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Chronic anthropogenic disturbance as a secondary driver of ant community structure: interactions with soil type in Brazilian Caatinga

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SUMMARY

Habitat loss is widely recognized as the major cause of global biodiversity decline, but remaining habitat is increasingly threatened by chronic human disturbances. Using a multi-model averaging approach we examined the association between five chronic disturbance surrogates and the richness and taxonomic and functional composition of ants in Brazilian Caatinga. Using pitfall traps in 47 plots near Parnamirim city (Pernambuco) across two soil types (sand and clay), we recorded 53 species from 27 genera. Ant species richness on sand was slightly higher than on clay, and was negatively related to most surrogates of anthropogenic disturbance. Soil type and human population size were the main predictors of ant species richness. Soil type was the most important predictor of functional group abundance. Taxonomic and functional composition were influenced by soil type and disturbance, but this relationship varied between clay and sandy soils. Ant functional composition showed a weak relationship with disturbance on sandy soils, but on clay soils it showed predictable winner–loser replacement. We attribute the greater effect of disturbance on clay soils to higher intensity of land use, and our study highlights the importance of considering context dependence when evaluating biodiversity responses to disturbance.

Keywords: ant diversity, ant functional groups, biodiversity, human disturbance, semi-arid vegetation

INTRODUCTION

Anthropogenic disturbance has severely reduced forest cover worldwide, and such habitat loss and associated fragmentation is widely recognized as the major cause of global biodiversity loss (Murcia 1995; Veldman *et al.* 2009; Ahrends *et al.* 2010; Laurance *et al.* 2011). Much of the remaining habitat, however, experiences chronic anthropogenic disturbance (CAD *sensu* Singh 1998) that does not result in habitat loss and fragmentation. Such disturbance includes firewood collection, exploitation of non-timber products, hunting, overgrazing by livestock and intentional introduction of invasive plant species (Martorell & Peters 2005). Moderate levels of CAD can actually promote diversity (Connell 1978; Grime 1979), but high levels typically have negative impacts (Singh 1998).

The ecological impacts of CAD have received far less research attention than those associated with acute disturbances that lead to extensive habitat loss. CAD can have a major effect on vegetation structure (Sagar *et al.* 2003; Shaanker *et al.* 2004; Ribeiro *et al.* 2015), and can also disrupt key ecological processes such as seed dispersal (Leal *et al.* 2014) and plant-protection against herbivores (Leal *et al.* 2015). Disruptions of such processes cause shifts in the functional composition of trees, from long-lived, highly specialized species to disturbance-tolerant, short-lived generalized species (Sagar *et al.* 2003; Uniyal *et al.* 2010; Ribeiro *et al.* 2015; Ribeiro *et al.* 2016). However, there have been few studies of the impact of chronic disturbances on faunal diversity (Ribeiro-Neto *et al.* 2016).

Ants have attracted considerable attention in disturbance studies because they are such a globally dominant faunal group and a popular bio-indicator in land management (Hoffmann & Andersen 2003; Andersen & Majer 2004). CAD can cause major shifts in ant species and functional composition, even with little or no change in overall species richness (Hoffmann 2010; Franklin 2012). Such shifts can be directly caused by habitat change, but can also be mediated by changes in the abundance of dominant species, which result in cascading indirect effects on subdominant and subordinate groups (Bestelmeyer & Wiens 1996; Hoffmann & Andersen 2003; Andersen & Majer 2004) and on ecological interactions (Leal *et al.* 2014; Leal *et al.* 2015). Ant communities show predictable replacement of disturbance 'losers' (disturbance-sensitive taxa) by disturbance 'winners' (disturbance-adapted taxa; see Tabarelli *et al.* 2012), with disturbance typically favouring

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*Supplementary material can be found online at http://dx.doi.org/10.1017/S0376892916000291 open-adapted taxa at the expense of highly specialized, forest-associated functional groups (Andersen 2000; Hoffmann & Andersen 2003; Beaumont *et al.* 2012; Leal *et al.* 2012). At a regional scale, disturbance is a secondary driver of variation in ant communities that is determined primarily by soil type, and ant responses to disturbance can vary markedly with soil type (Hoffmann & Andersen 2003; Hoffmann 2010; Ribeiro-Neto *et al.* 2016).

We examined ant community responses to CAD and its interaction with soil type in semi-arid Caatinga of north-eastern Brazil. We assessed the effects of CAD on both species and functional diversity, focusing on three key questions. First, what is the magnitude of effects of disturbance compared with those of soil type as the putative primary driver of local variation in ant communities? Second, to what extent do the effects of disturbance vary with soil type? Third, to what extent does functional composition show predictable winner–loser replacement involving the loss of highly specialized, forest-associated functional groups?

MATERIALS AND METHODS

Study site

Caatinga vegetation consists of mosaics of seasonally dry tropical forest (*sensu* Pennington *et al.* 2009) and scrub (Velloso *et al.* 2002) covering 826 411 km² of north-eastern Brazil (Brasil-MMA 2011). It is one the world's most biodiverse and densely populated semi-arid regions, with more than 23 million people at a density of 26 inhabitants/km² (INSA 2012). Nearly 10 million m^3 year^{-1} of firewood and charcoal are obtained via exploitation of native vegetation (Gariglio *et al.* 2010), and there are more than 16 million goats (IBGE 2010). Collectively, slash-and-burn agriculture, firewood collection, overgrazing and hunting impose a continuum of degradation varying from relatively minor biomass reduction to complete desertification (Leal *et al.* 2005; Brasil-MMA 2011; Ribeiro *et al.* 2015).

