










# Environmental filters and biotic interactions drive species richness and composition in ecotone forests of the northern Brazilian Amazonia

## Filtros ambientais e interações bióticas conduzem a riqueza e composição de espécies em florestas de ecótono do norte da Amazônia brasileira

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**Abstract:** The structure of tree communities in tropical forests depends on environmental filters and biotic interactions such as competition and facilitation. Many ecotone forests in Northern Amazonia are intriguingly populated by tree assemblages characterized by distinct abundances of a single species, *Peltogyne gracilipes* (Leguminosae). It is unclear whether this pattern solely reflects environmental filters or also antagonistic interactions among species with similar habitat requirements. The aim of this study was to determine the response of species richness and composition to environmental filters, and analyze the role of *P. gracilipes* in structuring tree communities in ecotone forest areas of the Northern Brazilian Amazonia. We sampled 129 permanent plots along a hydro-edaphic gradient. All arboreal individuals with stem diameter  $\geq 10$  cm were measured and identified. Multiple regressions were performed to test the effects of environmental filters, and abundance of *P. gracilipes* on the tree species richness and composition. Species richness and composition responded to the same filters which, in turn, affected species composition directly and indirectly, through the abundance of *P. gracilipes*. Our results indicate that both abiotic filters and biotic interactions shape the studied tree communities. *P. gracilipes* can be considered an indicator species of hydro-edaphic conditions, but also is itself a driver of tree community structure.

**Keywords:** Community structure. Maracá Island. Roraima. Seasonal forests. Tree species.

**Resumo:** Estrutura de comunidades de árvores em florestas tropicais depende de filtros ambientais e interações abióticas, como competição e facilitação. Muitas florestas de ecótono no norte da Amazônia são intrigantemente povoadas por assembleias de árvores, caracterizadas por abundâncias distintas de uma única espécie, *Peltogyne gracilipes* (Leguminosae). Não está claro se este padrão isoladamente reflete filtros ambientais ou também interações antagonísticas entre espécies com requisitos de *habitats* semelhantes. O objetivo deste estudo foi determinar a resposta da riqueza e composição de espécies aos filtros ambientais, analisando o papel de *P. gracilipes* na estruturação de comunidades arbóreas em áreas de floresta de ecótono do norte da Amazônia brasileira. Amostramos 129 parcelas permanentes ao longo de um gradiente hidro-edáfico. Todos os indivíduos arbóreos com diâmetro do caule  $\geq 10$  cm foram medidos e identificados. Regressões múltiplas foram realizadas para testar os efeitos dos filtros ambientais, e da abundância de *P. gracilipes* na riqueza e composição das árvores. Riqueza e composição de espécies responderam aos mesmos filtros, os quais, por sua vez, afetaram a composição das espécies direta e indiretamente, por meio da abundância de *P. gracilipes*. Nossos resultados indicam que tanto os filtros abióticos quanto as interações bióticas moldam as comunidades arbóreas estudadas. *P. gracilipes* pode ser considerada uma espécie indicadora de condições hidroedáficas, mas também é ela própria uma impulsionadora da estrutura da comunidade arbórea.

**Palavras-chave:** Estrutura da comunidade. Ilha de Maracá. Roraima. Florestas sazonais. Espécies de árvores.

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## INTRODUCTION

Amazon region is recognized as the largest continuous area of tropical forest on Earth, holding a rich tree flora estimated at 15,000 species (ter Steege et al., 2020). The global importance of the Amazon is reflected in their ecosystem services provided by the forest standing, including carbon stocks, hydrological cycle and conservation of biodiversity (Fearnside, 2013; Le Clec'h et al., 2019). The region concentrates a huge diversity of forest ecosystems conditioned by different environmental filters and biotic factors which do not allow simplistic assessments for use in ecosystem services policies or environmental modeling (Ometto et al., 2014; Tejada et al., 2020). In general, species richness and composition of tree communities has been used to create an identity to the regional forest ecosystems and associate them with studies related to ecosystem functions and processes (Gomes et al., 2018; F. R. Costa et al., 2020; Sousa et al., 2020). Although the number of investigations has grown in recent years, there are still spatial gaps that need to be filled to improve our understanding of how environmental filters act synergistically with biotic factors, promoting variations in the species richness and composition that model ecosystem identity for the different forest types in the Amazon (Oliveira-Filho et al., 2021). This is an environmental key issue with direct implications for theories of species coexistence, natural resource management, and conservation in Amazon (Householder et al., 2021).

Most ecological studies have been done in areas closer to the Amazon river channel (central Amazonia), and they have shown that edaphic and topographic filters affect the species richness and composition of plants at different spatial scales (Toledo et al., 2017; Figueiredo et al., 2018; Oliveira et al., 2019). Main analyses have shown that species distribution is related mainly to soil macronutrient and clay contents (Fine et al., 2005; Quesada et al., 2010; Moser et al., 2014), which vary along topographic gradients (Bohlman et al., 2008; Zuleta et al., 2020). It is assumed that these factors represent the main environmental conditions along which plant communities are structured

in Amazonia (F. V. Costa et al., 2015). Likewise, soil micronutrients also function as environmental filters which can affect species distribution and community structure (Baldeck et al., 2013). Soil micronutrient availability can be both limiting and toxic to plants (Sperotto et al., 2014), or even affect indirectly the availability of other nutrients that limit plant growth even on more fertile tropical soils (Kaspari et al., 2008; Barron et al., 2009).

