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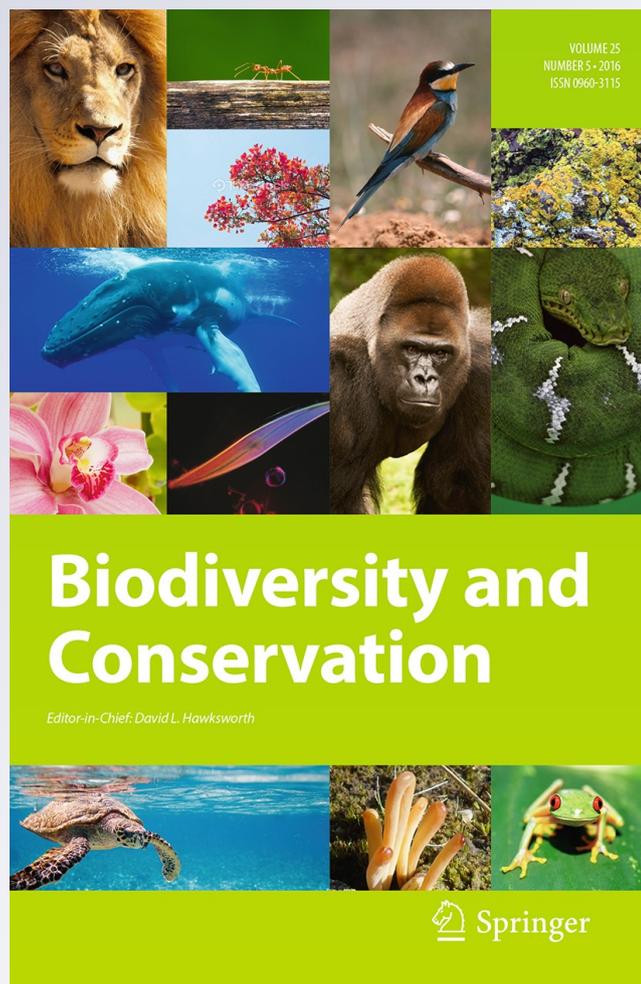
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Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga

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Abstract Although chronic anthropogenic disturbance (CAD) represents a significant threat to the integrity of tropical biotas, few efforts have been made to understand its impacts. We address the effects of CAD on plant and ant communities in the Caatinga, a seasonally dry tropical forest in northeast Brazil. Both taxa were recorded across 25 0.1-ha plots within a 220-km² landscape dominated by old-growth vegetation exposed to human activities. CAD was measured indirectly via a disturbance index, which was calculated from proxies of human disturbance such as plot distance to roads and villages, and density of people and livestock. Plant and ant abundance was not correlated to the CAD index. However, CAD had negative, positive or neutral effects on species diversity, depending upon diversity measure, taxa and soil type; e.g. plants were more negatively affected than ants. Furthermore, several plant and ant species exhibited higher abundance in the most disturbed vegetation patches while some exhibited lower abundance. Species-level responses resulted in taxonomic responses at the community level and increments in cross-plot species similarity as CAD increased. Our results indicate that: (1) CAD affects several community-level attributes, but with differing intensities; (2) community-level effects can be either positive or negative, and effects are soil dependent; (3) plants are more negatively affected than ants; (4) some species benefit, while others are negatively affected by CAD;

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and (5) by affecting the abundance and occurrence of particular species, CAD causes biotic homogenization towards the higher end of the disturbance gradient.

Keywords Biotic homogenization · Cross-taxa congruence · Soil conditions · Species diversity · Tropical dry forests · Cascading effects

Introduction

Tropical forests have been converted into commodity production systems, where habitat loss and fragmentation have been recognized as a major threat to biodiversity persistence (Laurance et al. 2002; Clark and Covey 2012). The major process subjacent to these disturbance-driven changes is the replacement of a diverse group of disturbance-sensitive species by a less diverse group of disturbance-adapted species; this phenomenon of increased community similarity through space and time, as anthropogenic disturbances increase, has been called biotic homogenization (adapted from Olden and Rooney 2006 who defined the term for invasive non-native species). However, much less is known about the effects of the subtle but frequent removals of small proportions of forest biomass due to firewood collection, exploitation of non-timber forest products, damage to the vegetation caused by overgrazing by livestock and competitive exclusion of native species by invasive species, the so called chronic anthropogenic disturbances (CAD sensu Singh 1998; Ticktin 2004; Ahrends et al. 2010; Schulz et al. 2016). Although CAD does not result in habitat loss and fragmentation, there are reports in the literature of reductions in stem density, basal area, species richness and community evenness, favoring disturbance-adapted species in detriment of forest-dependent and long-lived plant species (Sagar et al. 2003; Ribeiro et al. 2015); however, to our knowledge, no biotic homogenization processes have so far been reported for areas under pressure from CAD.