Our study was conducted in a continuous patch of Caatinga vegetation near Parnamirim city (8°5'S; 39°34'W; 393 m asl) in Pernambuco state. The climate is semi-arid, with an average temperature of 26°C and most of the 550 mm mean rainfall falling between January and May (IBGE 1985). The soils are predominantly non-calcic brown soils, planosols (clay soils) and regosols (a sandy soil; IBGE 1985). The human population size in the immediate Parnamirim region is approximately 20 000, with about half living in rural areas (IBGE 2011).

We established 47 plots (average ± standard deviation distance between plots 7 ± 4.4 km) on two soil types (26 on sand and 21 on clay) and representing a range of intensities of anthropogenic disturbance. Areas that had experienced acute rather than chronic disturbance, such as slash-and-burn agriculture, were not included. Vegetation cover tended to be higher on clay than on sandy soil ($t = 2.7026$, $df = 23$, $p = 0.006$).

Measurement of disturbance

We used the five measurements of disturbance that have been previously described for the study plots (Leal *et al.* 2014), based on surrogates related to population density and intensity of land use, which tend to decrease with increasing distance from cities and roads (Ahrends *et al.* 2010). These surrogates were: the number of people ('people') and combined number of cattle and goats ('stock') in the farms within 2 km of each plot; the distance to the nearest road ('distance to road'); the distance to the nearest farm ('distance to farm'); and the distance to Parnamirim ('distance to city') (Leal *et al.* 2014; Ribeiro *et al.* 2015). People ($W = 315$, $p = 0.824$), stock ($W = 268.5$, $p = 0.466$) and distance to road ($W = 289.5$, $p = 0.366$) did not vary with soil type (Wilcoxon matched-pair tests), whereas distance to farm ($W = 451$, $p < 0.001$) and distance to city ($W = 199$, $p = 0.050$) tended to be lower for sites with clay soils.

Ant sampling and functional classification

Ants were sampled using six pitfall traps (13 cm height and 12 cm diameter) with 10 m spacing in each plot. Traps were partly filled with a 90% ethanol solution, and were operated for a 48-hr period. Twenty-four of the plots (13 on clay and 11 on sand) were sampled from February to May 2010, and the remaining 23 (eight on clay and 15 on sand) were sampled from March to May 2013. All ants were sorted into species and, where possible, named. Unnamed species were assigned code numbers that apply only to this study. A complete set of mounted voucher specimens is held in the ant collection at Universidade Federal de Pernambuco (Pernambuco, Brazil).

For classifying ant species into functional groups we adapted Andersen's (1995) widely used scheme based on global-scale responses of ants to environmental stress and disturbance (see also Andersen 1997; Hoffmann & Andersen 2003) to be more specific to the regional fauna. Our groups were: Army Ants (species of *Neivamyrmex* and *Nomamyrmex*); Dominant Dolichoderinae (primarily *Dorymyrmex*), Fire Ants (*Solenopsis* subgenus *Solenopsis*); Generalized Myrmicinae (*Pheidole, Crematogaster, Monomorium* and *Solenopsis* subgenus *Diplorhoptrum*), Lower Attini (*Cyphomyrmex*); higher Attini (*Acromyrmex*); Opportunists (*Brachymyrmex*, *Ectatomma*, *Gnamptogenys*, *Nylanderia* and *Tapinoma*); Specialist Predators (*Dinoponera*, *Leptogenys*, *Ponera* and *Thaumatomyrmex*); Subordinate Camponotini (*Camponotus*); and Tree Specialists (*Myrmelachista, Cephalotes* and *Pseudomyrmex*; see Table S1 for a comprehensive classification).

For each plot, we quantified the abundance of each species as the number of traps in which they occurred (i.e., frequency of occurrence), ranging from one to six per plot. For functional groups we combined frequencies of occurrence of their constituent species.

Table 1 Model-averaged effect size (β), unconditional standard error (SE) and the sum of Akaike weights (ΣW) for the effects of soil type and five chronic anthropogenic disturbance metrics on ant total species richness and ant functional group abundance in Caatinga ecosystems. Par = Averaged parameter of the model.

Response variable	*Par*	*Soil*	*People*	*Stock*	*Distance to road*	*Distance to farm*	*Distance to city*
Total species richness	β	0.025	–0.022	0.011	0.016	-0.003	0.010
	SE	0.015	0.015	0.017	0.018	0.017	0.020
	ΣW	0.670	0.330	0.300	0.390	0.350	0.540
Army Ants	β	-0.126	9.523	-0.784	-0.615	-0.251	0.405
	SE	4.311	11.182	4.308	9.186	3.013	5.667
	ΣW	0.250	0.310	0.240	0.210	0.260	0.800
Dominant Dolichoderinae	β	0.440	–0.043	-0.153	-0.119	0.547	-0.499
	SE	0.191	0.186	0.171	0.193	0.340	0.339
	ΣW	0.860	0.340	0.320	0.670	0.580	0.260
Fire Ants	β	0.402	–0.329	-0.077	-0.076	0.184	0.001
	SE	0.160	0.150	0.199	0.207	0.184	0.221
	ΣW	0.950	0.320	0.410	0.300	0.290	0.810
Generalized Myrmicinae	β	-0.444	–0.227	-0.070	0.414	0.119	-0.341
	SE	0.156	0.163	0.173	0.335	0.200	0.374
	ΣW	0.730	0.280	0.310	0.440	0.370	0.370
Lower Attini	β	0.139	–0.112	0.459	0.037	0.133	0.205
	SE	0.165	0.192	0.166	0.225	0.181	0.198
	ΣW	0.340	0.950	0.310	0.320	0.420	0.320
Opportunists	β	0.589	0.409	0.034	-0.286	0.201	0.574
	SE	0.145	0.138	0.165	0.248	0.144	0.236
	ΣW	0.970	0.280	0.520	0.490	0.960	0.960
Specialist Predators	β	0.230	–0.323	-0.101	-0.325	0.062	0.503
	SE	0.154	0.160	0.178	0.297	0.180	0.285
	ΣW	0.540	0.310	0.280	0.520	0.820	0.750
Subordinate Camponotini	β	-0.116	–0.713	0.500	0.047	-0.430	-0.008
	SE	0.167	0.186	0.184	0.182	0.166	0.195
	ΣW	0.330	0.930	0.930	0.270	0.260	0.980
Tree Specialists	β	0.054	–0.218	0.262	0.047	-0.160	-0.302
	SE	0.175	0.218	0.205	0.293	0.193	0.238
	ΣW	0.280	0.480	0.350	0.320	0.530	0.390

