



RESEARCH ARTICLE

# Pioneer palm tree as an ecosystem engineer: Effects on ant community structure

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## Abstract

Ecosystem engineer species can affect the assembly and maintenance of biological communities by altering local environmental conditions. Several palm tree species play this role in changing the surrounding environment mainly through the fall of entire rachis and the formation of a thick and homogeneous leaf litter layer beneath the canopy. However, their impact on soil animal communities remains unclear. In particular, soil organisms (e.g. ants) can be negatively affected by palm-driven local changes, since they are especially susceptible to leaf litter changes. Our objective was to test if the presence of palm trees reduces alpha and beta diversities of ant communities at taxonomic and morphometric levels. We also tested if palm tree understory mound (debris pile just below the canopy) area and population density reduce ant community alpha and beta diversities (at the taxonomic and morphometric levels) in tropical rainforests. To do so, we described taxonomic and morphometric diversity patterns of ant communities in a relictual landscape of the Atlantic Rainforest (northeastern Brazil) using Hill's numbers approach in two habitats: understory mounds surrounding the palm tree species *Acrocomia intumescens*, and forest understory without *A. intumescens* (non-palm understory). Our main findings were: (1) Taxonomic and morphometric alpha diversity were similar between *A. intumescens* understory mound and non-palm understory; (2) Ant communities in non-palm understory presented higher beta diversity than communities from *A. intumescens* understory mounds considering both rare species and morphometric traits; (3) *A. intumescens* understory mound area negatively affected common and dominant ant species; and (4) the interaction between understory mound area and the population density of *A. intumescens* affected dominant ant species in complex ways and the outcomes depend on the balance between both predictors. Our findings point to an important role of palm trees as ecosystem engineers in reducing ant biodiversity and changing the functional signature of human-modified tropical rainforests.

## KEY WORDS

beta diversity, human-modified tropical rainforest, morphometric diversity, palm tree hyperproliferation, taxonomic diversity

## INTRODUCTION

Ecosystem engineer species promote physical and/or chemical changes in the environment affecting the availability of resources for other species, shifting microclimatic conditions, and altering surrounding communities (Losapio et al., 2021). For example, the presence of pioneer palm tree species (e.g. Arecaceae: *Atalaya oleifera*) leads to the deposition of old rachises (and other debris), creating a thick leaf litter layer, which results in a structurally simplified environment at the ground level (Peters et al., 2004). Consequently, the presence of palm trees can impose reductions in species richness and compositional changes in tropical rainforest plant communities by preventing seed germination and seedling recruitment (Aguiar & Tabarelli, 2010). This natural process keeps the ground-level environment surrounding palm trees, which is covered by their fallen debris (the palm tree understory mounds) in a constant stage of initial succession, since it limits the occurrence of shade-tolerant species (Aguiar & Tabarelli, 2010), and could drive plant communities into biotic homogenization, with lower beta diversity if compared to the forest understory free of palm trees influence (Martínez-Ramos et al., 2016).

In human-modified tropical rainforests, the organizational dynamics of natural communities have been severely altered (Carrara et al., 2015). For example, after habitat loss, fragmentation, and formation of forest edges, there is a consistent change in species composition of tree communities, with a small number of pioneer tree species replacing a greater number of shade-tolerant tree species (Tabarelli et al., 2012). In this scenario, several palm tree species, belonging to different genera and from different tropical ecosystems increase their population density (Aguiar & Tabarelli, 2010; Martínez-Ramos et al., 2016; Souza & Martins, 2003). The increase in palm tree recruitment rates occurs in response to edge-induced increased light availability (Souza & Martins, 2003) and changes in the dynamics of seed predation and seed dispersal, as reported for *Atalaya oleifera* (Pimentel & Tabarelli, 2004). The high population density of such palm tree species reinforces the mechanisms which allow their hyperproliferation, preventing full forest regeneration after disturbances (i.e. treefall gaps, habitat loss and edge effects), and could contribute to the so-called arrested succession (Schnitzer et al., 2000) in edge-affected forests.

Because of this edge-driven palm tree hyperproliferation, a high proportion of tropical rainforest understory could be altered by the fallen rachises which dominate leaf litter under palm tree canopies and those alterations might spread from plants throughout ground-dwelling organisms, like arthropods. The impact of hyperproliferation of uncultivated palm trees on plant communities is well known and documented (Aguiar & Tabarelli, 2010; Martínez-Ramos et al., 2016), but their impact on edaphic animal assemblages, like ants, remains barely explored. For instance, it is known that arthropod communities, including ant communities (Franken et al., 2013), in areas affected by fallen palm tree branches and rachises present lower species richness (Holmquist et al., 2011) if compared to areas free of palm trees influence. However, we still do not know to what extent bigger palm trees, which may produce more leaf litter and bigger forest canopy gaps, elicit more shifts in ant communities, and it is poorly understood if ant communities also face biotic homogenization due to the simplified ground environmental conditions generated by the presence of palm trees (i.e. simplified leaf litter; Peters et al., 2004).

Additionally, the effects of simplified habitats on ant communities might spread from taxonomic to functional level and such environments may support functionally similar ant species and harbour ant communities which also face functional biotic homogenization. Functional diversity can be

assessed based on species morphometric characteristics which represent species adaptation to environmental conditions (Silva & Brandão, 2010). Then, assessing morphometric trait values and their between-sites variations provides important insights into functional community structure, ecosystem resilience, and response capacity to future disturbances (Liu et al., 2016; Martello et al., 2018).

Ants are present in almost all terrestrial ecosystems, and they are abundant (Underwood & Fisher, 2006), develop interactions that are important for population maintenance of several plant species (Oliveira & Koptur, 2017), and influence soil physical and chemical properties (Gomes et al., 2010). Simultaneously, plant diversity (and also the diversity of produced leaf litter) is important to maintain ant diversity since plants provide habitat structure, food sources, and suitable local microclimatic conditions (Ribas et al., 2003). Additionally, through litter deposition, they alter the roughness of the substrate on which the ants move (Alma et al., 2019; Kaspari & Weiser, 1999), affecting ant nesting behaviour, foraging activity, and species richness (Queiroz et al., 2013). Consequently, modified leaf litter surrounding palm trees may act on ant morphometric traits related to foraging activity (e.g. leg, mandible, and eye length), preferential food resource (e.g. mandible length), and environmental chemical perception (e.g. antenna length). Based on this, ants are an excellent model to understand whether the negative effects of palm trees leaf litter on plants extend to other organisms. Particularly, in this study, it is expected that: (1) ant communities in *A. intumescens* understory (i.e. region just below the canopy which is covered by fallen debris) present lower taxonomic and morphometric alpha and beta diversities if compared to areas free of palm trees influence (non-palm understory), and (2) increases in *A. intumescens* understory mounds area (i.e. area of the region just below the canopy which is covered by fallen debris) and population density may reduce taxonomic and morphometric alpha and beta diversities of ant communities.