Despite these findings on areas closer to the Amazon river channel, it is unclear what is relative importance of different environmental conditions for the structure of tree communities in terms of species richness and composition in the ecotones dispersed on peripheral areas of Amazonia (Canetti et al., 2019). Ecotone is a known general term to define a multi-dimensional environmentally stochastic interaction zone between two or more ecological systems or communities (Hufkens et al., 2009). In Amazon region, they are extensive ecosystems located in the peripheral northern and southern borders representing transition zones between large open vegetation (savannas) and different forest types, which are of great importance from the perspective of biological conservation (Santos et al., 2013; Marques et al., 2019). The lack of better clarity on how species richness and composition are structured in the Amazonian ecotone areas are mainly due to the lack of spatialization of investigations relating both biotic and environmental drives acting synergistically in the plant distribution. The paucity of studies is more noticeable in Northern Brazilian Amazonia, where ecotone forests have been increasingly threatened by anthropogenic disturbances as deforestation and fires (Barni et al., 2015; Almeida et al., 2016).

In peripheral zone of Northern Amazonia, a region encompassing much of the Brazilian state of Roraima, at the boundary with Venezuela and Guyana, the ecotone represent a wide transition area between the large Rio Branco-Rio Rupununi savanna and continuous areas of different forest types (Desjardins et al., 1996; Barbosa et al., 2007). The continuous forest area is formed by an interaction range comprising ombrophilous forests, seasonal

forests and some few enclaves of savanna dispersed on hydro-edaphic gradients (Milliken & Ratter, 1998; Carvalho et al., 2018; W. Silva et al., 2019b). *Peltogyne gracilipes* Ducke (Leguminosae), a tree endemic species occurring along whole ecotone zone, can dominate forest stands until reaching monodominant status (Nascimento & Proctor, 1997; Nascimento et al., 2007). Monodominance by *P. gracilipes* was first documented in 1924-25 (ter Steege et al., 2019), and it has been related to hydro-edaphic conditions, such as poorly drained soils and high Fe<sup>+2</sup> content (Nascimento et al., 2017; Villacorta, 2017). However, it is unclear whether this pattern solely reflects exclusion of most tree species from such areas due to their physiological requirements, or whether agonistic interactions with *P. gracilipes* can exclude other species from sites where they could occur otherwise.

To better understand the effects of environmental filters and biotic interactions with *P. gracilipes* in structuring tree communities in ecotone forests of Northern Amazonia, we tested the hypothesis that hydro-edaphic gradients shape species richness and composition both directly and indirectly. Direct effects would result from species sorting along hydro-edaphic gradients due to niche partitioning and local adaptation, whereas indirect effects would result from environmentally-driven changes in *P. gracilipes* abundance, which would affect the abundances of other species due to *P. gracilipes* being a better competitor for soil resources under restrictive soil conditions. We predicted that altitude – a topographic proxy indicating the risk of seasonal flooding – and soil nutrients content would be the main drivers of *P. gracilipes* abundance, species richness and species composition, whereas *P. gracilipes* would have a negative effect on species richness and would change species composition independently of environmental conditions.

## MATERIAL AND METHODS

### STUDY AREA

This study was performed in eastern of Maracá Island, the largest part of the Maracá Ecological Station (3° 15'

- 3° 35' N and 61° 22' - 61° 58' W), a conservation area managed by the Chico Mendes Institute for Biodiversity Conservation (ICMBio) located in state of Roraima, Northern Brazilian Amazonia (Figure 1). Maracá has moist tropical climate, and it is situated in a region characterized by the transition between savanna (Aw) and monsoon (Am) climatic subtypes in Köppen's classification (Barbosa, 1997; Barni et al., 2020). Average annual temperature and rainfall are 26 °C and 2.086 ± 428 mm, respectively, with a rainier period from May to August, and a drier period from December to March (Couto-Santos et al., 2014). The vegetation of Maracá Island reflects the climatic and biogeographic transition zone in which it is inserted (Milliken & Ratter, 1998), presenting a mosaic of ombrophilous and seasonal forests spreader over a hydro-edaphic gradients which are related to the structure, species richness and composition of each forest type (Robison & Nortcliff, 1991; Carvalho et al., 2018).