Statistical analysis

To avoid multi co-linearity between the predictor variables, we first ran an analysis of variance inflation factor (VIF) of each predictor using the car package for R version 3.2.4 (R Core Team 2015). The highest VIF was 2.7, which indicates no co-linearity (Neter *et al.* 1990) and therefore allowing them all to be included in our models.

To test the effects of soil type and the five disturbance measures on each response variable we used a multi-model inference approach (Burnham & Anderson 2002) that ranks all mathematical models (i.e., models built with all possible combinations of the six explanatory variables excluding interactions) according to the Akaike Information Criterion (AIC). To evaluate the strength and relative importance of soil type and the various disturbance measures we then computed model averaged parameter estimates (averaged across the whole set of models) based on the Akaike weights (W), which represent the probability that a given model is the best model for the data. Then, for each of the six explanatory variables (averaged across the whole set of models), we calculated: (1) β as a measure of effect direction and size (Grueber *et al.* 2011); (2) sum of W (ΣW), which represents the probability that a predictor variable affects the response variable; and (3) the relative importance of the variables (which combines effect size and the weights of a predictor). A multi-model inference approach (with averaged parameters) is more stable and reliable than inference based on a unique best model chosen among the several possible candidates (Burnham & Anderson 2002; Grueber 2011).

For the count data, we used generalized linear models with a Poisson error distribution and log-link function, and the AIC for overdispersed count data corrected for small sample sizes (QAICc) instead of AIC (Burnham & Anderson 2002; Grueber *et al.* 2011). We also transformed data to a mean of zero and standard deviation of 0.5 (Gelman 2008). Using this transformation, all parameter estimates are set to the same scale allowing the comparison between categorical and continuous predictors (Hereford *et al.* 2004; Gelman 2008; Schielzeth 2010). We also estimated the goodness-of-fit of the models by calculating the adjusted R^2 considering log likelihood for the full model (soil type and five disturbance