## MATERIAL AND METHODS

### Study area

The study was carried out at the Mata do Pau Ferro State Park, located in the municipality of Areia, state of Paraíba, Northeastern Brazil, is a remnant of the Atlantic Rainforest at the Borborema mountains, which is considered a relictual landscape of Atlantic Tropical Rainforest embedded in a semi-arid region covered by Caatinga vegetation (Barbosa et al., 2004), a seasonally dry tropical forest (Pennington et al., 2009). The Mata do Pau Ferro State Park is a 600ha forest fragment, with an altitude ranging between 400 and 600m, average annual temperature of 22°C, relative air humidity around 85%, and annual rainfall of 1500 mm (Pôrto et al., 2004). Mata do Pau Ferro State Park is home to a great floristic richness with 309 species of angiosperms described, with speciose plant families like Rubiaceae, Malvaceae, and Solanaceae (Barbosa et al., 2004). The occurrence of two species of the family Arecaceae, *Attalea oleifera* Barb. Rodr and *Acrocomia intumescens* Drude is registered. The Atlantic Tropical Rainforest covering the coast of Northeastern Brazil (including the high-altitude relictual tropical rainforests) is reduced to a small fraction of its original area, with high levels of forest fragmentation (Crouzeilles et al., 2019). The impact of forest loss and fragmentation in this region rendered a landscape in which 48% of forest remnants are smaller than 10 hectares (Lôbo et al., 2011). In particular, the Borborema mountains region is currently hyper-fragmented due to human activities that promoted the change in land cover, with the

original forest being replaced with various agricultural uses (pastures and monocrops; Pôrto et al., 2004). Even though the establishment of the Mata do Pau Ferro State Park has reduced habitat loss, more localized disturbances such as illegal logging still occur.

## Sampling procedure

### Focal species, *A. intumescens* understory area, and population density

*Acrocomia intumescens* is a palm tree endemic to Northeastern Brazil (de Lima et al., 2018). It forms unique and well-defined understory mounds with old rachises and ripe fruits that are detached from the bunch, forming piles under the canopy around the parent plant stem (hereafter *A. intumescens* understory). We selected 10 palm trees, at least 100m away from each other, based on a georeferenced information system. All palm trees were growing in similar soil and topographic conditions (always flat areas), furthermore, they were intentionally selected to represent different palm tree sizes, understory mounds area, and population density. Additionally, as *A. intumescens* occurs in patchy aggregates of individuals, the 10 selected individuals were growing in different patches. In each of the 10 selected palm trees, we measured the understory mound area by inspecting the distribution of leaf litter from the palm tree (specially composed of old and easily identifiable rachises and fruits) on the ground surface. We considered that palm tree gaps exhibit a near-to-ellipse geometric shape. Consequently, we visually identified and measured the two largest diameters ( $d_1$  and  $d_2$ ) perpendicular to each other and calculated the palm tree understory mound area according to the equation  $A = \pi d_1 d_2$ . *A. intumescens* understory mound area ranged between  $2.12\text{ m}^2$  and  $7.52\text{ m}^2$  (mean  $4.41\text{ m}^2$ ; standard deviation,  $\pm 1.51$ ). To assess population density, we delimited a radius of 10 m around each palm tree considered as an experimental unit, within which we counted the number of palm tree individuals. On average we found 5.20 individuals ( $\pm 6.19$ ) per plot. In two plots, we recorded only the focal palm tree and, considering that we did not include the focal individual in the measurements, the population density of these plots was considered zero. In the plot with the highest density, we recorded 20 palm trees around the focal individual.

## Ant fauna collection

Two collections were carried out, in March and September 2019. For each selected palm tree and its respective palm tree understory mound (i.e. *A. intumescens* understory), we also established an experimental control unit in the forest understory (hereafter non-palm tree understory) at least 20 m away from any palm tree and free of palm tree leaf litter influence. In the two habitats, in the first sample, we set two pitfall traps spaced a half meter apart (traps in the clearings were also spaced half a meter away from palm tree stems). In the second sample, we set six traps per experimental unit. Each trap was made with colourless plastic containers measuring 20 cm in diameter  $\times$  10 cm in height, buried at the ground level, and filled with 200 ml of water, as indicated by Agosti et al. (2000). The samples from the two sampling periods were pulled together before describing taxonomic and morphometric community structures.

The collected specimens were identified to the species level, when possible, following available taxonomic keys (Baccaro et al., 2015; Bolton

et al., 2005). For cases where we were unable to perform species-level identification, we separated them into morphospecies and assigned a code valid only for this study. We considered the abundance of each species as the total number of workers collected in the traps. We are aware of possible bias towards widespread and lonely foraging species (e.g. *Dinoponera quadriceps* in our study system) if trap capture frequency is taken as abundance data, and we are also aware of the bias towards huge ant colonies near traps (i.e. army ants in our study system) if workers count is taken as abundance data (Andersen, 1991). We then opted for the workers counting approach because, according to Andersen (1991) and Arccoverde et al. (2018), data can be treated to control for biases raised by a very high number of individuals from the same colony falling into one or few traps. Consequently, in this work, we counted the number of workers per sampling unit up to the maximum of 100 workers (Arccoverde et al., 2018) and used a square root transformation to minimize the discrepancy in abundance values between species. To check the efficiency of our data collection, we calculated the Chao coverage estimator. The estimator provides a probability between 0 and 1, which means that the closer to 1 is the Chao estimator value, the more efficient is the sample (Chao et al., 1988). A complete set of mounted specimens is kept in the invertebrate collection of the Center of Agrarian Sciences, Federal University of Paraíba.

## Morphometric characterization

In this work, we characterized the morphometric diversity of ant communities based on five morphological traits (body size, relative mandible length, relative eye length, relative antenna length, and relative leg length). For information on ecological meaning and definition of attributes, please, see Table S1. Only the worker caste was considered for the measurements (Silva & Brandão, 2010) and we measured three individuals of each species to obtain an average value of each attribute, except for species that had less than three individuals collected. All morphometric measurements were standardized by dividing their value by the ant body size, except for the body size itself (Arnan et al., 2018). Morphometric traits were measured at the Laboratory of Plant Ecology of the Center of Agricultural Sciences, Federal University of Paraíba, using a stereoscopic microscope with a 10 mm micrometre eyepiece reticle.

## Taxonomic and morphometric alpha diversity

We calculated the taxonomic alpha diversities of each sampling unit using Hill numbers (Jost, 2006). Hill numbers can be calculated using the general equation  ${}^qD = \left( \sum_i^S P_i^q \right)^{1/(1-q)}$ , and depend on the value of the parameter “ $q$ ” (called order of diversity) and the relative abundance ( $P$ ) of the species “ $i$ ” (detailed information, Jost, 2006). In this work, we used three orders of diversity to calculate the Hill numbers:  $q = 0$  (hereafter,  ${}^0D$ ), which equals species richness and assigns disproportionate weight to rare species;  $q = 1$  ( ${}^1D$ ), which equals Shannon entropy and weights species importance by its relative abundance, assigning greater weight to common species; and  $q = 2$  ( ${}^2D$ ), which is equivalent to the inverse Simpson concentration, and gives more importance to dominant species in a community (Jost, 2006; Ribeiro-Neto et al., 2016). All analyses were performed using the Vegan package (Oksanen et al., 2020) of the R software (R Development Core Team 2020).