### SAMPLING DESIGN

We sampled arboreal individuals (trees + palms) in 129 permanent plots (10 m x 50 m; 6.45 ha) spread over six East-West trails belonging to a sampling grid established by the Brazilian Biodiversity Research Program (PPBio) on the eastern of Maracá Island (PPBio, n.d.). The PPBio grid (25 km<sup>2</sup>) is a mesoscale sample of the ecotone forest covering eastern of Maracá Island (mosaic of ombrophilous and seasonal forests). It is a representative area showing us how environmental filters and biotic factors act conditioning variation in species richness and composition in the studied ecotone zone. Each trail is 5 km long, along which 18-29 plots were established in each one with at least a distance of 150 m between them. This sampling design aimed at capturing small-scale structural variation in tree communities of this ecotone forest (W. Silva et al., 2019b). Swamps and enclaves of savannas were not considered in this study. All plots were georeferenced in UTM coordinates and had their altitudes determined topographically (Vale & Romero, 2015). The permanent plots have been measured annually since 2015.



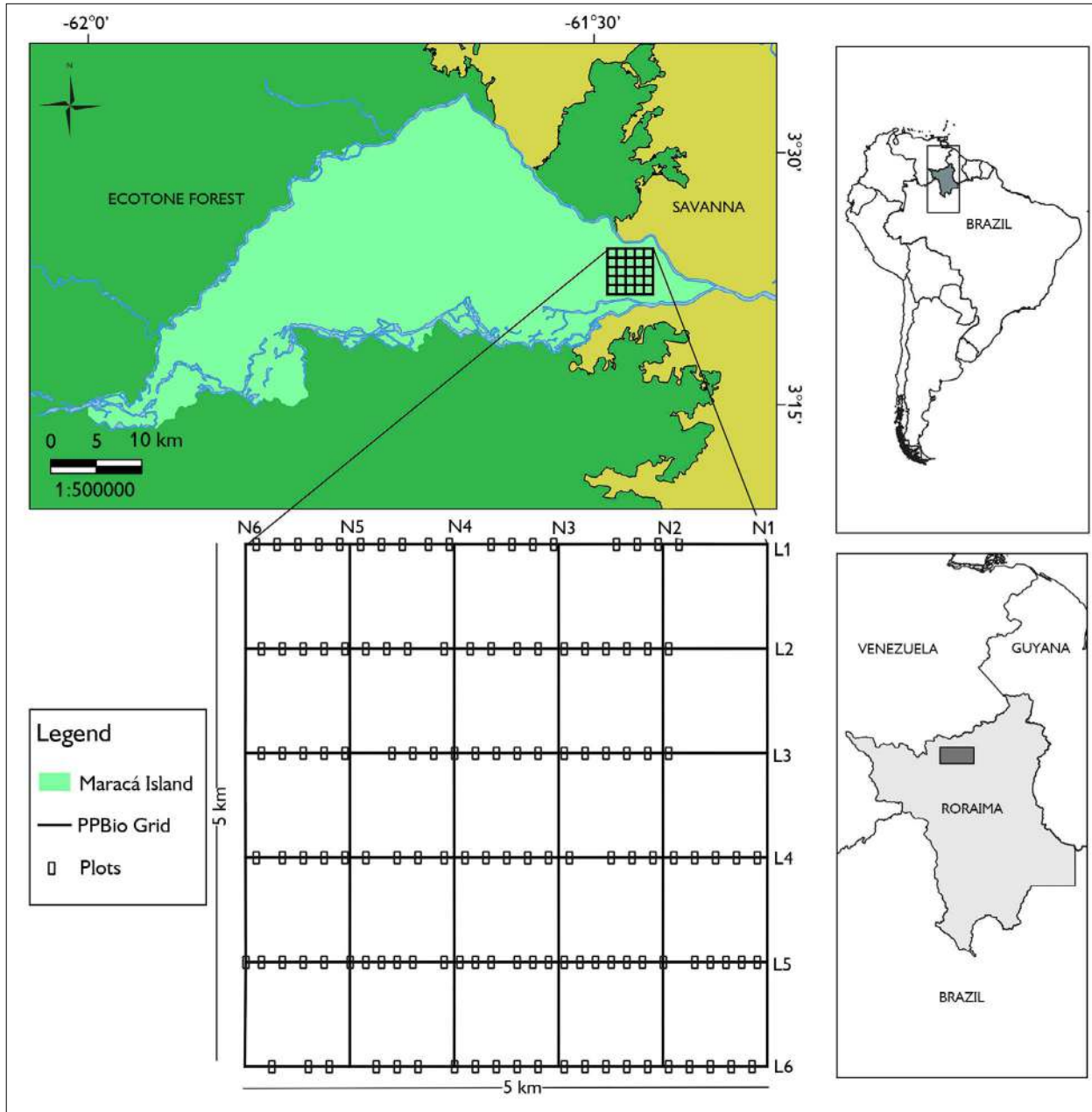


Figure 1. Study area indicating the grid of the Biodiversity Research Program (PPBio) and Geographic location of 129 permanent plots on the eastern of Maracá Island, state of Roraima, Northern Brazilian Amazonia. Map: A. C. Citó (2020).

