Is the *Peltogyne gracilipes* monodominant forest characterised by distinct soils?

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ABSTRACT

Various explanations have been put forward for monodominance in otherwise diverse tropical forests. This study assesses if the monodominance of *Peltogyne gracilipes* on Maraca Island in the northern Amazon can be related to edaphic factors. The basal area of *P. gracilipes* and the five other most common tree species on Maraca Island (*Astrocaryum aculeatum, Attalea maripa, Ecclinusa guianensis, Licania kunthiana* and *Pradosia surinamensis*) were recorded in 30 regularly-spaced 0.5 ha plots distributed over an area of 25 km², for which data on topography and concentration of mineral elements in the soil were also obtained. Stems of *P. gracilipes* accounted for ≥50% of the basal area in five of the plots, which we consider indicative of monodominance, whilst the highest relative basal area that any of the other species achieved in any plot was 31%. The soils data explained more of the variation in the basal area of *P. gracilipes* than it did for the other five species. The presence vs. absence and basal area of P. gracilipes was positively related to concentrations of magnesium (Mg), aluminium (Al), iron (Fe), phosphorus (P) and silt in the soil and to Mg:Ca ratios. These soils were found in the plots at the lowest elevations, which suggests that drainage factors may also be important. Overall, our results suggest that edaphic factors may explain, at least partially, monodominance in this Amazonian forest.

1. Introduction

Tropical forests are widely renowned for their high tree diversity, with the stems in any given forest being divided amongst many rare species. The occurrence of one or a few tree species dominating large areas of tropical forest was considered uncommon until the mid 1980s. However, monodominant forests, in which a single late successional tree species comprises greater than 50% of the total basal area (Connell and Lowman, 1989; Hart et al., 1989), have since been found in many regions of the tropics (see Connell and Lowman, 1989). They can occur side by side with forests comprised of many rare species and often have similar species composition and overall species richness, but very different dominance characteristics (Connell and Lowman, 1989; Hart et al., 1989; Nascimento et al., 1997; Marimon et al., 2001; Torti et al., 2001; Peh et al., 2011; van der Velden et al., 2014). Single-species dominance is often related to extreme environments such as flooded, saline or fertile soils (Hart et al., 1989; van der Velden et al., 2014). However, several examples of monodominant forest have been reported

with no significant differences in soil-bound nutrients from adjacent mixed forest (Hart et al., 1989; Martijena, 1998; Nascimento et al., 1997; Peh et al., 2011b). Given that monodominant forests belie the general pattern in tropical rain forests of communities comprised entirely of rare species, determining how and why some forests are prone to monodominance can contribute to a more general understanding of tropical plant diversity (Connell and Lowman, 1989; Torti et al., 2001).

An interesting case study is that of *Peltogyne gracilipes* Ducke (Fabaceae), which forms monodominant forests in areas of the northeastern Amazon Basin of Brazil. Large *P. gracilipes* forests exist in and around Maraca Island, a protected area (3°15′N, 61°22′W) located in Roraima State. The island has *c.* 100,000 ha, covered mainly by evergreen and semi-evergreen forest with savanna occurring in small patches. Other common trees of the canopy layer include *Ecclinusa guianensis* Eyma, *Licania kunthiana* Hook f. and *Pradosia surinamensis* (Eyma) T. D. Penn. as well as the palms *Astrocaryum aculeatum* Barb.-Rodr. and *Attalea maripa* Mart. (Nascimento and Proctor, 1997; Nascimento et al., 1997). Annual rainfall on the island is *c.* 2100 mm, with a distinct dry
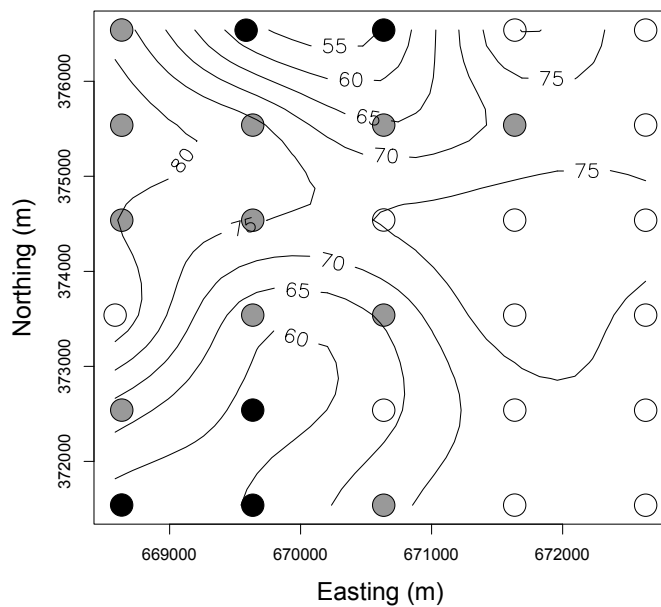

Fig. 1. Map of the study area with contour lines giving the elevation (m a.s.l.). The circle for each plot is coloured according to its status with respect to *Peltogyne gracilipes* (black: monodominant *P. gracilipes* forest, ≥ 50% total basal area; grey: *P. gracilipes* present, but < 50% total basal area; white: *P. gracilipes* absent).

season from December to March. Soils on Maracá Island are generally poor in nutrients, particularly phosphorus (Nortcliff and Robison, 1998). *P. gracilipes*-dominated forest occurs on lower slopes and on soils with high Magnesium (Mg) concentrations (Nascimento et al., 1997; Nortcliff and Robison, 1998).