We used the approach proposed in Chao et al. (2014) to describe morphometric alpha diversity because it presents a mathematical framework to adapt Hill numbers to functional data (Chao et al., 2014; Chiu & Chao, 2014). In summary, the derivation for morphometric alpha diversity of Hill numbers is based on Rao Entropy (Botta-Dukát, 2005), and it can integrate the values of morphometric traits measured in a set of species from a community despite abundance distribution, giving more importance to rare ecological functions if  $q = 0$  ( $^0D$ ). Alternatively, it can control for the abundance distribution and gives more importance to common morphometric traits if  $q = 1$  ( $^1D$ ), or it can weight disproportionately abundance distribution, giving more importance to dominant morphometric traits if  $q = 2$  ( $^2D$ ; Chiu & Chao, 2014).

## Taxonomic and morphometric beta diversity

We calculated beta diversity based on Hill numbers as it can be applied to measure both taxonomic and morphometric beta diversities (Chao et al., 2014; Chiu & Chao, 2014). Characterizing beta diversity based on Hill numbers does not require a minimum number of species to calculate morphometric diversity, as in measurements based on functional space (Mason et al., 2013), allowing for unifying the characterization of taxonomic and morphometric diversity. The taxonomic beta diversity is based on local dissimilarity, and, if  $q = 0$ ,  $^0D$  derives from the classic Sørensen index, based on richness, which weights all species equally. If  $q = 1$ ,  $^1D$  approximates the Horn index, based on Shannon entropy, and it is weighted according to the relative abundance of species. Finally, if  $q = 2$ ,  $^2D$  approximates the classic Morisita-Horn index, which is very sensitive to dominant species (detailed information in Chao et al., 2014).

Morphometric beta diversity followed the same Hill numbers approach used in taxonomic beta diversity, and the indices of morphometric beta diversity measure the average proportion of the effective distance in morphometric traits between pairs of species in a given pair of local communities that is shared with all other pairs of communities (Chao et al., 2014; Chiu & Chao, 2014). Then, if  $q = 0$ ,  $^0D$  is calculated from a functional derivation of the Sørensen index, which is insensitive to abundance and gives more importance to rare morphometric traits. If  $q = 1$ ,  $^1D$  is the functional derivation of the Horn index, which weights morphometric traits proportionally to their abundance, and, if  $q = 2$ ,  $^2D$  is the functional adaptation of the Morisita-Horn index, which assigns disproportionate weight to dominant morphometric traits in a community (Chiu & Chao, 2014).

## Data analysis

### Diversity patterns between habitat types

To test whether the sites under the influence of palm trees and their understory mounds (*A. intumescens* understory) harbour communities with lower alpha diversity, both taxonomic and morphometric, in relation to forest sites free of the influence of palm trees understory mounds (non-palm understory), we adjusted pairwise Wilcoxon tests, given that our data did not meet the assumptions of normality and homoscedasticity. To test if *A. intumescens* habitats harbour ant communities presenting lower beta diversity (both, taxonomic and morphometric) if compared to non-palm understory, we fitted Multiple Regression on Distance Matrices (MRM), based on 999 permutations, following (Lichstein, 2007).

## Effect of the *A. intumescens* understory mound area and population density

To test if increased *A. intumescens* understory mound area (measured in m<sup>2</sup>) and population density reduce taxonomic and morphometric alpha diversity (both taxonomic and morphometric) of ant communities, we used adjusted generalized linear models (GLM) with Gaussian error distribution, except for order <sup>0</sup>D of the taxonomic alpha diversity, for which we fitted the model to the Poisson error distribution, as the data did not meet assumptions of normality and homoscedasticity. To test if increasing area of *A. intumescens* understory mounds and population density reduces ant communities' beta diversity (both taxonomic and morphometric), we used Multiple Regression on Distance Matrices (MRM) with Gaussian distribution and 999 permutations (Lichstein, 2007). All analyses were performed in R software (R Development Core Team 2020).

## RESULTS

### Description of local fauna

We sampled 1593 ant workers, 968 in *A. intumescens* understory mounds and, 625 in non-palm understory habitats, belonging to seven subfamilies, 22 genera and, 31 species/morphospecies. On average, we collected 7.50 ( $\pm 1.71$ ) ant species per experimental unit in *A. intumescens* understory mounds and 8.40 ( $\pm 2.27$ ) in non-palm understory habitats. Our sampling appears to have captured the local fauna well, both for the *A. intumescens* understory mounds (Chao estimator = 0.98) and the non-palm understory habitats (Chao estimator = 0.99). The subfamily Myrmicinae was the most diverse (15 morphospecies), followed by Ponerinae (five) (see species list in the Table S2). *Dinoponera quadriceps* was the most frequent ant species in both habitat types. Additionally, six ant species occurred in only one *A. intumescens* understory mound sample, while eight ant species occurred in only one non-palm understory sample (Figure S1). Abundance distribution amongst ant species showed a pattern of a few species occurring at high abundance and several species occurring at low abundance (Figure S2). The morphospecies *Nomamyrmex* sp1 was the most abundant in both habitats, while different groups of low-abundance species (three in *A. Intumescens* understory mounds and four in the non-palm understory) occurred in both habitat types (Figure S2).

In general, individual morphometric traits were not affected by the presence of *A. intumescens* understory, with the exception of relative leg length, which was about 5% longer in non-palm understory habitats (mean  $\pm$  SD:  $0.956 \pm 0.19$ ) if compared to non-palm understory habitats ( $0.918 \pm 0.17$ ;  $t = 2.12$ ;  $p = 0.044$ ). For more detailed description of morphometric trait variation between habitats, please see Table S3.

### Effects of *A. intumescens* understory mounds on the taxonomic and morphometric structure of ant communities

Both taxonomic and morphometric alpha diversities were not affected by the presence of *A. intumescens* understory mounds. Regardless of the order of diversity in question, *A. intumescens* understory and non-palm understory areas supported ant communities with similar levels of rare, common, and dominant species and morphometric traits (Table 1).

**TABLE 1** Taxonomic and morphometric alpha diversity of ant communities from understory mounds surrounding *Acrocomia intumescens* individuals (*A. Intumescens* understory) and from forest understory free of *A. intumescens* influence (non-palm understory) in a relictual landscape of the Brazilian Atlantic Tropical Rainforest. Data represented are median and interquartile range: Median<sub>(iqr range)</sub>. <sup>0</sup>D, <sup>1</sup>D and <sup>2</sup>D refer to the different diversity orders of Hill numbers.