All biometric data can be freely accessed by the Mendeley Data repository (W. Silva et al., 2019a), and ForestPlots platform (ForestPlots.NET, n.d.) under the codes ETA, ETB, ETC, ETD, ETE and ETF.

#### FOREST INVENTORY

We obtained tree data using the protocol for forest inventory in PPBio research sites (Castilho et al., 2014). We sampled all trees and palms with stem diameter  $\geq 10$  cm

(hereafter only trees), within each of the 129 sampling plots. When trees had deformities or aerial roots, stem diameter was measured 0.5 m above these features (cf. Castilho et al., 2014). Measurements were taken using a diameter tape (model 283D/5m).

All individuals were morphotyped based on field observations and collection of biological material between 15-23/12/2017 for posterior taxonomic identification. Collected material represented most sampled species and were deposited in the herbarium of the *Instituto Nacional de Pesquisas da Amazônia* (INPA), *Museu Integrado de Roraima* (MIRR) and *Universidade Federal Roraima* (UFRR) (acronyms follow Thiers, 2020 [continuously updated]). Species identification was mainly performed by A. T. Mello by comparison with material from INPA's botanical collection, with further checking by R. O. Perdiz and R. I. Barbosa using the botanical collections of INPA, UFRR and MIRR, and consultations to the Reflora virtual herbarium (Reflora, 2020). Scientific names were verified and corrected with reference to the species list of the Brazilian Flora (BFG et al., 2015); family-level groupings followed APG et al. (2016). A total of 3,040 stems (tree = 2,815; palm = 225), corresponding to 140 species (42 botanic families) were used in the analysis. Species composition by sampling plot is presented in the study of W. Silva et al. (2019b), and it is also freely available in the Brazilian Biodiversity Information System (W. Silva et al., 2020).

### SOIL SAMPLING AND ANALYSIS

Soil samples (20-cm deep) were collected at two points within each of the 129 sampling plots. The two subsamples were mixed forming a compound soil sample and, subsequently, each one was air-dried and sieved (2-mm mesh size). Physical (soil clay content, %), and chemical edaphic variables (contents of available  $K^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$ , P,  $Fe^{2+}$ ,  $Zn^{2+}$ ,  $Mn^{2+}$ , B and  $Cu^{2+}$ , and soil organic matter) were obtained using standard protocols (EMBRAPA, 2011). All soil data are freely available through Mendeley Data repository (Barbosa et al., 2019).

### STATISTICAL ANALYSIS

Tree community structure was described as species richness (defined as the number of species found in a plot) and species composition, defined as the combination of species abundances in a plot. The latter was summarized in a single variable using the first axis of a Principal Coordinate Analysis (PCoA), based on Bray-Curtis dissimilarities computed from Hellinger-transformed species abundances (Legendre & Legendre, 2012). We considered the following environmental variables as potential drivers of tree species abundance: (i) altitude (m a.s.l.) as a topographic proxy indicating the risk of seasonal flooding, and (ii) edaphic variables such as soil clay content (%), soil organic matter, sum of bases ( $K^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$ ;  $cmol\ kg^{-1}$ ), sum of micronutrients ( $Fe^{2+}$ ,  $Zn^{2+}$ ,  $Mn^{2+}$ , B and  $Cu^{2+}$ ;  $mg\ kg^{-1}$ ), and soil available P ( $mg\ kg^{-1}$ ). Clay content was adopted to represent the soil texture while bases and micronutrients were grouped by both affinity and reaction forms in the soil. Correlation matrix of the environmental variables used as predictors in the regression models of tree community structure was performed (Appendix 1). Multiple regressions were performed in three analyses: (i) testing for the effects of environmental variables on the abundance of *P. gracilipes*; (ii) testing for the effects of environmental variables and *P. gracilipes* abundance on the richness of remaining species; and (iii) testing for the effects of environmental variables and *P. gracilipes* abundance on the composition of remaining species, as represented by the first Principal Coordinate (PCo1). This allowed us to examine the extent to which *P. gracilipes* could shape community structure on its own, independently of environmental variables. Nutrient predictors were log-transformed to account for non-linear species responses due to strong nutrient limitation when their availability is low. Predictor effects were visualized using partial residual plots, which control for variation in remaining predictors (Breheny & Burchett, 2017). We tested spatial autocorrelation among plots showing that there is no residual spatial autocorrelation in any of the analyzed models because the residuals are independent in analyses involving the regression models (Appendix 2). All analyses were

performed in R 3.6.3 (R Core Team, 2020), with the aid of packages 'vegan' for ordination (Oksanen et al., 2015) and 'visreg' for partial residual plots to visualize predictor effects (Breheny & Burchett, 2017).