Plants and ants are suitable study groups to address cross-taxa responses to CAD because their local diversity can be used as surrogates of total biota diversity and can also be used as a predictor of biota responses to disturbance (Andersen et al. 2004; Leal et al. 2010). In addition, plants and ants interact in many different ways, with vegetation affecting ants through modulation of resource availability and microclimate conditions (Andersen 1983; Sanders et al. 2003; Arnan et al. 2007), while ants play roles ranging from plant mutualists to antagonists (Rico-Gray and Oliveira 2007). Although CAD has been proven to negatively affect both plants and ants (Leal et al. 2014; Ribeiro et al. 2015), there has been no comparison of the intensity of their responses to CAD. We, thus far, do not know if plants, which are directly exploited by humans, are more negatively affected by this disturbances regime than are ants (Lucena et al. 2007; Silva et al. 2015).

CAD has been well documented in seasonally dry tropical forests (SDTF sensu Prado 2003) in Mexico (Martorell and Peters 2005, 2009; Villarreal-Barajas and Martorell 2009), India (Sagar et al. 2003; Kumar and Ram 2005; Yen 2015) and recently in the Brazilian SDTF Caatinga (Leal et al. 2014, 2015; Ribeiro et al. 2015, *in press*). Caatinga is a mosaic of xerophytic, deciduous, semiarid thorn scrubs and seasonally dry tropical forests occupying 884,453 km² of north-eastern Brazil (Pennington et al. 2009), and it is one of the world's most diverse dry ecosystems (MMA 2011). Caatinga supports very dense (i.e. 26 inhabitants per km²; Medeiros et al. 2012) and low-income (Ab'Sáber 1999) rural populations, which are widely dependent on forest resources for their livelihoods (Davidar et al. 2010; Djoudi et al. 2015).

Firewood collection (Cavalcanti et al. 2015), exploitation of tree bark and leaves for medicinal proposes (Lucena et al. 2007; Silva et al. 2015), overgrazing by livestock (Leal et al. 2003; Schulz et al. 2016) and hunting (Alves et al. 2009) impose a continuum of degradation, varying from relatively minor biomass reduction to complete desertification (Leal et al. 2005; Ribeiro et al. 2015). Caatinga, is therefore, an ecosystem under pressure from high levels of CAD, and offers an interesting opportunity to examine the potential effects of this kind of disturbance on dry forest biotas (Leal et al. 2014; Ribeiro et al. 2015).

We address the effects of CAD simultaneously on plant and ant communities in a landscape of the Caatinga. As Caatinga biodiversity is intrinsically influenced by soil types (Pereira et al. 2003; Araújo et al. 2004; Moro et al. 2015), we also addressed how differences in soil type influence the response of plants and ants to CAD. Because CAD directly targets plants, and ants are indirectly affected, we hypothesized larger disturbance effects on plants than on ants. More specifically, as disturbance increases, we predict: (i) the overall abundance and species richness of both communities will decrease, but at a greater rate in plants than in ants; (ii) species similarity of both plant and ant communities will increase (biotic homogenization), but at a greater rate in plants than in ants; and (iii) there will be no soil-related differences in the responses of plant and ant communities to anthropogenic disturbance. We examine the uncovered patterns in the light of CAD theory, biotic homogenization, and cross-taxa responses to human disturbances.

Materials and methods

Study site

This study was undertaken in a continuous patch of Caatinga vegetation near Parnamirim municipality (8°5'S; 39°34'W; 393 m asl) in Pernambuco state, Brazil. The climate is semi-arid, with an average temperature of 26 °C, and the majority of the 431 mm mean annual rainfall received between January and May (CPRM - Serviço Geológico do Brasil 2005). Soils in the region can be classified into two main categories: clay and sandy soils. Clay soils are typically shallow and rocky luvisols, but contain high amounts of clay and have high cation exchange capacity, which increases fertility (IUSS Working Group WRB 2014). Sandy soils are typically mineral regosols, are very weakly developed due to low levels of weathering and contain high proportions of silt/clay, which make this kind of soil nutrient-poor and highly susceptible to erosive processes (IUSS Working Group WRB 2014). Parnamirim was founded in the nineteenth century, with its origin related to livestock farming, a common economic activity in semiarid regions of Brazil. The present-day local economy also includes smallholder agriculture, and the human population in Parnamirim is around 20,000 people, with 11,000 living in rural areas (IBGE 2011).

Disturbance measures

We established twenty-five 20 m × 50 m plots (distance between plots: 6.46 ± 3.48 km, mean ± SD) within a 220 km² landscape dominated by old-growth vegetation that is exposed to CAD. In order to avoid undesired effects from acute disturbances, we considered old-growth vegetation to be forest stands not exposed to slash-and-burn agriculture

in the last 50 years (Leal et al. 2014; Ribeiro et al. 2015). Plots were distributed on two soil types (10 on clay and 15 on sandy soils).