Order	Component	<i>A. Intumescens</i> understory	Non-palm understory	df	V	p
<sup>0</sup> D	Taxonomic	7.00 <sub>(6.25–7.75)</sub>	8.5 <sub>(6.50–9.75)</sub>	9	18	0.351
<sup>1</sup> D	Taxonomic	6.13 <sub>(5.55–7.02)</sub>	7.22 <sub>(5.22–8.66)</sub>	9	21	0.556
<sup>2</sup> D	Taxonomic	5.40 <sub>(5.08–5.92)</sub>	6.33 <sub>(4.26–7.75)</sub>	9	23	0.697
<sup>0</sup> D	Functional	7.27 <sub>(6.56–7.70)</sub>	8.93 <sub>(6.96–9.65)</sub>	9	15	0.232
<sup>1</sup> D	Functional	6.59 <sub>(6.07–6.9)</sub>	7.89 <sub>(5.99–8.86)</sub>	9	20	0.490
<sup>2</sup> D	Functional	6.00 <sub>(5.4–6.4)</sub>	7.06 <sub>(5.3–7.9)</sub>	9	22	0.620

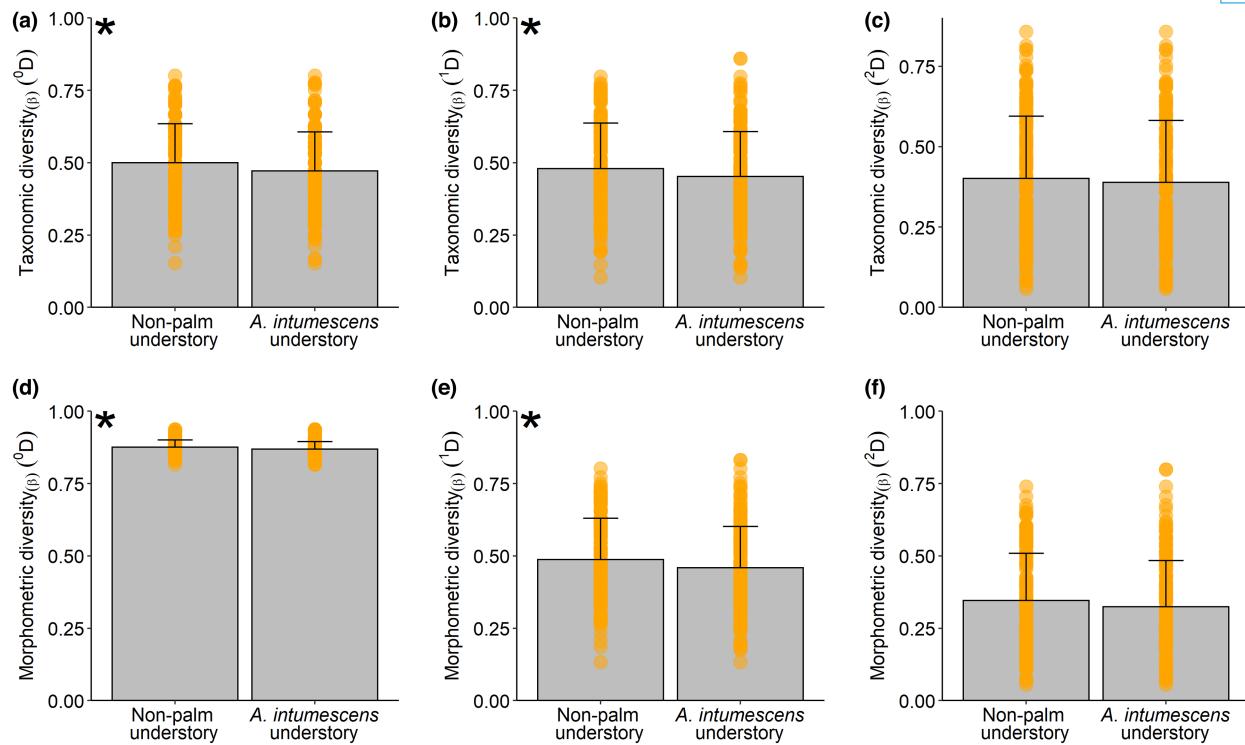
**TABLE 2** Taxonomic and morphometric beta diversity of ant communities from understory mounds surrounding *A. intumescens* individuals (*A. Intumescens* understory) and from forest understory free from *A. intumescens* influence (non-palm understory) in a relictual landscape of the Brazilian Atlantic Tropical Rainforest. Data represented are mean and standard deviation: Mean<sub>(sd range)</sub>. Significant differences according to the multiple regression on distance matrices (MRM) are highlighted in bold. <sup>0</sup>D, <sup>1</sup>D and <sup>2</sup>D refer to the different diversity orders of Hill numbers.

Order	Component	<i>A. Intumescens</i> understory	Non-palm understory	F	p
<sup>0</sup> D	Taxonomic	0.472 <sub>(0.13)</sub>	0.501 <sub>(0.13)</sub>	4.03	<b>0.019</b>
<sup>1</sup> D	Taxonomic	0.453 <sub>(0.15)</sub>	0.481 <sub>(0.16)</sub>	4.32	<b>0.027</b>
<sup>2</sup> D	Taxonomic	0.391 <sub>(0.19)</sub>	0.401 <sub>(0.19)</sub>	3.05	0.080
<sup>0</sup> D	Morphometric	0.874 <sub>(0.02)</sub>	0.892 <sub>(0.02)</sub>	4.42	<b>0.015</b>
<sup>1</sup> D	Morphometric	0.462 <sub>(0.14)</sub>	0.493 <sub>(0.14)</sub>	5.02	<b>0.017</b>
<sup>2</sup> D	Morphometric	0.331 <sub>(0.16)</sub>	0.353 <sub>(0.16)</sub>	3.04	0.065

The presence of *A. intumescens* understory mounds reduced the taxonomic and morphometric beta diversity of ant communities, but, this effect depended on the order of diversity. Considering the diversity of rare species and morphometric traits, when compared to the *A. intumescens* understory mounds, the non-palm understory areas presented order of diversity <sup>0</sup>D about 6% and 2% higher for taxonomic and morphometric beta diversity, respectively (Table 2, Figure 1a,d). For the order of diversity <sup>1</sup>D, taxonomic and morphometric beta diversities were about 7% higher in non-palm understory than in *A. intumescens* understory mounds (Table 2, Figure 1b,e). In contrast, for dominant species and morphometric traits, *A. intumescens* understory mounds and non-palm understory habitats had similar beta diversity levels (Table 2, Figure 1c,f).