To assess whether the monodominance of *P. gracilipes* is related to edaphic factors at a mesoscale, we examined the distribution and abundance of *P. gracilipes* and other common species on Maracá Island in relation to soil attributes, taking advantage of an existing network of 30 permanent plots systematically spread over an area of 25 km² (Fig. 1).

2. Material and methods

2.1. Study plots

The study was conducted in 30 plots that had been established following the guidelines of Magnusson et al. (2005) and Pezzini et al. (2012) and that were adopted by the Brazilian Programme for Biodiversity Research (PPBio). Each plot was defined by a 250-m central line that followed topographic isoclines. The width of the plot was 20 m (0.5 ha) for trees with diameter at breast height (DBH) ≥ 30 cm and 10 m (0.25 ha) for trees with dbh ≥ 10 cm. All trees sampled were mapped, tagged and measured for DBH by the PPBio inventory team between 2007 and 2008, while the aforementioned six most abundant species were identified in 2009. Using these data, we calculated basal area per hectare for each species in each plot.

Topographic characteristics of plots (elevation and slope) and chemical and texture data for soils were obtained from Pimentel and Baccaro (2011). Physical (gravimetric humidity, particle size) and chemical (Ca, Fe, K, Mg, Mn, P and Zn in mg/kg; pH) analyses were carried out at the Soil and Plant Thematic Laboratory - LTSP/INPA (Pimentel and Baccaro, 2011) on a bulked mixture of six soil surface (0–15 cm) samples collected from each plot at 50 m intervals (0, 50, 100, 150, 200 and 250 m) using the 250-m central line. The samples were air-dried at room temperature and sieved through a 2 mm mesh. We additionally calculated the Mg:Ca ratio given that previous research has shown it to be potentially important variable explaining monodominance in *Peltogyne*-dominated forests (Nascimento et al., 1997;

Milliken and Ratter, 1998; Nortcliff and Robison, 1998).

2.2. Data analysis

We aimed to determine how the natural logarithm of basal area (m²/ha) for the six dominant species was related to topographical and soil variables. Slope, Ca, Fe, Mg, Mn, and Zn were log-transformed prior to modeling to bring in extreme values and reduce heteroscedasticity. We then used a principal component analysis (based on the correlation matrix among variables) to reduce the dimensionality of the data and the number of explanatory variables for use in downstream analyses. The first three variables each explained > 10% of the variation in the raw environmental data (30%, 18%, and 13% respectively) and a scree plot visualization showed a significant drop off in variation explained amongst subsequent axes (all < 8%). We therefore selected these three axes for statistical modeling. The variables with the greatest loadings (correlation coefficients ≥ 0.30) on the first three axes were the following (numbers in brackets are correlation coefficients with the given axis): Mn (0.42), Ca (0.39) and Al (−0.31) on the first axis; elevation (0.41), Mg:Ca ratio (−0.39), P (−0.37), Mg (−0.33), Al (−0.33), Fe (−0.32) and silt (−0.30) on the second axis; and sand(-0.44), pH (−0.40), elevation (0.37), clay (0.35) and Fe (−0.33) on the third axis.

As most species are absent in at least a few of the plots, we employed hurdle models with a log-normal response to model the variation in basal area over environmental gradients on Maracá Island. These models are analogous to zero-inflated models often used for count data (e.g. zero-inflated poisson), except that they are suitable for continuous (i.e. non-integer), positive data where the response variable has many zeros (Croissant et al., 2014). Essentially, these are two-part models where the 'first part' of the model represents a binomial presence/absence model and the 'second part' of the model models the variation in basal area when the species is present. This modeling approach is advantageous as it allows simultaneous consideration of presence/absence and basal area variation within the same statistical framework, which in turn allows for straightforward comparisons of all possible models within an information criterion framework (Burnham and Anderson, 2002).

Following recommendations in Burnham and Anderson (2002), we first constructed a 'full model' where we incorporated the first three principal components. We compared this to a null model without any explanatory variables on either side of the model using the Akaike Information Criterion, corrected for small sample size (AICc). If the null model gave a lower AICc value than the full model, we did not consider any further models and concluded that the measured edaphic variables did not significantly explain variation in presence/absence or basal area of species. If the full model gave a lower AICc value, we then dropped all explanatory variables that were not significant (p > 0.05) based on the value of their t-statistic (Cade, 2015). The AICc of this reduced model was evaluated and then compared to models where we dropped each of the remaining explanatory variables in turn. If the AICc value did not drop by > 2 units when a given variable was removed, it was dropped from the final model. For final model validation, we extracted the residuals and examined them for normality, homoscedasticity, and spatial autocorrelation using spatial correlograms with Moran's I. In order to evaluate and compare model fit across species, we used a pseudo-R^2 value based on the relative value of the residual sum of squares compared to the total sum of squares (Croissant et al., 2014). All analyses were conducted in the R Statistical Environment v3.02 (R Core Development Team 2016) using functions in the base, vegan (Oksanen et al., 2014), and mhurdle packages (Croissant et al., 2014).