The typical structure of Caatinga vegetation (the lack of a grass layer, low tree height and patchy tree distribution) combined with the chronic, rather than acute nature of the disturbance regime makes direct anthropogenic disturbance measures impossible (Leal et al. 2014). Instead, we adopted a landscape scale perspective to obtain a gradient of CAD intensity. We used five measures of chronic disturbance that have been described as important surrogates of human disturbance in tropical forests studies. They were: (i) proximity to the nearest house (hereafter, proximity to house) (ii) proximity to the nearest road (proximity to road) (iii) proximity to Parnamirim city center (proximity to city) (iv) density of people living near the plot (people) and (v) density of livestock (livestock) (Sagar et al. 2003; Martorell and Peters 2005; Leal et al. 2014, 2015; Ribeiro et al. 2015). The first three measures are related to the access people have to Caatinga resources, and the last two are related to the pressure human activities impose on Caatinga ecosystems. All measures of CAD were equally weighted to calculate the disturbance index.

We used satellite imagery from the Advanced Land Observing Satellite (ALOS) to locate plots and human settlements, and we estimated the measures 'proximity to house', 'proximity to road' and 'proximity to city' as the reciprocal smallest distance from the center of each plot. We later conducted 34 interviews, in which we collected information on the number of people living in, and the number of livestock managed by, each dwelling in a buffer (2 km radius) around each plot's geographic center. The total area of human settlements covered by interviews was 12.56 km², as described in Ribeiro et al. (2015). We selected this buffer size because local people reported that the maximum dispersal distance of herd animals is 2 km.

The measures 'people' and 'livestock' were log-transformed. We also transformed (1/logX) distance based measures to make these measurements positively related to anthropogenic disturbance, as Ahrends et al. (2010) suggest that disturbance levels may increase in sites nearer to roads, cities and human settlements. Thus, anthropogenic disturbance is positively related to all our disturbance measures (Martorell and Peters 2005, 2009). We then calculated a disturbance index as follows: we scored each disturbance descriptor from 0 (low disturbance) to 5 (high disturbance) and summed up the scored values to obtain a global Disturbance Index. Thus, our disturbance index ranges from 0 (lowest level of disturbance) to 25 (highest level of disturbance; maximum sum for the five disturbance measures). We calculated the disturbance index separately for sandy and clay soils, aiming to control for differences in plant species composition between contrasting soil types, which are considerable in Caatinga ecosystems (Pereira et al. 2003; Moro et al. 2015).

Plant and ant surveys

We conducted floristic inventories at 19 of our plots during the rainy season of 2011 and at the remaining 6 plots in the rainy season of 2012; there was no relationship between sampling year and the disturbance level of plots. We surveyed the whole area in each plot and recorded all woody plants (trees and shrubs) and cacti with diameter at soil height (DAS) >3 cm and height >1.5 m. Plant individuals were identified, where possible, to species level and flowering materials were deposited at the herbarium of the Federal University of Pernambuco (Pernambuco–Brazil); nomenclature followed APG III (2009). We sampled the ant community of all 25 plots in 2012 using 6 pitfall traps (13 cm in height

and 12 cm in diameter, filled with ethanol 92 %) that were active for 48 h. Pitfall traps were placed on a central line in the plot and were 10 m away from each other. All ants were sorted into morphospecies and identified to species level, where possible. If identification to species level was not possible, individuals were assigned a code applicable only to this study. The abundance of each species in each plot was registered as the proportion of the six pitfall traps where a given species was found. A complete set of mounted voucher specimens is held in the ant collection at the Federal University of Pernambuco.

Data analysis

Overall abundance per plot of plants and ants was computed as the sum of the abundance of each plant and ant species occurring in a plot, respectively. In addition to estimating overall abundance, we estimated diversity indices for three different diversity levels: species richness (or 0D), the exponential of Shannon entropy (or 1D) and the inverse Simpson concentration (or 2D) (Jost 2006). 0D , 1D and 2D are in the same units and satisfy the replication principle (Jost 2006), which is required in biodiversity assessments as it considers the uniqueness of each species that composes an assemblage (Gotelli and Chao 2013). The formulas of 0D , 1D and 2D are detailed elsewhere (Jost 2006). 0D is not sensitive to species abundance and so gives disproportionate weight to rare species (Jost 2006), 1D weights species by their abundance without disproportionately favoring either rare or abundant species, while 2D favors abundant species and can be interpreted as the number of very abundant or dominant species in the community (Jost 2006). To make overall abundance and diversity values comparable across plants and ants, we divided each value (separately for total abundance and each diversity level) by the higher value from the respective soil and diversity level (only in the case of diversity estimations). These analyses were performed with the package Entropart in R (R Development Core Team 2014).