### *A. intumescens* mound area, population density, and patterns of taxonomic and morphometric structure of ant communities

Considering taxonomic alpha diversity, the diversity of rare ant species (<sup>0</sup>D) was not affected either by *A. intumescens* understory mound area or by population density (Table 3). The diversity of common (<sup>1</sup>D) and dominant (<sup>2</sup>D) ant species, however, were negatively affected by the increasing



**FIGURE 1** Comparison of taxonomic and morphometric beta diversity of ant communities from tropical rainforest plots influenced by *Acrocomia intumescens* understory mounds (*A. intumescens* understory) and forest understory free of *A. intumescens* influence (non-palm understory) in a relictual landscape of the Brazilian Atlantic Tropical Rainforest. (a) Diversity of order <sup>0</sup>D, which means the beta diversity of rare species. (b) Diversity of order <sup>1</sup>D, which represents the beta diversity of common species. (c) Diversity of order <sup>2</sup>D, which represents the beta diversity of dominant species. (d) Morphometric diversity of order <sup>0</sup>D, which represents the beta diversity of rare morphometric traits. (e) Morphometric diversity of order <sup>1</sup>D, which represents the beta diversity of common morphometric traits. (f) Morphometric diversity of order <sup>2</sup>D, which represents the beta diversity of dominant morphometric traits. \*points to statistically significant differences ( $p \leq 0.05$ ). Yellow dots depict observed values. Grey bars represent the mean and error bars represent the standard error.

*A. intumescens* understory mound area (Table 2; Figure 2a,b) but did not respond to increasing population density of *A. intumescens*.

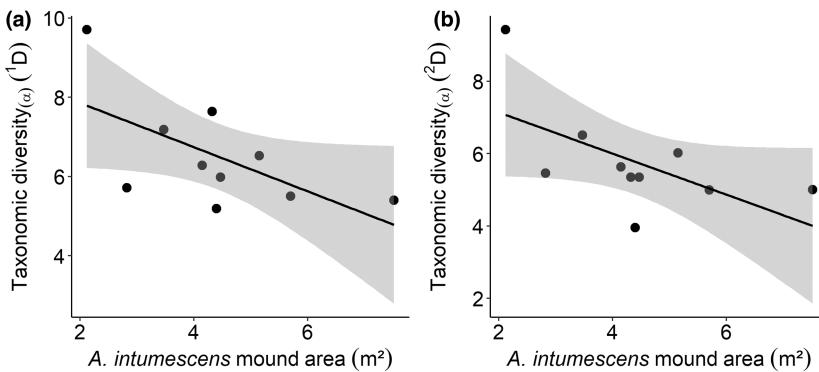
Additionally, we found an interactive effect between *A. intumescens* understory mound area and population density on the diversity of dominant ant species (<sup>2</sup>D; Table 3; Figure 3). Forest spots harbouring a high population density of small *A. intumescens* individuals, which produce small understory mounds, presented the highest <sup>2</sup>D values (Figure 3). In such a scenario, increasing area of *A. intumescens* mounds led to decreasing dominant ant species diversity (<sup>2</sup>D), but this effect tended to fade out towards forest patches where *A. intumescens* occurred in low population density (Figure 3). Similarly, forest spots harbouring a high population density of big *A. intumescens* individuals, which produce big understory mounds, presented the lowest values of <sup>2</sup>D (Figure 3). The reduction in *A. intumescens* population density, however, elicited opposite effects in forest patches affected by big *A. intumescens* mounds. On one side, if *A. intumescens* understory mounds are huge, reduced population density led to increased dominant ant species diversity (<sup>2</sup>D). Otherwise, if *A. intumescens* understory mounds are small, decreasing *A. intumescens* population density reduced dominant ant species diversity (Figure 3). Additionally, if population density is small, increasing *A. intumescens* understory mound area did not affect dominant ant species diversity (<sup>2</sup>D). Finally, the morphometric alpha diversity patterns, as well as the taxonomic and morphometric beta diversity patterns, were not affected either by the understory mounds area or by the population density of *A. intumescens*, regardless of the order of diversity (Table 3).

**TABLE 3** Effects of understory mound area and population density of *A. intumescens* on taxonomic and morphometric alpha (tested through generalized linear models – GLM) and beta (tested through multiple regression on distance matrices – MRM) diversity patterns of ant communities in a relictual landscape of the Brazilian Atlantic Tropical Rainforest. Significant differences are highlighted in bold. <sup>0</sup>D, <sup>1</sup>D and <sup>2</sup>D refer to the different diversity orders of Hill numbers. NA – Not available.

Order	Diversity	Component	Explanatory variable	R <sup>2</sup>	df	F	p
<sup>0</sup> D	Alpha	Taxonomic	<i>A. intumescens</i> understory mound area	0.29	8	3.51	0.373
			Population density		7	2.31	0.984
			<i>A. intumescens</i> understory mound area*Population density		6	2.30	0.643
<sup>1</sup> D	Alpha	Taxonomic	<i>A. intumescens</i> understory mound area	0.65	8	6.26	<b>0.046</b>
			Population density		7	1.06	0.341
			<i>A. intumescens</i> understory mound area*Population density		6	3.89	0.096
<sup>2</sup> D	Alpha	Taxonomic	<i>A. intumescens</i> understory mound area	0.75	8	8.06	<b>0.030</b>
			Population density		7	3.20	0.123
			<i>A. intumescens</i> understory mound area*Population density		6	7.24	<b>0.036</b>
<sup>0</sup> D	Alpha	Morphometric	<i>A. intumescens</i> understory mound area	0.190	8	1.20	0.370
			Population density		7	0.00	0.980
			<i>A. intumescens</i> understory mound area*Population density		6	0.22	0.650
<sup>1</sup> D	Alpha	Morphometric	<i>A. intumescens</i> understory mound area	0.400	8	2.75	0.140
			Population density		7	0.29	0.600
			<i>A. intumescens</i> understory mound area*Population density		6	0.99	0.350
<sup>2</sup> D	Alpha	Morphometric	<i>A. intumescens</i> understory mound area	0.580	8	4.27	0.060
			Population density		7	1.07	0.330
			<i>A. intumescens</i> understory mound area*Population density		6	2.34	0.170
<sup>0</sup> D	Beta	Taxonomic	<i>A. intumescens</i> understory mound area	0.040	NA	0.05	0.335
			Population density		NA	0.04	0.667
<sup>1</sup> D	Beta	Taxonomic	<i>A. intumescens</i> understory mound area	0.030	NA	0.68	0.340
			Population density		NA	0.67	0.742
<sup>2</sup> D	Beta	Taxonomic	<i>A. intumescens</i> understory mound area	0.020	NA	0.43	0.405
			Population density		NA	0.42	0.815
<sup>0</sup> D	Beta	Morphometric	<i>A. intumescens</i> understory mound area	0.050	NA	0.66	0.324
			Population density		NA	0.65	0.460
<sup>1</sup> D	Beta	Morphometric	<i>A. intumescens</i> understory mound area	0.030	NA	0.41	0.286
			Population density		NA	0.42	0.839
<sup>2</sup> D	Beta	Morphometric	<i>A. intumescens</i> understory mound area	0.020	NA	0.38	0.407
			Population density		NA	0.37	0.773