## RESULTS

### RESPONSE OF *P. GRACILIPES* ABUNDANCE TO TOPOGRAPHIC AND EDAPHIC VARIABLES

Mean altitude, soil Clay content and sum of micronutrients explained 52% of the variation in the abundance of *P. gracilipes*

(Table 1). Abundance was lower at both higher altitude and soil clay content, but sum of micronutrients had the strongest positive effect on *P. gracilipes* abundance (Figure 2). Correlation analysis between altitude (topographic proxy for drainage) and micronutrients ( $r = -0.33$ ;  $P < 0.05$ ) was significant as while as clay content and micronutrients ( $r = 0.39$ ;  $P < 0.05$ ) (Appendix 1). This result indicate that environments populated by higher abundance of *P. gracilipes* is characterized by seasonal flooding in association with both higher micronutrients content and lower soil Clay content.

Table 1. Multiple regression models relating *Peltogyne gracilipes* abundance, species richness and species composition to hydro-edaphic (soil variables and altitude as a proxy for soil drainage) and biotic drivers in an ecotone landscape in Northern Amazonia ( $n = 129$ ). Bold numbers represent statistically significant effects ( $P < 0.05$ ).

Response	$R^2$	Predictor	Coefficient	$t$	$P$
Abundance of <i>P. gracilipes</i>	0.52	Intercept		-	-
		Mean altitude	-0.15	-3.86	<b>0.001</b>
		Clay content	-0.19	-2.76	<b>0.006</b>
		SOM	0.07	1.30	0.196
		Log base sum	-0.76	-1.15	0.252
		Log P content	0.21	0.82	0.411
		Log micronutrient sum	0.03	6.97	<b>0.001</b>
Species richness	0.32	Intercept	6.24	-	-
		Mean altitude	0.08	1.97	<b>0.050</b>
		Clay content	-0.04	-0.61	0.539
		SOM	0.08	1.46	0.144
		Log base sum	-0.75	-1.15	0.251
		Log P content	0.41	1.63	0.103
		Log micronutrient sum	0.00	1.16	0.869
		<i>P. gracilipes</i>	-0.42	-4.79	<b>0.001</b>
Species Composition (PCo1)	0.80	Intercept	-5.59	-	-
		Mean altitude	8.34	4.85	<b>0.001</b>
		Clay content	6.38	2.07	<b>0.039</b>
		SOM	-1.61	-0.64	0.518
		Log base sum	-3.13	-1.13	0.259
		Log P content	6.30	0.05	0.953
		Log micronutrient sum	-1.04	-0.04	0.962
		<i>P. gracilipes</i>	-2.96	-7.90	<b>0.001</b>





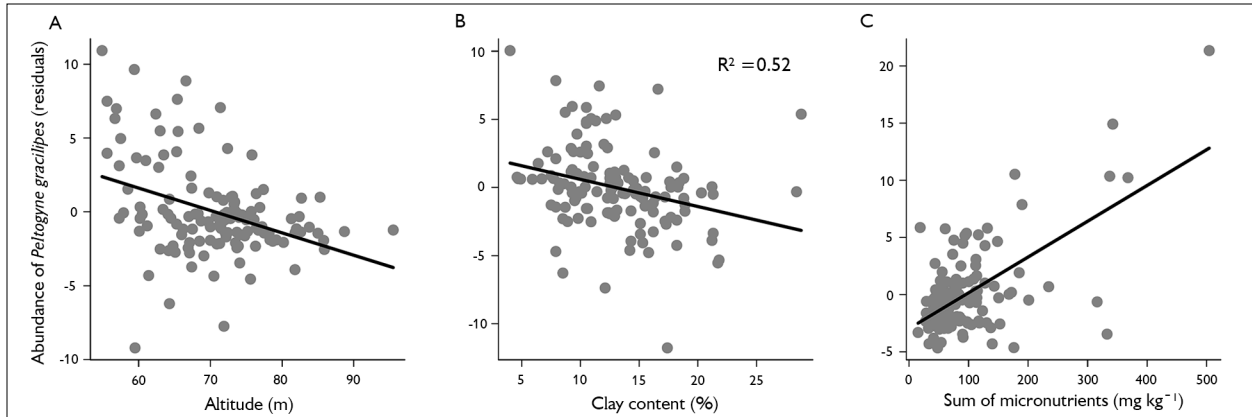


Figure 2. Relationship between abundance of *Peltogyne gracilipes* and (A) average altitude (B) clay content and (C) sum of soil micronutrients in an ecotonal landscape in Northern Brazilian Amazonia. Each point represents one sampling plot ( $n = 129$ ). Lines represent regression fits.

### RESPONSE OF SPECIES RICHNESS TO ENVIRONMENTAL GRADIENTS AND *P. GRACILIPES* ABUNDANCE

Altitude and the abundance of *P. gracilipes* together explained 32% of the variation in tree species richness observed in the study area (Table 1). The abundance of *P. gracilipes* was the strongest predictor of tree species richness, which decreased with the former (Figure 3A). Moreover, forest stands in higher areas tended to have more species (Figure 3B).

### RESPONSE OF SPECIES COMPOSITION TO ENVIRONMENTAL GRADIENTS AND *P. GRACILIPES* ABUNDANCE

The joint effect of altitude, soil Clay content and abundance of *P. gracilipes* explained 80% of the strongest pattern of change in species composition (as represented by PCo1) (Figure 4). Altitude and the abundance of *P. gracilipes* were the strongest predictors of species composition, whereas soil Clay content had a more subtle effect (Table 1).