To test the hypothesis that CAD exerts stronger effects on plants than on ants, we constructed general linear mixed models (GLMM) separately for each soil type (clay and sandy). Taxa (plants or ants) and disturbance index and their interaction were fixed factors, while plot was treated as a random factor. The dependent variables were the overall abundance and the three diversity levels. We expected to find a significant effect in the interaction term if the slope for plants was steeper than the slope for ants, indicating that plants would be more negatively affected by CAD than ants.

To test the hypothesis that high levels of CAD impose greater degrees of biotic homogenization on plants than on ants, we based our analysis on pairwise comparisons of disturbance and community dissimilarity matrices separately for each soil type (clay and sandy). First, we calculated the mean pairwise disturbance as the averaged disturbance level for plots taken in pairs separately for each soil type (45 and 105 pairs of plots in clay and sandy soils, respectively). Subsequently, we computed Bray–Curtis dissimilarity matrices for plants and ants and calculated a vector of community dissimilarity values for each pairwise plot comparison. We then constructed a generalized linear model (GLM) for each soil type, encompassing the effect of taxa (plant or ant) and the mean pairwise disturbance (continuous predictor) on the pairwise community dissimilarity (dependent variable). To control for possible spatial autocorrelation in community similarity, we applied Mantel tests that analyzed the correlation between the matrix of geographic distances and the matrix of community dissimilarities (using Bray–Curtis dissimilarity) based on 999 permutations; we perform four different tests, one for each combination of taxa (plants and ants) and soil type (clay and sandy soils).

Results

We recorded 80 plant species (from 15 families) and 45 ant species (from 7 subfamilies). For plants, the most species rich families were Fabaceae (16 species) and Euphorbiaceae (11), while Bignoniaceae, Burseraceae, Celastraceae, Cochlospermaceae, Erythroxylaceae, Nyctaginaceae and Olacaceae only presented 1 species each. Plots contained an average of 20.4 (\pm SE: \pm 4.8) plant species. For ants, the most species rich subfamilies were Myrmicinae (20 species) and Formicinae (11), while Pseudomirmecinae (2) and Ecitoninae (1) presented the lowest number of species. Plots contained an average of 14.6 (\pm 3.03) ant species (see Supplementary Material S1 for plant and ant species lists).

Throughout the whole set of plots the disturbance index varied from 1.01 to 18.53 (both values obtained in clay soil plots), while it varied between 4.26 and 14.08 in sandy soil plots (see Supplementary Material S2 for a frequency distribution of the disturbance index scores from plots in sandy and clay soils). Contrary to our expectations, overall abundance was insensitive to either the taxa or the disturbance index for both soil types; we did not observe a significant interaction term between these two fixed factors (Table 1). In spite of no effects at the community level, we found changes in individual species abundance and/or occurrence patterns along the disturbance gradient in both soil types (Supplementary Material S3). For example, plant species such as *Erythroxylum pungens* E. O. Schulz (Erythroxylaceae) and *Fraunhoferia multiflora* Mart. (Celastraceae), in sandy soils, and *Senna macranthera* (DC ex Collad.) H. S. Irwin & Barneby (Fabaceae) and *F. multiflora*, in clay soils, showed lower abundance in plots facing higher levels of CAD. However, the abundance of plant species like *Sennegalia polyphylla* (DC) Briton & Rose and *Amburana*

Table 1 Effects of taxa (plants or ants), chronic anthropogenic disturbance intensity and their interaction on overall abundance, and diversity levels concerning rare (0D), common (1D) and dominant (2D) species on sandy and clay soils in Caatinga vegetation from Parnamirim municipality, Brazil