## DISCUSSION

Alterations promoted by *A. intumescens* partially affected the ant fauna, since: (1) taxonomic and morphometric alpha diversities remain unchanged despite the presence or absence of palm trees, suggesting a mechanism for maintaining alpha diversity between habitats; (2) ant communities in non-palm understory habitats present higher beta diversity than ant communities in areas under the influence of *A. intumescens* understory mounds considering both rare species and rare morphometric traits; (3) *A. intumescens* understory mound area negatively affects common and dominant species in ant communities; and (4) interactive effects between

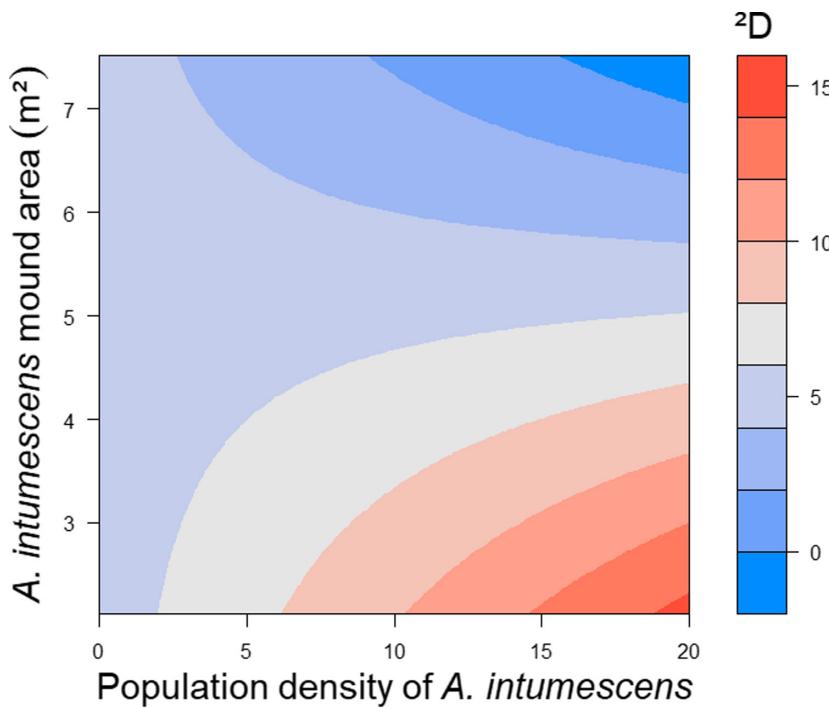


**FIGURE 2** Effect of increasing understory mound area surrounding individuals of *Acrocomia intumescens* on the taxonomic alpha diversity of ant communities in a relictual landscape of the Brazilian Atlantic Tropical Rainforest. (a) Diversity of order <sup>1</sup>D, which represents the diversity of common species. (b) Diversity of order <sup>2</sup>D, which represents the diversity of dominant species.

understory mound area and population density of *A. intumescens* are complex, affect only dominant ant species diversity and their outcomes depend on the balance between both predictors. Taken together, these results suggest that, in disturbed forests, increased habitat area affected by palm trees (due to both increases in palm tree size, producing high amount of debris, and palm trees population density) can lead to losses of taxonomic and morphometric diversity of ant communities in tropical rainforests.

Our findings differ from those observed for plants, which demonstrated a consistent reduction in alpha diversity in areas under the influence of palm trees compared to areas of the tropical rainforests free of their influence (Aguiar & Tabarelli, 2010). Theoretically, for organisms that forage interstitially, like ants, it is expected that more heterogeneous habitats (leaf litter in the understory of non-palm areas, in our study) harbour greater alpha diversity (taxonomic and morphometric) since more species (with more diverse morphometric traits) can meet their demand for resources (Fahrig et al., 2011). For ants, particularly, diversified leaf litter may be a very important environmental feature as described in the literature (Kaspari & Weiser, 1999; Queiroz et al., 2013). Nevertheless, the relationships between environmental heterogeneity and increased alpha diversity are not always simple and positive, as the increase in environmental heterogeneity may represent a decrease in the availability of preferred habitats for some species, which may lead to population reduction and/or the need to migrate to the suitable/preferred habitat (Fahrig et al., 2011). The maintenance of taxonomic and morphometric diversity emerges at multiple locations and scales due to changes in species composition, local adaptations, and niche preferences (Vellend et al., 2013). In particular, we relate our findings to species-specific habitat requirements, leading to the replacement of species and morphometric traits between different types of habitats (i.e. *A. intumescens* and non-palm understory), keeping alpha diversity unchanged. For example, in our data set, species of the genus *Anochetus* and *Rasopone* were found just in non-palm understory samples, while the species *Megalomyrmex ayri* was recorded only in *A. intumescens* understory patches.

Areas under the influence of palm trees showed reduced beta diversity (taxonomic and morphometric), particularly of rare species and morphometric traits which may indicate some degree of biotic homogenization. One of the best known and widely studied mechanisms that promote a decline in beta diversity is the simplification of habitats (Filgueiras et al., 2021), in our



**FIGURE 3** Effect of the interaction between *A. intumescens* mound area ( $\text{m}^2$ ) and population density of *A. intumescens* on taxonomic alpha diversity of order  ${}^2\text{D}$  of ant communities from a relictual landscape of the Brazilian Atlantic Tropical Rainforest.  ${}^2\text{D}$  represents the diversity of dominant species in the community. Cool colours represent lower diversity values, while warm colours represent higher diversity values.

case, it is promoted by palm trees mainly through the constant deposition of leaf litter around the stem (Martínez-Ramos et al., 2016). *Acrocomia intumescens* acts similarly to other ecosystem engineer species, such as *Atta* leaf-cutting ants, which have been proven to promote the simplification of natural habitats through cutting off seedlings that grow on nests (Meyer et al., 2011) in several ecosystems like seasonally dry tropical forests (Knöchelmann et al., 2020), Cerrado, the Brazilian savannas (Costa et al., 2018), and tropical rainforests (Meyer et al., 2011). In simplified habitats, there is a consistent reduction in beta diversity in assemblages of various taxa, such as plants, spiders and, beetles (Merckx et al., 2018; Ribeiro-Neto et al., 2016), which can be dominated by organisms with similar life-history traits that make them adapted to disturbances (Merckx et al., 2018). Our results support the view suggested by Martínez-Ramos et al. (2016), which places the proliferation of palm trees as a filter of diversity in tropical forests, and indicates that damage to ant biodiversity may be more severe on rare species and morphometric traits, which theoretically should exhibit greater risk of local extinction.