## DISCUSSION

### EFFECT OF ENVIRONMENTAL VARIABLES ON THE ABUNDANCE OF *P. GRACILIPES*

Our results indicate a strong effect of environmental conditions (altitude, soil clay content and sum of micronutrients) on

the abundance of *P. gracilipes*. The spatial distribution of this species is shaped by different environmental filters in the eastern of Maracá Island, supporting the proposals of Nascimento and Proctor (1997) and Nascimento et al. (2017). Seasonally flooded areas located in bottomlands with higher micronutrient content are seemingly more suitable for the occurrence of this species in the study area. These findings are similar to those of Villacorta (2017), who suggested that *P. gracilipes* would not occur or would have low abundance in non-flooded soils, but could become monodominant in areas with higher hydro-edaphic restrictions.

Poorly structured soils, low sum of bases content and seasonally flooded, as those where *P. gracilipes* is more abundant in eastern Maracá Island, can be considered limiting to the growth and survival of other tree species, causing root systems to be shorter and underdeveloped due to the low tolerance of most species to restrictive soils (Gale & Barfod, 1999; Quesada et al., 2012). This was also demonstrated by Ramírez-Narváez (2017), who found lower root biomass in areas where *P. gracilipes* is more abundant, indicating that this species has greater tolerance to environments with stronger hydro-edaphic restrictions relative to other species occurring in eastern Maracá Island. Thus, higher abundance of *P. gracilipes* is expected in more restrictive environments (e.g. seasonally flooded areas) in eastern Maracá Island and, depending

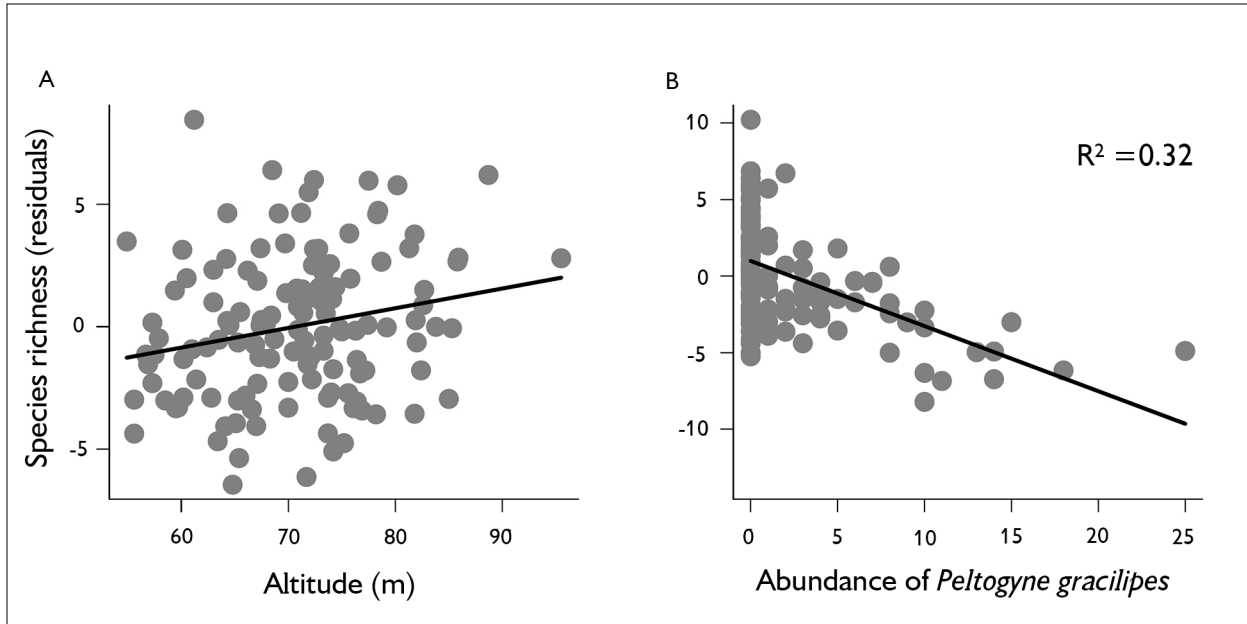


Figure 3. Relationship between species richness and (A) average altitude and (B) abundance of *Peltogyne gracilipes* in an ecotonal landscape in Northern Brazilian Amazonia. Each point represents one sampling plot ( $n = 129$ ). Lines represent regression fits.

on the prevalence of this species, monodominance can result, as discussed by Nascimento and Proctor (1997) and Milliken and Ratter (1998).

#### EFFECT OF ENVIRONMENTAL VARIABLES AND ABUNDANCE OF *P. GRACILIPES* ON SPECIES RICHNESS

Our results showed that altitude, used as a topographic proxy for risk of seasonal flooding, and the abundance of *P. gracilipes* control tree species richness in the studied area. The positive effect of altitude on species richness is related to the fact that bottomlands have greater hydro-edaphic restrictions (hydromorphic; sum of bases-poor soils), as also observed by Nascimento et al. (2017) and Villacorta (2017).