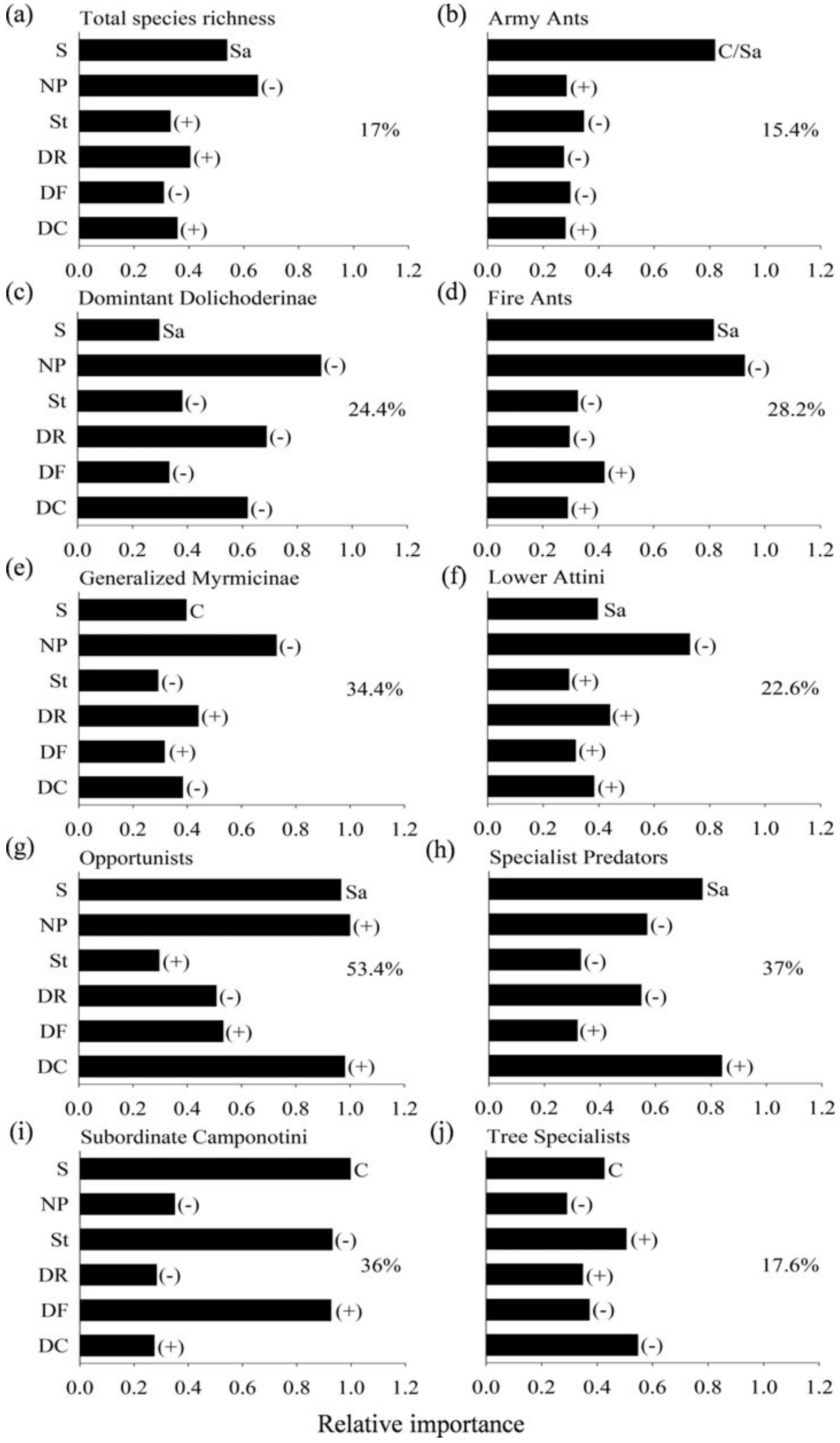

Figure 1 Relative importance of soil type and five chronic anthropogenic disturbances as predictors of total ant species richness and ant functional group abundance in Caatinga ecosystems from northeast Brazil. Signal (+/−) depicts the direction of model-averaged effect size (β) for each variable and percentage alongside each graph depicts the proportion of variation on data explained by the full model. Total species richness was higher on sand than clay. The letter (C = clay soil; Sa = sandy soil) next to the column for soil effect depicts the soil type with higher functional group abundance. DC = Distance to Parnamirim city; DF = Distance to the nearest farm; DR = Distance to the nearest road; NP = Number of people; S = Soil type; St – Stock (goats and cattle summed).

Table 2 Influence of soil type and the five chronic disturbance metrics on species and functional composition (based on 10 000 randomizations in a Canonical Correspondence Analysis). Only significant results are shown.

Community data	*Data*	*Source*	*df*	*Chi-square*	*F*	*p*
Species composition	All	Soil	1	0.158	5.659	0.000
		People	1	0.053	1.909	0.019
		Distance to farm	1	0.061	2.176	0.008
		Distance to city	1	0.061	2.192	0.006
		Residual	40	1.114		
	Sandy soil	People	1	0.139	3.480	0.000
		Distance to city	1	0.073	1.813	0.038
		Residual	20	0.800		
	Clay soil	People	1	0.104	1.684	0.043
		Stock	1	0.115	1.859	0.026
		Distance to road	1	0.104	1.684	0.047
		Distance to city	1	0.138	2.231	0.007
		Residual	15	0.927		
Functional composition	All	Soil	1	0.077	10.769	0.000
		People	1	0.020	2.742	0.011
		Distance to city	1	0.028	3.860	0.001
		Residual	40	0.285		
	Sandy soil	People	1	0.025	1.989	0.036
		Residual	20	0.250		
	Clay soil	People	1	0.035	2.096	0.050
		Stock	1	0.053	3.157	0.009
		Distance to city	1	0.076	4.568	0.001
		Residual	15	0.250		

measures) and the null model (only the intercept) according to Magee (1990) and Nagelkerke (1991). All analyses were performed using the packages arm and MuMIn for R (R Core Team 2015).

We evaluated variation in ant species composition in relation to soil type and disturbance using Canonical Correspondence Analysis (CCA) (Ter Braak 1986; Legendre *et al.* 2011). The analysis was performed for all sites combined to assess soil type and disturbance effects, and also separately for each soil type to assess differential disturbance effects according to soil type, and was based on frequency data, considering only those species that occurred in at least five plots to avoid any bias caused by rare species. We performed a randomization test (10 000 aleatorizations) to obtain the statistical significance of our explanatory variables (Legendre *et al.* 2011). These analyses were repeated for functional group composition (based on functional group abundance), again considering only those functional groups with more than one constituent species. The analyses were performed using the packages Vegan and BiodiversityR for R (R Core Team 2015).

RESULTS

We recorded 53 ant species from 27 genera and seven subfamilies. Myrmicinae (24 species) and Formicinae (12) were the richest subfamilies, and *Pheidole* (11) and *Camponotus* (eight) the richest genera (Table S1). Thirteen (25%) species were recorded in only one plot and 10 (21%) were found in more than 30 plots, with *Solenopsis globularia* the most frequent (46 plots). The richest functional groups were Generalized Myrmicinae (16 species), Subordinate Camponotini (eight) and Opportunists (seven). Ant species richness was slightly higher on sandy (14.5 ± 2.98, mean ± standard deviation) than clay soils (12.6 ± 3.2; $t = 2.1605$, $df = 45$, $p = 0.036$). Twelve species occurred only on sandy and six species only on clay soil.

Our full model explained 17% of the variance in ant species richness. Soil type showed the strongest effect on total species richness and, amongst the five CAD metrics, only human population size and distance to farm exerted a significant (in both cases negative) effect on total ant species richness (Table 1). Soil type was a more important predictor of total ant species richness than any disturbance measure (Table 1 and Fig. 1 (*a*)). Among disturbance measures, human population size was the most important predictor, and livestock and distance to farm the least important (Fig. 1 (*a*)).