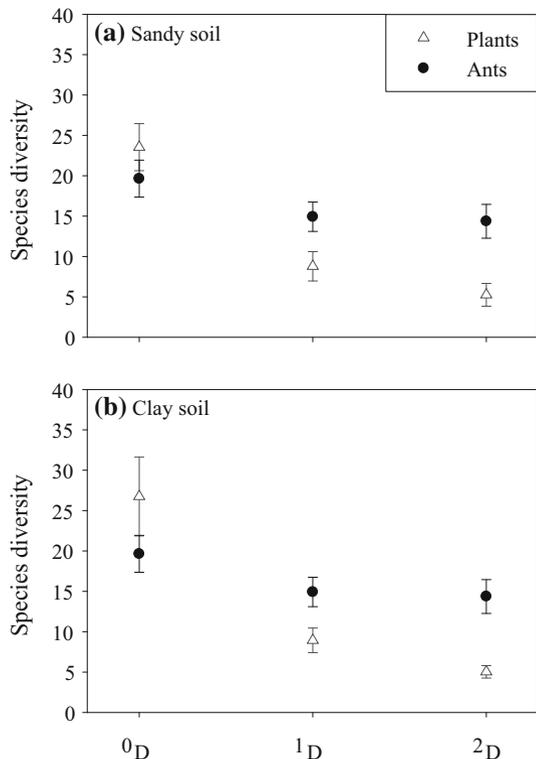
Diversity level	Effect	Sandy soil				Clay soil			
		R ²	df	F	p	R ²	df	F	p
Overall abundance	Taxa	0.33	1, 26	0.3	0.568	0.22	1, 16	0.5	0.505
	Disturbance index		1, 26	0	0.855		1, 16	1.3	0.288
	Taxa \times disturbance index		1, 26	3.5	0.086		1, 16	0.2	0.677
0D	Taxa	0.07	1, 26	0	0.992	0.52	1, 16	1.7	0.232
	Disturbance index		1, 26	0.8	0.374		1, 16	2.3	0.166
	Taxa \times disturbance index		1, 26	1.5	0.248		1, 16	5.4	0.048
1D	Taxa	0.03	1, 26	0.5	0.475	0.45	1, 16	1.7	0.228
	Disturbance index		1, 26	0	0.985		1, 16	1.7	0.235
	Taxa \times disturbance index		1, 26	0.3	0.594		1, 16	8.6	0.019
2D	Taxa	0.08	1, 26	1.69	0.216	0.44	1, 16	7.237	0.027
	Disturbance index		1, 26	0.412	0.532		1, 16	0.489	0.504
	Taxa \times disturbance index		1, 26	0.283	0.604		1, 16	7.266	0.027

Significant effects are shown in bold ($p < 0.05$)

cearensis (Alemão) A. C. Sm. (Fabaceae), in sandy soils, and *Jatropha mollissima* (Pohl) Baill. and *Cnidocolus quercifolius* Pohl (Euphorbiaceae) in clay soils, was positively related to CAD level. Amongst ant species, *Thaumatomyrmex mutilatus* Mayr (Ponerinae) in sandy soils and *Camponotus cingulatus* Mayr (Formicinae) were negatively affected by CAD. In contrast, *Pheidole diligens* Smith (Myrmicinae) was benefited from high levels of CAD on both sandy and clay soils. While some ant species, such as *Dinoponera quadriceps* Kempf (Ponerinae), did not exhibit clear trends across the gradient.

Diversity profiles were quite similar for plants and ants, with decreasing scores from 0D towards 2D and a stronger reduction for plants than for ants in both soil types (Fig. 1a, b). Species diversity was higher for plants than for ants when considering 0D in clay (paired Student's *t* test, $t = -2.6$, $df = 9$, $p = 0.019$) and sandy ($t = -2.3$, $df = 14$, $p = 0.032$) soils. For other levels, diversity was higher for ants than for plants in both clay (1D : $t = 5.6$, $df = 9$, $p < 0.0001$; 2D : $t = 9.3$, $df = 14$, $p < 0.0001$) and sandy (1D : $t = 5.1$, $df = 9$, $p < 0.0001$; 2D : $t = 7.7$, $df = 14$, $p < 0.0001$) soils. These results indicate that plants have more rare species and less common and dominant species than do ants. We found a significant interaction effect between the disturbance index and the taxa for all diversity levels in clay soil plots (Table 1). Thus, there was a negative effect of the disturbance index on 0D , 1D and 2D for plants, while for ants it tended to be neutral for 0D and positive for 1D and 2D (Fig. 2). In contrast, there was no significant interaction effect on any of the diversity levels in sandy soil plots, which is in contrast to our prediction of similar patterns between soil types. There were no effects of the two fixed

Fig. 1 Diversity levels for rare (0D), common (1D) and dominant species (2D) of plants (grey triangles) and ants (black circles) on sandy (a) and clay soils (b) in Caatinga vegetation from Parnamirim municipality, Brazil. Circles and triangles depict the mean diversity value, while bars show the 95 % confidence intervals