Our analyses are similar to those of other studies performed in different regions of tropical forest, which indicated that environments with greater hydro-edaphic restrictions tend to have lower species richness (Jones et al., 2008; J. Silva et al., 2010; Mosquera & Hurtado, 2014). For instance, in an ecotone area between Brazilian Amazonia and

'Cerrado' (savanna), Elias et al. (2019) also reported that tree species richness is related to topography, indicating that hydric restrictions function as a filter to species in environments of sandy soils. Likewise, Lozada et al. (2012) indicated that environments with poorly drained soils in eastern Venezuela can generate restrictive hydric conditions which reduce local species richness and contribute to the formation of monodominance. This observation is similar to that found in our study area, where environments with greater hydro-edaphic restrictions featured higher abundance of *P. gracilipes*, which often achieved monodominance (sensu Connell & Lowman, 1989).

In this context, we suggest that monodominant aggregations of *P. gracilipes* individuals in eastern Maracá Island tend to exclude other tree species through competitive interactions (e.g. tolerance to seasonal anoxia), optimizing its growth and survival in environments with greater hydro-edaphic restrictions. As *P. gracilipes* is a slow-growing species (Carvalho, 2014), it could have greater fitness under these conditions by being able to accumulate biomass under low



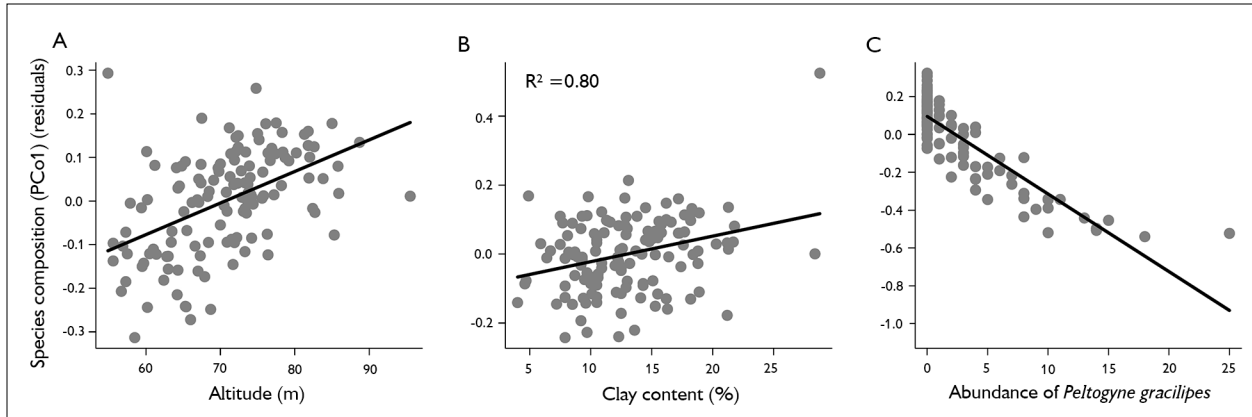


Figure 4. Relationship between species composition and (A) average altitude, (B) clay content and (C) abundance of *Peltogyne gracilipes* in an ecotonal landscape in Northern Brazilian Amazonia. Each point represents one sampling plot ( $n = 129$ ). Lines represent regression fits.

soil nutrient levels (e.g. low sum of bases) which tend to exclude most tree species also occurring in this area. A plausible explanation is that fitness differences among species can negatively impact species richness because abundant soil nutrients are not necessarily available equally to all plants, as pointed by Chesson (2000). Therefore, the forests of eastern Maracá indicate to be an example of how species richness can vary significantly in environments with small differences in soil nutrient contents, and where the flooding seasonality seems to be the determining factor for a species (*P. gracilipes*) can achieve dominance of the environment through competitive exclusion.

#### EFFECT OF ENVIRONMENTAL VARIABLES AND ABUNDANCE OF *P. GRACILIPES* ON SPECIES COMPOSITION

Tree species composition in eastern Maracá Island was related to the same predictors of species richness, varying as a function of the risk of seasonal flooding. These findings indicate that bottomlands with lower Clay content favour the survival of specialist species (*P. gracilipes*), contrary to uplands, where species composition is more diversified, as also observed by Nascimento and Proctor (1997) and W. Silva et al. (2019b).