For functional groups, full models explained between 15.4% (Army Ants) and 53.4% (Opportunists) of the variation in functional group abundance. Soil type was the strongest predictor of the abundance of three functional groups (Fire Ants, Generalized Myrmicinae and Opportunists), human population size and distance to city were each the strongest predictors for two functional groups, and distance to farm and stock size were each the strongest predictor of one functional group each (Table 1). Soil type presented higher ΣW than any disturbance measure in four out of the nine functional groups considered. For the five remaining functional groups, distance to city (for Army Ants and Subordinate Camponotini), distance to farm (for Specialist Predators and Tree Specialists) and human population size (for Lower Attini) presented higher ΣW than soil type (Table 1). The relative importance (which combines effect size and the weights of a predictor) of predictor variables for functional group abundance varied markedly (Fig. 1 (*b*)–(*j*)). For example, soil was the most important factor in models for Dominant Dolichoderinae, Fire Ants, Generalized Myrmicinae, Lower Attini and Opportunists, while distance to city (for Specialist Predators and Tree Specialists) and distance to farm (for Army Ants and Subordinate Camponotini) achieved higher relative importance than soil type for two functional groups each (Fig. 1 (*b*)–(*j*)).

CCA showed that sandy and clay soils supported distinct ant communities (F = 5.659, df = 1, $p < 0.001$) and, orthogonal to the soil effect, variation in species composition was significantly correlated with human population size and distance to roads and city (see Table 2 for significant results and Table S2 for complete CCA results; Fig. 2 (*a*) and Fig. S1 (*a*)). The abundances of *Pseudomyrmex termitarius* and *Pheidole obscurithorax* were negatively related to human population size and to the distances to road and city. Different sets of disturbance surrogates were related to ant communities from each soil type (Table 2). At sandy sites (Fig. 2 (*b*) and Fig. S1 (*b*)), communities varied in relation to human population size (positively related to *Gnamptogenys sulcata* abundance) and distance to city (negatively related to the abundance of several species of *Pheidole*). At clay sites (Fig. 2 (*c*) and Fig. S1 (*c*)), communities varied in relation to human population size and stock size (with *Gnamptogenys sulcata*, *Ectatomma muticum* and *Cyphomyrmex* sp. increasing in abundance), and to distances to road and city (with *Gnamptogenys moellery* and *Solenopsis tridens* increasing in abundance).

The two soil types also supported very distinct ant communities in terms of functional group composition, with Dominant Dolichoderinae, Fire Ants, Opportunists and Specialist Predators all having higher abundance on sandy soils (Table 2 for significant results and Table S2 for complete CCA results; Fig. 3 (*a*) and Fig. S2 (*a*)). The relationship between functional group composition and