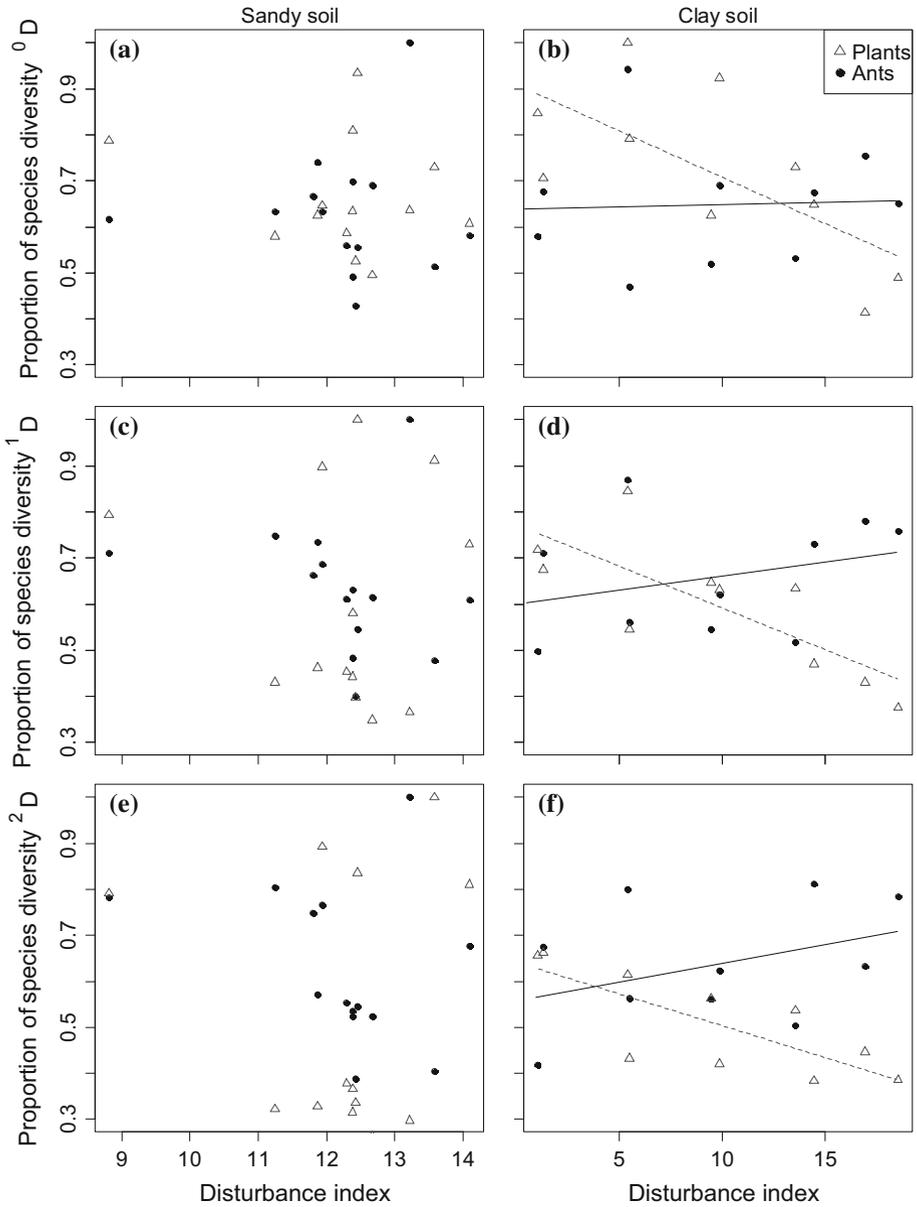


Fig. 2 Relationship between the intensity of chronic anthropogenic disturbance (CAD) and diversity levels for rare (0D ; a, b), common (1D ; c, d) and dominant species (2D ; e, f) on sandy (left side) and clay soils (right side) of plants (triangles) and ants (circles) in the Caatinga vegetation from Parnamirim municipality, Brazil. Diversity estimations are given as the proportion of the maximum diversity value separately for each diversity level and soil type. Dashed lines represent plants, while solid lines represent ants

factors (disturbance index and taxa) on any of the three diversity levels in either of the two soil types, except for the effect of taxa on 2D in clay soils, whereby 2D was higher in ants than in plants.

Mantel tests indicated no spatial autocorrelation in community similarity among plots, for both plants (clay soils: Pearson $r = -0.07$, $p = 0.70$; sandy soils: Pearson $r = 0.25$, $p = 0.10$) and ants (clay soils: Pearson $r = -0.04$, $p = 0.69$; sandy soils: Pearson $r = 0.24$, $p = 0.08$). For sandy soil plots, taxa, mean pairwise disturbance and the interaction term significantly influenced community dissimilarity (Table 2; Fig. 3). The slope for the relationship between mean pairwise disturbance and community dissimilarity was negative for both taxa, which means that plots with higher CAD scores are more similar in species composition than plots with lower values of CAD. However, the slope was much steeper in plants than in ants (Fig. 3a), emphasizing a stronger biotic homogenization process working on plants. For clay soil plots, dissimilarity in species composition was affected by taxa, while mean pairwise disturbance and the interaction term showed no effect (Table 2; Fig. 3b).

