel.



**Figure 3.** Species abundances distribution along environmental gradients on the 41 plots near Km 158 of the BR-319 highway in the Madeira-Purus interfluvium, Central Amazonia. a) Ordination of species was based on the partial gradient of litter depth; and b) silt content, obtained from a model including the effects of litter depth, percentage of canopy openness, cation content and silt content on assemblage composition.

**Figura 3.** Distribuição da abundância de espécies ao longo de gradientes ambientais nas 41 parcelas próximas ao Km 158 da rodovia BR 319- no interflúvio Madeira-Purus, Amazônia Central. a) Ordenação das espécies foi baseada nos gradientes parciais de profundidade de serapilheira; e b) conteúdo de silte, obtidos pelo modelo incluindo o efeito da profundidade de serapilheira, porcentagem de abertura de dossel, conteúdo de cátion e conteúdo de silte sobre a composição da assembléia.

barrier for seed and seedlings, which might prevent seeds reaching the soil and inhibit emergence of seedlings or sprouts (Facelli & Pickett 1991, Molofsky & Augspurger 1992). Hence, the effects of leaf litter on seed germination and growth could be species-specific and could contribute for species coexistence by promoting variation in species relative abundance and occurrence in small spatial scales.

Chauvel et al. (1987) showed that soil types in Central Amazonia are largely associated with altitude and that there is a variation in soil type along the topographic gradient. Therefore, it might be hard to evaluate the relative importance of edaphic gradients in plant species composition and distribution without interference of the topographic gradient (Tuomisto & Ruokolainen 1994, Clark et al. 1999, Harms et al. 2004, Costa et al. 2005). It might be that plants differ in their tolerance and requirements associated to these gradients and therefore, it is important to understand how each of these gradients affect plant species to be able to explain diversity in terra firme forests. This study demonstrated that composition of the *Piper* assemblage was strongly associated with the soil texture gradient, which had probably low interference of the topographic gradient, as the sampled area is characterized by low topographic variation (0 - 20 m). Environmental factors such as water availability and aeration might be associated with soil texture and thus be the causal factor that is influencing species occurrence at different parts of the soil texture gradient. However we cannot conclude which of these associated environmental factors are influencing *Piper* assemblage composition.

Silvertown et al. (1999) demonstrated that hydrological defined niches structure communities in temperate forests and showed that plants are sensitive to hydrology in a fine scale. Our study area is characterized by a great variation in microtopography and soil texture fractions (mainly silt). The latter results in unstable structured soils, which greatly influences the movement of water through the soils, which may result in the presence of several small ponds, which flood throughout several months of the year. Therefore, we suggest that soil texture might be associated with water and oxygen availability gradients and hence *Piper* species respond to variation in soil texture due to species-specific variation in tolerance to water availability or water-logging.

The significant effect of soil texture and litter depth on *Piper* assemblage composition and the high percentage of variation explained by these environmental variables, suggest that *Piper* species are segregated along various environmental niche axes, including gradients of soil moisture, and therefore that niche segregation plays a significant role in structuring the assemblage.

Soil fertility, represented by cation content, did not have a significant effect on *Piper* assemblage composition as was observed for other plant assemblages studied in western Amazonia (Vormisto et al. 2000, Poulsen et al. 2006, Tuomisto 2006). Given that *Piper* species development does not have a significant response to variation in soil fertility (Denslow et al. 1987, Fredeen et al. 1991) we may expect that this environmental variable would not affect *Piper* species differentially at a mesoscale and therefore do not structure *Piper* assemblage. However, the absence of a response to fertility may be only due to the absence of a broad gradient in fertility at our study site, considering that Central Amazonia has poor soils, compared to other Amazonian regions. The range of cation content observed at our study site (0.15-0.78 cmol.kg<sup>-1</sup>) represents 40% of the fertility gradient studied by Poulsen et al. (2006) (0.47-2.06 cmol.kg<sup>-1</sup>) and only 3% of those studied by Vormisto et al. (2004) (0.30 – 20.54 cmol.kg<sup>-1</sup>) in western Amazonia. The lack of plots representing the other 60 or 97% of the fertility gradient at our study site might be one possible explanation for the absence of significance observed between cation content and *Piper* species distribution, considering

that cation content has been shown to be the cause of plant species substitution in other tropical forests.

Our study detected a significant relationship between *Piper* assemblage composition and light availability at a mesoscale. The effect is remarkable, considering that the values of canopy openness sampled at the plots (3-10%) were confined to the darker end of the gradient, being far from regularly spread along the possible range of canopy openness, which can go from 0 to 100%. Although the important role of light in germination and development of tropical forest *Piper* species was shown in previous studies (Fleming 1985, Denslow et al. 1990, Greig 1993, Vázquez-Yanes et al. 1990, Chazdon & Kaufman 1993, Daws et al. 2002), those were observed along a wide range of light variation, and measurements were centered on individual plants. The effect of light on assemblage composition at a mesoscale is not commonly documented (but see Jones et al. 2006, Zuquim et al. 2009), but as we have shown, helps explain part of its variation.

Based on our results, we conclude that *Piper* assemblage composition is strongly affected by litter depth, soil texture and canopy openness at a mesoscale. This conclusion supports the view that deterministic processes related to environmental conditions within terra-firme forests are involved in explaining assemblage structure at this scale.

Effects of edaphic factors on plant assemblage structure have been reported for different plant groups, however the strong effect of litter depth at a mesoscale had not yet been highlighted. We can expect that litter depth variation not only influences the structure of *Piper* assemblages, but also of other plant groups at the mesoscale, as it has a direct or indirect effect on species germination and establishment.

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