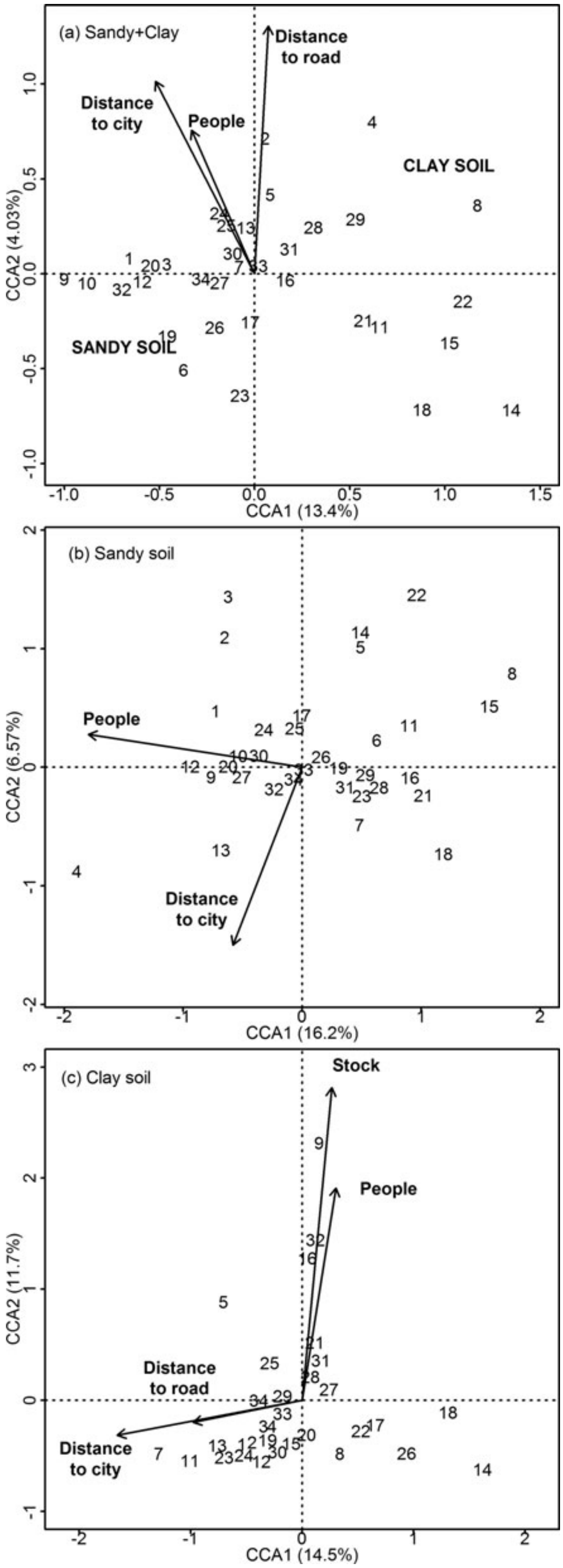

Figure 2 Associations between soil type and five anthropogenic disturbance metrics and species composition considering both sand and clay soil types combined (*a*; centroids for soil types are depicted as sandy soil and clay soil) and separately for sand (*b*) and clay (*c*) according to CCA. Only variables significantly related to ant species composition according to a randomization test based on 10 000 randomizations are shown. 1 = *Nylanderia* sp. 1; 2 = *Pheidole* sp. 7; 3 = *Cyphomyrmex transversus*; 4 = *Pheidole* sp. 9; 5 = *Pheidole radoskowiskii*; 6 = *Camponotus atriceps*; 7 = *Gnamptogenys moellery*; 8 = *Crematogaster* sp. 1; 9 = *Gnamptogenys sulcata*; 10 = *Acromyrmex rugosus*; 11 = *Pheidole* sp. 8; 12 = *Pheidole* sp. 4; 13 = *Camponotus cingulatus*; 14 = *Pseudomyrmex termitarius*; 15 = *Pheidole* sp. 3 grupo *flavens*; 16 = *Cyphomyrmex* sp. 1; 17 = *Dorymyrmex spurius*; 18 = *Pheidole obscurithorax*; 19 = *Dorymyrmex thoracicus*; 20 = *Solenopsis geminata*; 21 = *Camponotus* (*Myrmaphaenus*) sp. 2; 22 = *Crematogaster* sp. 2; 23 = *Solenopsis tridens*; 24 = *Pheidole* sp. 5; 25 = *Brachymyrmex patagonicus*; 26 = *Forelius pusillus*; 27 = *Pheidole diligens*; 28 = *Camponotus crassus*; 29 = *Pheidole* prox *jelskii*; 30 = *Camponotus blandus*; 31 = *Camponotus* (*Tanaemyrmex*) sp. 1; 32 = *Ectatomma muticum*; 33 = *Solenopsis globularia*; 34 = *Dinoponera quadriceps*.

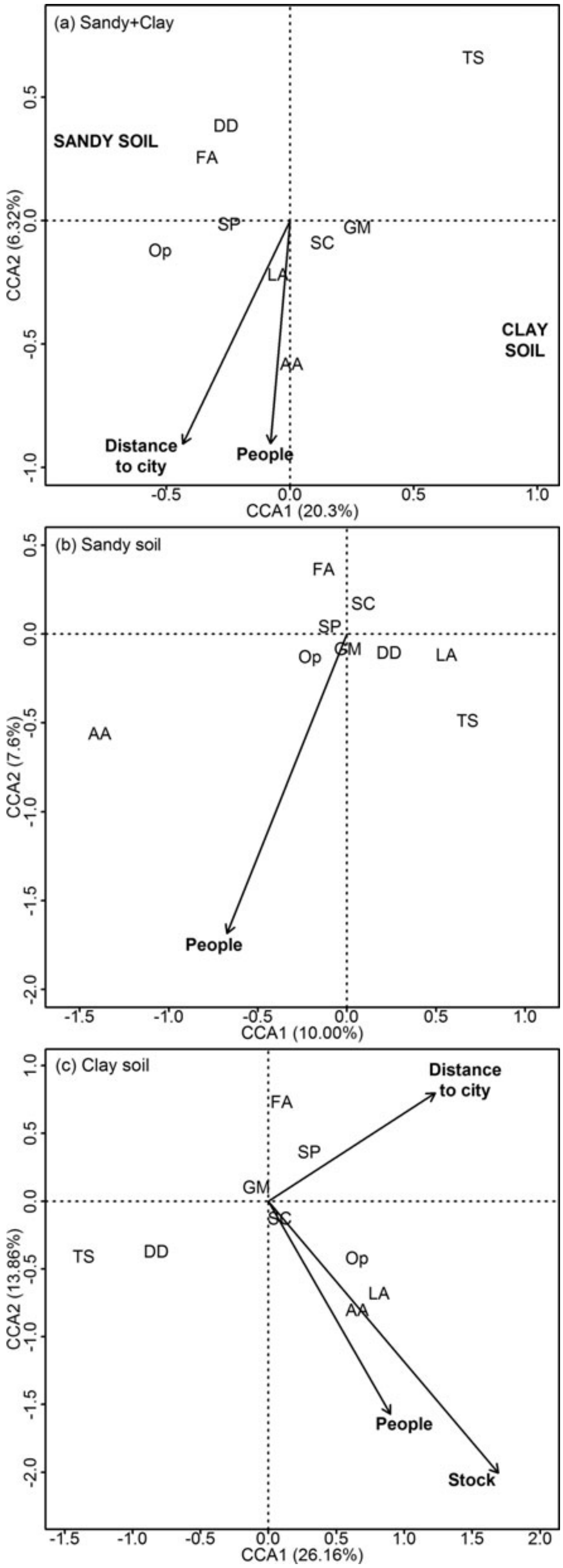

Figure 3 Effects of soil type and five anthropogenic disturbance metrics on functional group composition considering both sand and clay soil types combined (*a*; centroids for soil types are depicted as sandy soil and clay soil) and each separately (*b* and *c*), according to CCA. Only variables that were significantly related to functional group composition according to a randomization test based on 10 000 randomizations are shown. AA = Army Ants; DD = Dominant Dolichoderinae; FA = Fire Ants; GM = Generalized Myrmicinae; LA = Lower Attini; Op = Opportunist; SP = Specialist Predator; SC = Subordinate Camponotini; TS = Tree Specialists.

disturbance metrics varied markedly between the two soil types. On sandy soils, the abundances of different functional groups showed very weak relationships with disturbance surrogates (Fig. 3 (*b*) and Fig. S2 (*b*)). However, on clay soils the abundances of Opportunists, Lower Attini and Army Ants were positively related to the local densities of people and stock, and the abundances of Dominant Dolichoderinae and Tree Specialists were negatively, and that of Specialist Predators positively, related to distance to city (Fig. 3 (*c*) and Fig. S2 (*c*)).

DISCUSSION

Our study sought to examine ant community responses to CAD and its interaction with soil type in a densely populated semi-arid ecosystem. We found that CAD has a secondary effect on patterns of ant diversity and composition in Caatinga, which are influenced primarily by soil type. Ant communities on the two soil types were different functionally as well as taxonomically, with Dominant Dolichoderinae, Fire Ants, Opportunists and Specialist Predators all more abundant at sandy sites.