Discussion

Our results suggest that: (1) CAD affects several community-level attributes, but with differing intensities, e.g. the most conspicuous effects were on species diversity and taxonomic composition; (2) community-level effects can be either positive or negative, and effects are soil dependent; (3) plants are affected to a greater extent than ants; (4) some species benefit (i.e. higher abundance in the most disturbed plots), while others are negatively affected by CAD; and (5) by affecting the occurrence and abundance of particular species, CAD causes biotic homogenization towards the higher end of the disturbance gradient. These findings partially support our initial hypotheses with interesting implications for CAD theory and cross-taxa responses to human disturbances.

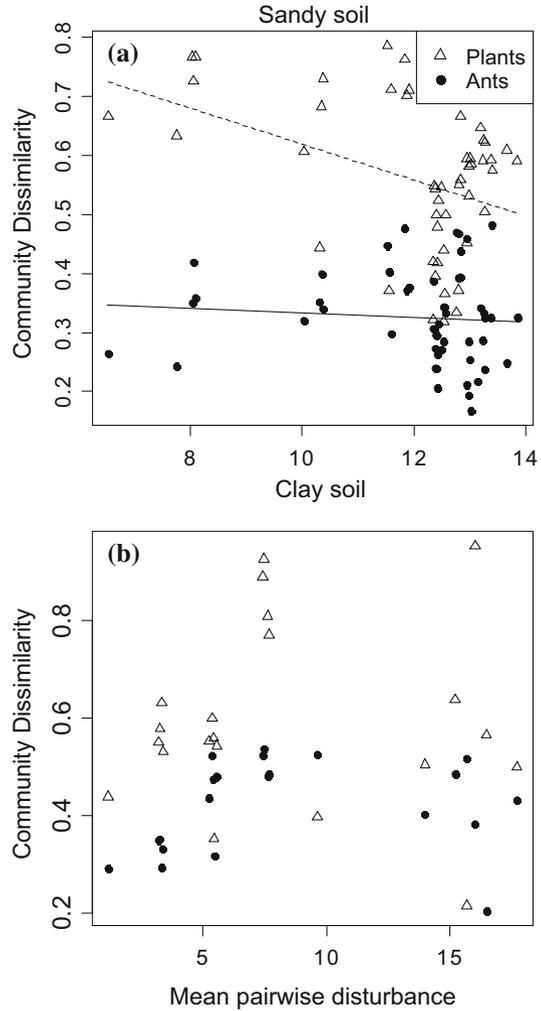
With the exception of hunting (Alves et al. 2009), studies addressing the effects of CAD are still relatively rare and limited in terms of vegetation structures, plant populations and communities (Martorell and Peters 2005; Villarreal-Barajas and Martorell 2009), despite the fact that CAD-related patterns in plant communities are expected to cascade to plant attendants (Leal et al. 2014, 2015). Overall, our results support an emerging view that CAD can impose biologically-relevant negative impacts on plant communities (Sagar et al. 2003;

Table 2 Effects of the intensity of chronic anthropogenic disturbances (CAD) on the Bray-Curtis dissimilarity in species composition for plants and ants in the 25 plots on sandy and clay soils in Caatinga vegetation from Parnamirim municipality, Brazil

Soil type	Source of variation	df	R ²	MS	F	p
Sandy soil	Taxa	1	0.57	1.4	128.8	<0.001
	Mean pairwise disturbance	1		0.08	7.36	0.01
	Taxa × mean pairwise disturbance	1		0.05	4.43	0.04
	Residuals	98		0.01		
Clay soil	Taxa	1	0.21	0.32	13.9	<0.001
	Mean pairwise disturbance	1		0.00	0.08	0.78
	Taxa × mean pairwise disturbance	1		0.00	0.05	0.83
	Residuals	38		0.02		

Significant effects are shown in bold ($p < 0.05$)

Fig. 3 Relationship between the Bray–Curtis dissimilarity in species composition of plants and ants and the mean pairwise disturbance level for the 25 plots on sandy (15 plots; **a**) and clay (10 plots; **b**) soils in Caatinga vegetation from Parnamirim municipality, Brazil. *Dashed lines* represent plants, while *solid lines* represent ants



Villarreal-Barajas and Martorell 2009). Studies in Africa and India have reported shifts in stem abundance, biomass, species diversity and taxonomic composition, along with increased invasions by exotic plant species in response to synergistic sources of disturbance, including grazing by livestock and firewood and fodder collection (Ticktin 2004; Ahrends et al. 2010). Surprisingly, we did not find evidence for a reduction in plant density, a community-level attribute that, similar to biomass, is usually sensitive to CAD (Ahrends et al. 2010). As previously documented, individuals from disturbance-sensitive plant species can be gradually replaced by individuals of disturbance-adapted species in response to increased environmental filtering, such as increased water stress (Kumar and Ram 2005). This winner/loser replacement (sensu Tabarelli et al. 2012) or successional process (Kumar and Ram 2005) is in accordance with the changes in species abundance we have documented in our study sites. For example, previous studies in the same region of the Caatinga have documented the increased abundance of the disturbance-adapted *Jatropha mollissima* and *Croton*