3. Results

We give a summary of the results from the hurdle models in Table 1. The presence/absence and basal area of *P. gracilipes* were negatively related to the second principal component (PC2), which means the

Table 1

Summary of hurdle model results for each species. The explanatory variables (principal components of environmental variation) retained in the final model for each species are given as well as the value of the t-statistic for the given variable (in brackets). The sign of the t-statistic indicates whether the presence or basal area of a species is positively or negatively related to the principal component, while the magnitude of the t-statistic provides a relative measure of the importance of the component. The R^2 values represent the pseudo-coefficient of determination. See main text for further details.

Species	Presence/Absence	Basal area	R^2
A. aculeatum	PC2 (+2.18), PC3 (+2.67)	NA	0.31
A. maripa	NA	NA	0.00
E. guianensis	NA	NA	0.00
L. kunthiana	PC2 (+2.27), PC3 (+2.78)	NA	0.44
P. gracilipes	PC2 (−2.31)	PC2 (−4.76), PC3 (−4.10)	0.66
P. surinamensis	NA	NA	0.00

species is more likely to occur and achieve higher basal in plots at lower elevations (see also Fig. 1) with higher values of the Mg:Ca ratio and higher P, Mg, Al and Fe concentrations and silt content in the soil. The basal area of *P. gracilipes* also showed a negative relationship with the third principal component (PC3), which means it is more likely to achieve high basal area in environments with high sand content, low clay continent and high pH values. In contrast to *P. gracilipes*, both *A. aculeatum* and *L. kunthiana* showed a lower probability of occurring at low values of PC2 and PC3. None of the final models for these three species showed significant spatial autocorrelation in the residuals. Meanwhile, the measured environmental variables did not show any significant relationships with the presence/absence or basal area of *A. maripa*, *E. guianensis* or *P. surinamensis*.

4. Discussion

In the forests of Maraca Island, *P. gracilipes* seems unique in being able to achieve extraordinarily high biomass (Nascimento et al., 2014). It is the only species to represent greater than 50% of basal area in any of the 30 plots surveyed, and it does so in five of them (Fig. 1). Our analyses of the potential drivers of this monodominance demonstrate that it is achieved in plots with particular environments, namely low elevation, soils with high silt and sand, but low clay content, high Mg:Ca ratios, high Mg, Fe and Al concentrations, and high pH values. Meanwhile, these are the same environmental conditions under which two of the five other species considered are significantly less likely to occur (*A. aculeatum* and *L. kunthiana*). Our observational approach does not allow us to distinguish whether it is the unique environmental characteristics of these plots or the high basal area of *P. gracilipes* that reduces the probability of occurrence of *A. aculeatum* and *L. kunthiana* in these plots. Similarly, our analyses cannot definitively demonstrate that the monodominance of P. gracilipes in these sites is due to the environmental conditions *per se*. However, it is noteworthy that the presence/absence and basal area of *P. gracilipes* show a stronger relationship with the measured environmental conditions than the other five most common species on Maraca Island (as measured by pseudo-R^2) and that *P. gracilipes* is the only species for which basal area shows a significant relationship with environmental conditions.

Given the small number of plots surveyed (n = 30) and that many of the measured environmental variables are correlated with each other, we were not able to distinguish which of the measured variables were most related to monodominance of *P. gracilipes*. However, areas dominated by *P. gracilipes* had Mg concentration on soils about 4 mmolc kg^{-1}, values higher than found for most Amazon soils (Quesada et al., 2010). Previous research (Nascimento et al., 1997; Nortcliff and Robison, 1998) has also suggested that the Mg:Ca ratio and Mg content are important factors to explain the dominance of *P. gracilipes* on Maracá Island. As pointed out by Villela and Proctor (1999, 2002), these differences in soil composition between areas dominated by *P. gracilipes* and areas where *P. gracilipes* is absent may be related to the

ability of *P. gracilipes* to accumulate Mg, with its litterfall being a source of Mg in surface soil. Meanwhile, the parent material is likely to be the primary source of magnesium in soils of areas dominated by *P. gracilipes* (Nascimento and Proctor, 1997). Parent material has been highlighted by different authors as an important source of mineral elements in surface soils of some tropical forests (Burnham, 1989; Melo et al., 2000).

Nascimento and Proctor (1997) suggested that *P. gracilipes*-dominated forests are expanding over Maracá, albeit slowly, owing to its poorly dispersed seeds. Our results here reinforce previous studies in showing a relationship between monodominance of *P. gracilipes* and high Mg soils, but they do not allow us to determine the relative importance of magnesium *per se* versus poor drainage in facilitating monodominance. A crucial and unanswered question is whether *P. gracilipes* can dominate on low-magnesium soils. To address this question, future research, ideally using an experimental approach, is needed to explore the potential interactions between magnesium and seasonally high water tables.

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