Soil has important direct effects on ant communities through its role as a nesting and foraging substrate (Hölldobler & Wilson 1990; Kaspari & Weiser 1999; Hoffmann 2010). Clay soils typically support distinct ant communities because of their poor drainage and propensity for waterlogging (Andersen *et al.* 2015). Soil also has important indirect effects on ant communities as a primary driver of vegetation structure. In Caatinga, sandy soils harbour plant communities that are less diverse and have lower vegetation cover than those of clay soils (Silva *et al.* 2003). Notably, Dominant Dolichoderinae were more species rich on sandy soils, which reflects its strong preference for open habitats (Andersen 1995). By contrast, Generalized Myrmicinae and Subordinate Camponotini were more diverse and abundant on clay soils. These two groups are behaviourally subordinate to Dominant Dolichoderinae and are competitively limited by them (Andersen & Patel 1994; Arnan *et al.* 2011); it is therefore possible that the association of generalized Myrmeicinae and Subordinate Camponotini with clay soils reflects competitive interference from Dominant Dolichoderinae on sandy soils.

CAD had complex effects on ant richness and composition, and these effects varied markedly between soil types. Ant communities on clay soils had stronger associations with disturbance measures than those on sand. Although this may reflect intrinsic differences in ecosystem resilience between the soil types given the differences in plant and ant composition, we suspect that it more likely reflects higher levels of disturbance on clay. Clay soils have higher fertility than sandy soils, and are therefore likely to be preferentially selected for use. They also tended to be closer to farms and to Parnamirim city, which would also tend to make them more intensely used.

Previous studies of ant responses to disturbance in other biomes show predictable winner–loser replacement in relation to disturbance, typically involving the proliferation of highly generalized species and loss of highly specialized, forest-associated taxa (Andersen 1997; Hoffmann & Andersen 2003; Leal *et al.* 2012). In our study, ant functional composition was only weakly related to CAD on sandy soils. However, on clay soils it showed winner–loser replacement that is consistent with previous studies (Ribeiro-Neto *et al.* 2016), with the abundance of Opportunist (disturbance winners) increasing with CAD, and that of Specialist Predators (disturbance losers) decreasing.

In conclusion, we have shown that CAD reduces ant species richness in Brazilian Caatinga, and can also substantially re-organize the functional composition of ant communities. However, this varies markedly with soil type. Soil type therefore not only affects ant communities directly as a nesting and foraging substrate, and indirectly through vegetation type, but also indirectly by determining the level of disturbance experienced. Our study more generally highlights the importance of considering context dependence when evaluating biodiversity responses to disturbance.

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Supplementary material

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References

Ahrends, A., Burgess, N. D., Milledge, S. A. H., Bulling, M. T., Fisher, B., Smart, J. C. R., Clarke, G. P., Mhoro, B. E. & Lewis, S. L. (2010) Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 14556–14561.

Andersen, A. N. & Majer, J. D. (2004) Ants show the way down under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* **2**: 291–298.

Andersen, A. N. & Patel, A. D. (1994) Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia* **98**: 15–24.

Andersen, A. N. (1995) A classification of Australian ant communities based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* **22**: 15–29.

Andersen, A. N. (1997) Functional groups and patterns of organization in North American ant communities: a comparison with Australia. *Journal of Biogeography* **24**: 433–460.

Andersen, A. N. (2000) A global ecology of rain forest ants: functional groups in relation to stress and disturbance. In: *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, eds. D. Agosti, J. D. Majer, L. Alonso & T. Shultz, pp. 25–34. Washington D. C., USA: Smithsonian Institution Press.

Andersen, A. N., Del Toro, I. & Parr, C. L. (2015) Savanna ant species richness is maintained along a bioclimatic gradient of decreasing rainfall and increasing latitude in northern Australia. *Journal of Biogeography* **42**: 2313–2322.

Arnan, X., Gaucherel, C. & Andersen, A. N. (2011) Dominance and species co-occurrence in highly diverse ant communities: a test of the interstitial hypothesis and discovery of a three-tiered competition cascade. *Oecologia* **166**: 783–794.

Beaumont, K. P., Mackay, D. A. & Whalen, M. A. (2012) The effects of prescribed burning on epigaeic ant communities in eucalypt forest of South Australia. *Forest Ecology and Management* **271**: 147–157.

Bestelmeyer, B. T. & Wiens, J. A. (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecological Applications* **6**: 1225–1240.

Brasil-MMA (2011) Monitoramento do desmatamento nos biomas brasileiros por satélite: Monitoramento do bioma Caatinga. Brasília, Brazil: Ministério do Meio Ambiente.

Burnham, K. P. & Anderson, D. R. (2002) Model selection and inference: a practical information-theoretic approach. New York, USA: Springer.

Connell, J. H. (1978) Diversity in tropical rain forest and coral reefs. *Science* **199**: 1302–1310.

Franklin, K. (2012) The remarkable resilience of ant assemblages following major vegetation change in an arid ecosystem. *Biological Conservation* **148**: 96–105.

Gariglio, M. A., Sampaio, E. V. S. B., Cestaro, L. A. & Kageyama, P. Y. (2010) Uso sustentável e conservação dos recursos florestais da caatinga. Brasília, Brazil: Serviço Florestal Brasileiro.

Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* **27**: 2865–2873.

Grime, J. P. (1979) Plant strategies and vegetation processes. London, UK: Jon Wiley & Sons.

Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* **24**: 699–711.