In western Amazonia, the effect of topography on tree species composition was explained by Valencia et al. (2004) and Moser et al. (2014), who concluded that the topographic gradient imposes a restriction on species composition, even though most species are generalist relative to topographic variation. In Central Amazonia, Kinupp and Magnusson (2005) described that topography and a suite of variables (e.g. soil texture, water table depth and frequency of floods) restrict certain species to lower altitudes, although most species occurred both in bottomlands and uplands, even when species groups were analyzed separately. Similarly, Toledo et al. (2017) analyzed the effect of ecological characteristics separately and concluded that soil Clay content was responsible for 50% of the variation in species composition along the altitude gradient in Reserve Ducke, Central Amazonia. This observation is analogous to that by Damasco et al. (2013), who showed that soil Clay content was one of the most important predictors of tree species diversity in an ecotone area between ombrophilous forest and 'campinarana' open forest in the Viruá National Park, Northern Amazonia. Our study indicated that the altitude (a topographic proxy for risk of seasonal flooding) can be seen as an important predictor for determining the species composition in the ecotone forests of eastern Maracá, because it has a synergistic effect with both fertility and soil texture,

especially Clay content (Appendix 1). Different types of environments characterized by seasonal flooding are seen as important factors that support distinctions in the tree species composition in the Amazon (Assis et al., 2015; Alemán et al., 2019). However, the seasonal flooding should not be seen as a single environmental filter predicting tree species composition in Maracá.

Studies on different tropical forests (Peh et al., 2011a, 2011b; Marimon-Junior et al., 2019) have suggested that the clustering of specialist species is not conditioned by a single factor, but rather by a suite of environmental filters of different types (chemical, physical and biological) which favour species dominance. For instance, Marimon et al. (2001a, 2001b) showed that higher Mg:Ca ratio and higher micronutrients ( $\text{Fe}^{+2}$  and  $\text{Mn}^{+2}$ ) contents in the soil were responsible for the dominance by *Brosimum rubescens* (Moraceae), a tree species which prevails in environments considered unfavourable to other species due to chemical toxicity. An effect of  $\text{Fe}^{+2}$  was also observed by Lozada et al. (2012) in forests of eastern Venezuela which are dominated by *Mora excelsa* (Leguminosae). Iron ( $\text{Fe}^{+2}$ ) is a micronutrient of high content in the seasonally flooded soils of Maracá in which it could reach toxic levels to some tree species, but does not indicate any negative effect on *P. gracilipes* (Villacorta, 2017). In this light, our results in Maracá suggest that species composition is a complex synergism between hydro-edaphic restrictions, and distinctive abundances of *P. gracilipes*, where sites at lower altitudes, poorly drained and clay-poor soils have as characteristic species composition dominated by *P. gracilipes* (monodominance). Therefore, altitude assumes the role of driver of species composition modulate by different abundances of *P. gracilipes*, considering its synergistic role in the allocation of nutrients, soil texture and hydraulic conditions (seasonal flooding) in ecotone forests in eastern of Maracá Island.

## CONCLUSION

Tree species richness and composition in ecotone forests in eastern of Maracá Island, Northern Brazilian Amazonia,

respond primarily to the same environmental filters, i.e. altitude (topographic proxy for indicate risk of seasonal flooding) associated with texture (Clay content) and soil fertility (micronutrients and sum of bases). These finds indicate that hydro-edaphic restrictions are the drivers of environmental heterogeneity in the studied ecotone forests, with direct and indirect effects through the different abundances of *P. gracilipes*. Our results support the hypothesis that both abiotic filters (e.g. poorly drained soils) and biotic interactions (e.g. monodominant stands of *P. gracilipes*) shape the studied tree communities. *Peltogyne gracilipes* can be considered an indicator species of hydro-edaphic conditions, but also is itself a driver of tree community structure, distinguishing forest types where it occurs under lower (positive effect on species richness and composition) or higher (negative effect) abundance.

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## AUTHOR CONTRIBUTIONS

Williamar Silva contributed to conceptualization, methodology, investigation, writing (original draft) and data curation; Pedro Pequeno to formal analysis, validation and writing (reviewing and editing); Hugo Farias to conceptualization, investigation, writing (original draft) and data curation; Valdinar Melo to writing (original draft); Carlos Villacorta to writing (original draft) and data curation; Lidiany Carvalho to conceptualization and methodology; Ricardo Perdiz to writing (original draft) and data curation; Arthur Citó to visualization and writing (original draft); and Reinaldo Barbosa to project administration, funding acquisition, supervision and writing (reviewing and editing).



Appendix 1. Correlation matrix of environmental variables used as predictors in regression models of tree community structure. Numbers in bold indicate statistically significant correlations ( $P < 0.05$ ).

Environmental variables	Altitude	Clay	Base sum	P	Organic matter
Clay	-0.06	-	-	-	-
Base sum	-0.15	<b>0.23</b>	-	-	-
P	<b>-0.19</b>	0.00	-0.05	-	-
Organic matter	<b>-0.43</b>	<b>0.51</b>	<b>0.40</b>	0.15	-
Micronutrients	<b>-0.33</b>	<b>0.39</b>	0.06	0.07	<b>0.52</b>

Appendix 2. Residual spatial correlograms of regression models. The curve represents the estimated spatial correlation with varying distance between plots. The horizontal line indicates the null correlation (zero), and the grey bands indicate the 95% confidence interval. As confidence bands include the null correlation across distances, there is no evidence for significant residual spatial correlation.