Although our findings depart partially from our expectations because they are restricted to taxonomic alpha diversity, the interaction between understory mounds area and population density of palm trees can have a synergistic effect. Our results show that forest spots supporting a high number of huge palm trees, which produce huge understory mounds harbour less dominant ant species, but it is context-dependent as forest spots supporting lower numbers of huge palm trees harbour higher diversity of dominant ant species. Thus, tropical rainforest spots affected by palm trees can have important consequences for the diversity of ant species as anthropogenic disturbances favour the hyperproliferation of palm trees. It is expected that less disturbed tropical rainforest landscapes must present a low population density of palm trees (Souza & Martins, 2003), which, given enough

time, could reach a big size, producing big understory mounds. Under this scenario, it is expected higher habitat heterogeneity, particularly on the ground surface due to the canopy gaps produced by palm trees, which can lead to the occurrence of high sunlight spots in a shaded forest understory. It meets exactly the situation which rendered the highest diversity of dominant ant species in this work. Similarly, in tropical rainforest landscapes facing long-term deforestation, fragmentation, and edge effects, it is expected increased palm tree population density (Martínez-Ramos et al., 2016) and, given enough time, palm trees must become huge and produce huge understory mounds too. Under this scenario, it is expected a more homogeneous habitat at the ground surface because the huge palm tree understory mounds could become closer or even superimpose each other, and it meets the conditions that rendered the lowest diversity of dominant ants in this work. Literature also points out that in mature tropical rainforests, ant species may show niche complementarity, with every ant species being important to the total niche space of the community, while in tropical rainforests in earlier successional stages, ant species show lower niche complementarity and higher functional redundancy (Rocha-Ortega et al., 2018). Given that, this palm tree understory mound-adapted subset of ant species should be ecologically redundant and should spread out through the disturbed forest floor following the hyperproliferation of palm trees, potentially contributing to the arrested succession in edge-affected tropical rainforests (Lôbo et al., 2011).

The loss of habitats in tropical regions is predicted to intensify in the future (d'Annunzio et al., 2015), and so is the proliferation of disturbance-adapted organisms (Kress & Krupnick, 2022), such as *A. intumescens* (Aguiar & Tabarelli, 2010; Peters et al., 2004), which may reinforce the environmental conditions that trigger their hyperproliferation. Our findings, showing the negative effect of *A. intumescens* debris on taxonomic alpha diversity and taxonomic and morphometric beta diversities of ant communities, point to an important role of palm trees in reducing biodiversity in disturbed tropical rainforests. These effects should be linked to the role of *A. intumescens* as an ecosystem engineer, through modulating ecological filters in tropical forests (Martínez-Ramos et al., 2016), and through the simplification of leaf litter around palm tree stems. The small-scale *A. intumescens*-driven changes in ant biodiversity reinforce (and extend to soil arthropods) the notion that hyperproliferating pioneer plant species can change the functional signature of human-modified tropical rainforests. With this, the intensification of disturbances in tropical rainforests and the consequent increase in the palm tree-affected area could compromise the quality and efficiency of ecological services provided by ants throughout tropical ecosystems, potentially reducing ecosystem resilience and response capacity to future disturbances.

## AUTHOR CONTRIBUTIONS

**Anderson Dantas:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); writing – original draft (equal); writing – review and editing (equal). **Thais A. Vitoriano Dantas:** Investigation (equal); methodology (equal); project administration (equal); resources (equal). **José Domingos Ribeiro-Neto:** Conceptualization (equal); data curation (equal); formal analysis (equal); resources (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal).

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### CONFLICT OF INTEREST

The authors fully agree with the submission of the manuscript and have no conflicts of interest.

### DATA AVAILABILITY STATEMENT

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

### ETHICS APPROVAL

Not applicable.

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### REFERENCES

- Agosti, D., Majer, J.D., Alonso, L.E. & Schultz T.R. (2000) ANTS: *Standard methods for measuring and monitoring biodiversity*.  
Aguiar, A.V. & Tabarelli, M. (2010) Edge effects and seedling bank depletion: the role played by the early successional palm *Attalea oleifera* (Arecaceae) in the Atlantic forest. *Biotropica*, 42, 158–166.  
Alma, A.M., Farji-Brener, A.G. & Elizalde, L. (2019) When and how obstacle size and the number of foragers affect clearing a foraging trail in leaf-cutting ants. *Insectes Sociaux*, 66, 305–316.  
Andersen, A.N. (1991) Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. *Austral Ecology*, 16, 273–279.  
Arcoverde, G.B., Andersen, A.N., Leal, I.R. & Setterfield, S.A. (2018) Habitat-contingent responses to disturbance: impacts of cattle grazing on ant communities vary with habitat complexity. *Ecological Applications*, 28, 1808–1817.  
Arnan, X., Arcoverde, G.B., Pie, M.R., Ribeiro-Neto, J.D. & Leal, I.R. (2018) Increased anthropogenic disturbance and aridity reduce phylogenetic and functional diversity of ant communities in caatinga dry forest. *Sci. Total Environ.*, 631-632, 429–438.  
Baccaro, F.B., Feitosa, R.M., Fernandez, F., Fernandes, I.O., Izzo, T.J., Souza, J.D. et al. (2015) *Guia para os gêneros de formigas do Brasil*. Manaus: Editora INPA, p. 388.  
Barbosa, M.R.d.V., Agra, M.d.F., Sampaio, E.V.S.B., Cunha, J.P.d. & Andrade, L.A.d. (2004) Diversidade Florística na Mata do Pau-Ferro, Areia, Paraíba. In: *Brejos de altitude em Pernambuco e Paraíba: história natural, ecologia e conservação*. Brasília: Ministério do Meio Ambiente, pp. 111–122.  
Bolton, B., Alpert, G., Ward, P.S. & Naskrecki, P. (2005) *Bolton'S catalogue of ants of the world*. Cumberland, RI: Harvard University Press.  
Botta-Dukát, Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16, 533–540.  
Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J.H., Schondube, J.E., de Freitas, S.M. & Fahrig, L. (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biol. Conserv.*, 184, 117–126.  
Chao, A., Chiu, C.H. & Jost, L. (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, 45, 297–324.  
Chao, A., Lee, S.-M. & Chen, T.-C. (1988) A generalized Good's nonparametric coverage estimator. *Chinese J. Math.*, 16, 189.  
Chiu, C.H. & Chao, A. (2014) Distance-based functional diversity measures and their decomposition: a framework based on hill numbers. *PLoS One*, 9, e100014.