Hereford, J., Hansen, T. F., Houle, D. & Fenster, C. (2004) Comparing strengths of directional selection: how strong is strong? *Evolution* **58**: 2133–2143.

Hoffmann, B. D. & Andersen, A. N. (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* **28**: 444–464.

Hoffmann, B. D. (2010) Using ants for rangeland monitoring: global patterns in the responses of ant communities to grazing. *Ecological Indicators* **10**: 105–111.

Hölldobler, B. & Wilson, E. O. (1990) The ants. Berlin, London, Paris, Tokyo, Hong Kong: Springer-Verlag.

IBGE (1985) Atlas Nacional do Brasil: Região Nordeste. Rio de Janeiro, Brazil: Instituto Brasileiro de Geografia e Estatística.

IBGE (2010) Produção agrícola municipal para culturas temporárias e permanentes. Rio de Janeiro, Brazil: Instituto Brasileiro de Geografia e Estatística.

IBGE (2011) Censo demográfico 2010 – Características da população e dos domicílios. Rio de Janeiro, Brazil: Instituto Brasieiro de Geografia e Estatística.

INSA (2012) Sinopse do Censo Demográfico para o Semiárido Brasileiro. Campina Grande, Brazil: Instituto Nacional do Semiárido.

Kaspari, M. & Weiser, M. D. (1999) The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology* **13**: 530–538.

Laurance, W. F., Camargo, J. L. C., Luizao, R. C. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., Stouffer, P. C., Williamson, G. B., Benitez-Malvido, J., Vasconcelos, H. L., Van Houtan, K. S., Zartman, C. E., Boyle, S. A., Didham, R. K., Andrade, A. & Lovejoy, T. E. (2011) The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation* **144**: 56–67.

Leal, I. R., Filgueiras, B. K. C., Gomes, J. P., Iannuzzi, L. & Andersen, A. N. (2012) Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. *Biodiversity and Conservation* **21**: 1687–1701.

Leal, I. R., Silva, J. M. C., Tabarelli, M. & Lacher, T. E. Jr (2005) Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil, pp. 701–706. Oxford, UK: Blackwell Science Inc.

Leal, L. C., Andersen, A. N. & Leal, I. R. (2014) Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. *Oecologia* **174**(1): 173–181.

Leal, L. C., Andersen, A. N. & Leal, I. R. (2015) Disturbance winners or losers? Plants bearing extrafloral nectaries in Brazilian Caatinga. *Biotropica* **47**: 468–474.

Legendre, P., Oksanen, J. & ter Braak, C. J. F. (2011) Testing the significance of canonical axes in redundancy analysis. *Methods in Ecology and Evolution* **2**: 269–277.

Magee, L. (1990) R^2 measures based on Wald and likelihood ratio joint significance tests. In: *The American Statistician*, pp. 250–253. Abingdon, UK: Taylor & Francis.

Martorell, C. & Peters, E. M. (2005) The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. *Biological Conservation* **124**: 199–207.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* **10**: 58–62.

Nagelkerke, N. J. D. (1991) A note on a general definition of the coefficient of determination. *Biometrika* **78**: 691–692.

Neter, J., Wasserman, W. & Kutner, M. H. (1990) Applied linear statistical models. Chicago, USA: Irwin.

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.

R Core Team (2015) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ribeiro, E. M. S., Arroyo-Rodríguez, V., Santos, B. A., Tabarelli, M. & Leal, I. R. (2015) Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. *Journal of Applied Ecology* **52**: 611–620.

Ribeiro, E. M. S., Santos, B. A., Arroyo-Rodríguez, V., Tabarelli, M., Souza, G. & Leal, I. R. (2016) Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. *Ecology* **97**(6): 1583–1592.

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.

Sagar, R., Raghubanshi, A. S. & Singh, J. S. (2003) Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. *Forest Ecology and Management* **186**: 61–71.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* **1**: 103–113.

Shaanker, R. U., Ganeshaiah, K. N., Krishnan, S. A., Ramyar, R., Meera, C., Aravind, N. A., Kumar, A., Rao, D., Vanaraj, G., Ramachandra, J., Gauthier, R., Ghazoul, J., Poole, N. & Chinappa Reddy, B. V. (2004) Livelihood gains and ecological costs of non-timber forest product dependence: assessing the roles of dependence, ecological knowledge and market structure in three contrasting human and ecological settings in south India. *Environmental Conservation* **31**: 242–253.

Silva, R. A. D., Santos, A. M. M. & Tabarelli, M. (2003) Riqueza e diversidade de plantas lenhosas em cinco unidades de paisagem da Caatinga. In: *Ecologia e conservação da Caatinga*, eds. I. R. Leal, M. Tabarelli & J. M. C. Silva, pp. 337–366. Recife, Brazil: Editora Universitária – UFPE.

Singh, S. P. (1998) Chronic disturbance, a principal cause of environmental degradation in developing countries. *Environmental Conservation* **25**: 1–2.

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.

Ter Braak, C. J. F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167–1179.

Uniyal, P., Pokhriyal, P., Dasgupta, S., Bhatt, D. & Todaria, N. P. (2010) Plant diversity in two forest types along the disturbance gradient in Dewalgarh Watershed, Garhwal Himalaya. *Current Science* **98**: 938–943.

Veldman, J. W., Mostacedo, B., Peña-Claros, M. & Putz, F. E. (2009) Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. *Forest Ecology and Management* **258**: 1643–1649.

Velloso, A. L., Sampaio, E. V. S. B. & Pareyn, F. G. C. (2002) Ecorregiões propostas para o bioma Caatinga. Recife, Brazil: APNE Associação Plantas do Nordeste; Instituto de Conservação Ambiental The Nature Conservancy do Brasil.