sonderianus (Euphorbiaceae) combined with the decreased abundance of disturbance-sensitive *Fraunhoferia multiflora*, *Bauhinia cheilantha* (Bong.) Steud. (Fabaceae) and *Myracrodruon urundeuva* Fr. All. (Anacardiaceae) at most disturbed sites (Ribeiro et al. 2015, in press). This replacement might represent a plausible mechanism for (1) the unaltered plant density, at least for certain levels of disturbance, and (2) the biotic homogenization that we have documented here. Biotic homogenization can be driven by the rearrangement of native floras and faunas in response to anthropogenic disturbance (Lobo et al. 2011), as disturbance adapted species become highly prolific across the disturbed area. Higher levels of species similarity (i.e. biotic homogenization) can result, however, from other complementary forces, such as species loss and increases in species range (Godet et al. 2015). Our results have uncovered no shifts in species diversity in sandy soils, which is the soil type experiencing biotic homogenization, not even for rare species. All these pieces of evidence taken together, suggests that the biotic homogenization in sandy soils that we have reported here, is not driven by species loss, but by species replacements and increases in the range of species that were already extant in less disturbed areas. In the Caatinga, winner-loser replacements have been proposed to result from both increasing environmental filtering due to soil degradation and microclimatic shifts, and the population collapse experienced by exploited plant species, which result in the homogenization of important taxonomic groups (Ribeiro et al. 2015; Schulz et al. 2016).

We also offer additional evidence of the sensitivity of ants to CAD by documenting influences on the abundance of particular species, species diversity and taxonomic composition associated with variation in CAD. But in contrast to previously reported negative effects, such as the reduction of both large-bodied seed disperser ants (Leal et al. 2014) and extrafloral nectary attendant ants (Leal et al. 2015), our results suggest either no-effect or a positive effect (depending on diversity level), and in both cases the responses were contingent on soil type. Furthermore, our findings indicate that ants are similarly or less affected by CAD than plants. This may occur because plants are targeted by humans and livestock, and their deleterious effects are thus direct (Ribeiro et al. 2015). Disruption to plant-animal interactions, such as seed dispersal (Leal et al. 2014) and plant protection against herbivores (Leal et al. 2015), may also explain this finding. In contrast, ants are not directly affected by CAD, and as plastic generalists (Andersen 1983, 1992) and thermophilic insects (Diamond et al. 2012), several groups may even be favored by vegetation openness and aridity. For instance, in fire-prone ecosystems, the increase in environmental aridity favors the proliferation of several species, such as species of the genus *Iridomyrmex* in Australia (Andersen et al. 2014). In the Caatinga ecosystems, as CAD increases, we expect a reduction in soil cover by native vegetation and an increase in bare soil, which (similarly to fire) also increases the environmental aridity and helps to maintain high ant diversity.

Whatever the underlying mechanism causing reduced sensitivity among ant assemblages, our results show that plant and ant responses to CAD are soil dependent. Two distinct processes may be responsible for these differences. First of all, plant taxa contained a higher proportion of rare species than ants, while ant taxa showed a higher proportion of common and dominant species; this pattern was consistent across the two soil types. Because the three diversity levels for plants and ants did not differ between soil types, their differences in community diversity responses to CAD may not emerge as a result of the particular attributes of the communities harbored on sandy or clay soils, but due to the contrasting history of anthropogenic disturbances on these two soil types. As the clay soils in Caatinga ecosystems are more fertile than are sandy soils (IUSS Working Group WRB 2014), they have been preferentially occupied by humans, being managed and transformed

through time (Kauffman et al. 1993; Araújo et al. 2004). This difference in soil use has exacerbated the differences in community parameters among low and high disturbance levels in clay soils. Therefore, there may be a time-since-disturbance threshold (probably lower for plants) beyond which disturbances start to modify community parameters. Second, different responses according to the soil type might be due to different species compositions for both plants and ants, as species-specific traits play a major role in organism responses to environmental change (Swenson and Weiser 2010; Swenson et al. 2012; Arnan et al. 2014).

Caatinga vegetation is thus susceptible to CAD, and the most conspicuous response is the taxonomic restructuring across disturbance gradients, which affects multiple trophic levels. Proliferation of disturbance-adapted species in parallel to population collapse of sensitive species emerge as a key mechanism which may account for the majority of detected community-level responses, such as the relationships between CAD and species diversity. Because vegetation is the main targeted resource for human populations, this taxon is more severely impacted than ants, at least across the range of disturbance intensities we have assessed in this study (Kumar and Ram 2005). This suggests that responses to CAD first emerge in plants, particularly in terms of taxonomic composition, and as CAD intensifies its effects subsequently reach other attributes and higher trophic levels.

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