- Costa, A.N., Bruna, E.M. & Vasconcelos, H.L. (2018) Do an ecosystem engineer and environmental gradient act independently or in concert to shape juvenile plant communities? Tests with the leaf-cutter ant *Atta laevigata* in a neotropical savanna. *PeerJ*, 6.
- Crouzeilles, R., Santiami, E., Rosa, M., Pugliese, L., Brancalion, H.S.P., Rodrigues, R.R. et al. (2019) There is hope for achieving ambitious Atlantic Forest restoration commitments. *Perspect. Ecol. Conserv.*, 17, 80–83.
- d'Annunzio, R., Sandker, M., Finegold, Y. & Min, Z. (2015) Projecting global forest area towards 2030. *Forest Ecology and Management*, 352, 124–133.
- de Lima, N.E., Carvalho, A.A., Meerow, A.W. & Manfrin, M.H. (2018) A review of the palm genus *Acrocomia*: neotropical green gold. *Organisms, Diversity and Evolution*, 18, 151–161.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J. et al. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14, 101–112.
- Filgueiras, B.K.C., Peres, C.A., Melo, F.P.L., Leal, I.R. & Tabarelli, M. (2021) Winner–loser species replacements in human-modified landscapes. *Trends in Ecology & Evolution*, 36, 545–555.
- Franken, E.P., Baccaro, F.B. & Gasnier, T.R. (2013) Is there a refuge for ants in litter accumulated at the base of *Attalea attaleoides* (Barb.Rodr.) Wess.Boer (Arecaceae). *Entomotropica*, 28, 27–37.
- Gomes, J.P., Iannuzzi, L. & Leal, I.R. (2010) Response of the ant community to attributes of fragments and vegetation in a northeastern Atlantic rain forest area, Brazil. *Neotrop. Entomol.*, 39, 898–905.
- Holmquist, J.G., Schmidt-Gengenbach, J. & Slaton, M.R. (2011) Influence of invasive palms on terrestrial arthropod assemblages in desert spring habitat. *Biological Conservation*, 144, 518–525.
- Jost, L. (2006) Entropy and diversity. *Oikos*, 113, 363–375.
- Kaspari, M. & Weiser, M.D. (1999) The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology*, 13, 530–538.
- Knoechelmann, C.M., Oliveira, F.M.P., Siqueira, F.F.S., Wirth, R., Tabarelli, M. & Leal, I.R. (2020) Leaf-cutting ants negatively impact the regeneration of the caatinga dry forest across abandoned pastures. *Biotropica*, 52, 686–696.
- Kress, W.J. & Krupnick, G.A. (2022) Lords of the biosphere: plant winners and losers in the Anthropocene. *Plants, People, Planet*, 4, 1–17.
- Lichstein, J.W. (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology*, 188, 117–131.
- Liu, C., Guénard, B., Blanchard, B., Peng, Y.Q. & Economo, E.P. (2016) Reorganization of taxonomic, functional, and phylogenetic ant biodiversity after conversion to rubber plantation. *Ecological Monographs*, 86, 215–227.
- Lôbo, D., Leão, T., Melo, F.P.L., Santos, A.M.M. & Tabarelli, M. (2011) Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. *Diversity and Distributions*, 17, 287–296.
- Losapio, G., Schmid, B., Bascompte, J., Michalet, R., Cerretti, P., Germann, C. et al. (2021) An experimental approach to assessing the impact of ecosystem engineers on biodiversity and ecosystem functions. *Ecology*, 102, 1–12.
- Martello, F., De Bello, F., Morini, M.S.D.C., Silva, R.R., Souza-Campana, D.R.D., Ribeiro, M.C. et al. (2018) Homogenization and impoverishment of taxonomic and functional diversity of ants in eucalyptus plantations. *Scientific Reports*, 8, 1–11.
- Martínez-Ramos, M., Ortiz-Rodríguez, I.A., Piñero, D., Dirzo, R. & Sarukhán, J. (2016) Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest reserves. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 5323–5328.
- Mason, N.W.H., De Bello, F., Mouillot, D., Pavoine, S. & Dray, S. (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24, 794–806.
- Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L.F., Backeljau, T., Bonte, D. et al. (2018) Body-size shifts in aquatic and terrestrial urban communities. *Nature*, 558, 113–116.
- Meyer, S.T., Leal, I.R., Tabarelli, M. & Wirth, R. (2011) Ecosystem engineering by leaf-cutting ants: nests of *Atta cephalotes* drastically alter forest structure and microclimate. *Ecological Entomology*, 36, 14–24.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B. et al. (2020) Package ‘vegan’. [online]. Available from: <https://cran.r-project.org/web/packages/vegan/vegan.pdf>. [Accessed 20th June 2020].
- Oliveira, P.S. & Koptur, S. (2017) Ant-plant interactions: impacts of humans on terrestrial ecosystems. *Ant-Plant Interact. Impacts Humans Terr. Ecosyst.*, 1, 1–432.
- Pennington, R.T., Lavin, M. & Oliveira-Filho, A. (2009) Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and Systematics*, 40, 437–457.

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- Peters, H.A., Pauw, A., Silman, M.R. & Terborgh, J.W. (2004) Falling palm fronds structure Amazonian rainforest sapling communities. *Proceedings of the Royal Society B: Biological Sciences*, 271, 367–369.
- Pimentel, S.D. & Tabarelli, M. (2004) Seed dispersal of the palm *Attalea oleifera* in a remnant of the Brazilian Atlantic Forest. *Biotropica*, 36, 74–84.
- Pôrto, K.C., Cabral, J.J.P. & Tabarelli Biodiversidade, M. (2004) *Brejos de Altitude em Pernambuco e Paraíba*.
- Queiroz, A.C.M., Ribas, C.R. & França, F.M. (2013) Microhabitat characteristics that regulate ant richness patterns: the importance of leaf litter for epigaeic ants. *Sociobiology*, 60, 367–373.
- Ribas, C.R., Schoereder, J.H., Pic, M. & Soares, S.M. (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology*, 28, 305–314.
- Ribeiro-Neto, J.D., Arnan, X., Tabarelli, M. & Leal, I.R. (2016) Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian caatinga. *Biodiversity and Conservation*, 25, 943–956.
- Rocha-Ortega, M., Arnan, X., Ribeiro-Neto, J.D., Leal, I.R., Favila, M.E. & Martínez-Ramos, M. (2018) Taxonomic and functional ant diversity along a secondary successional gradient in a tropical forest. *Biotropica*, 50, 290–301.
- Schnitzer, S.A., Dalling, J.W. & Carson, W.P. (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*, 88, 655–666.
- Silva, R.R. & Brandão, C.R.F. (2010) Morphological patterns and community organization in leaf-litter ant assemblages. *Ecological Monographs*, 80, 107–124.
- Souza, A.F. & Martins, F.R. (2003) Spatial distribution of an undergrowth palm in fragments of the Brazilian Atlantic Forest. *Plant Ecology*, 164, 141–155.
- Tabarelli, M., Peres, C.A. & Melo, F.P.L. (2012) The ‘few winners and many losers’ paradigm revisited: emerging prospects for tropical forest biodiversity. *Biological Conservation*, 155, 136–140.
- Underwood, E.C. & Fisher, B.L. (2006) The role of ants in conservation monitoring: if, when, and how. *Biological Conservation*, 132, 166–182.
- Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D. et al. (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 19456–19459.

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