

Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga

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Abstract Anthropogenic disturbance can have important indirect effects on ecosystems by disrupting species interactions. Here we examine the effects of anthropogenic disturbance on distance dispersal by ants for the diaspores of myrmecochorous Euphorbiaceae in Brazilian Caatinga. Rates of diaspore removal and distances removed of *Croton sonderianus* and *Jatropha mollissima* were observed at 24 sites ranging from low to very high disturbance (primarily grazing by livestock, hunting and firewood collection). Despite a large number of seed-disperser ant species, there were only two species providing high-quality distance-dispersal services, *Dinoponera quadriceps* (40 % of all observed seed removals) and *Ectatomma muticum* (33 %). *D. quadriceps* was responsible for 97 % of all removals >2 m, and 100 % of all removals >5 m. Removal rates did not vary with disturbance for *C. sonderianus* (small elaiosome), but declined with increasing disturbance for *J. mollissima* (large elaiosome). The number of removals by *Ectatomma* was highest at intermediate levels of disturbance, whereas those by *Dinoponera* decreased

systematically with increasing levels of disturbance. Mean dispersal distance was four times higher at sites experiencing low disturbance, where removals >5 m represented a third of all removal events, compared with very highly disturbed sites, where no removals >5 m were observed. Despite high overall diversity there is very limited functional redundancy in disperser ant species, resulting in low disperser resilience in relation to disturbance. This is likely to have important implications for recruitment by myrmecochorous plants, and therefore on vegetation composition and structure, at sites subject to high anthropogenic disturbance.

Keywords Ants · *Croton sonderianus* · Ecological services · *Jatropha mollissima* · Mutualisms

Introduction

Anthropogenic disturbance is a ubiquitous driver of biodiversity decline, with few ecosystems remaining unaffected by people (Hanna et al. 1995; Murcia 1995). Most research on the effects of anthropogenic disturbance on biodiversity has focused on direct species losses or changes in community structure (e.g. Fahrig 2003; Martorel and Peters 2005; Santos et al. 2010; Laliberté et al. 2009). However, disturbance can also have important indirect effects through its impact on ecological processes. For example, disturbance-related changes in the richness and abundance of the litter decomposer fauna can reduce nutrient cycling and primary productivity (Riutta et al. 2012).

Many ecological processes are mediated by interactions between species (Bond 1995; Kremen et al. 2007; Marini et al. 2012), and such interactions play a key role in maintaining biodiversity and ecosystem functioning (Hooper

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et al. 2005; Bascompte and Jordano 2007). Human disturbance can affect these interactions by changing the abundance of one or more partners (Restrepo and Gomez 1998; Palmer et al. 2008), and/or by changing their behaviour (Bossard 1991; Farwig and Berens 2012). Interactions are increasingly susceptible to human disturbance with increasing specialization of partner species, as responses to environmental change are limited with low flexibility (Swihart et al. 2003; Colles et al. 2009; Aizen et al. 2012). Such disruptions may have cascading ecological effects that lead to further degradation of disturbed habitats (Kearns et al. 1998).

Seed dispersal establishes the initial template for plant distribution (Brunn et al. 2008; Markl et al. 2012), and so is a key biotic interaction that can be affected by human disturbance (Farwig and Berens 2012). Effective seed dispersal is especially at risk when interactions between diaspores and dispersal agents are highly specialized. Myrmecochory (seed dispersal by ants) is generally considered to be a diffuse mutualism because seeds are transported by a wide variety of generalised ant species (Beattie 1985; Lengyel et al. 2010). Myrmecochory is therefore expected to be highly resilient in relation to human disturbance, because ants are so ubiquitous even with relatively high levels of disturbance (Hoffmann and Andersen 2003; Woodcock et al. 2011). However, recent studies have shown that ants vary markedly in the quality of seed-dispersal services they provide (Giladi 2006; Gove et al. 2007; Ness et al. 2009). In particular, ant body size is strongly related to the distance that seeds are dispersed (Ness et al. 2004), an important component of seed-disperser quality (e.g. Andersen 1988; Gomez and Espadaler 1998; Ness et al. 2004). Changes in ant species composition with disturbance may therefore have important implications for the effectiveness of seed dispersal, especially if large-bodied species are particularly affected. Large-bodied invertebrates are known to be especially sensitive to human disturbance (Tschamtko et al. 2002; Filgueiras et al. 2011). Myrmecochory might therefore be more sensitive to anthropogenic disturbance than expected.

In this study we examine the effect of anthropogenic disturbance on seed dispersal by ants in Caatinga, a semi-arid ecosystem of north-eastern Brazil. Myrmecochory is one of the most important seed-dispersal types in Caatinga, with more than 100 plant species having seeds that are specialized for dispersal by ants (I. R. Leal, unpublished data). Caatinga ants vary markedly in the dispersal services they provide, and include a limited range of high-quality dispersers (species of *Dinoponera*, *Extatomma* and *Camponotus*) that regularly transport diaspores significant distances (Leal 2010). Other species typically feed on the ant-attracting appendage (elaiosome) in situ without transporting the diaspore, and therefore can be considered as mutualism cheaters (Leal 2010).

Our study specifically addresses the following series of hypotheses. First, anthropogenic disturbance changes ant disperser species composition. Second, high-quality disperser ant species are particularly sensitive to anthropogenic disturbance. Third, there is therefore a lower quality seed-dispersal service, as measured by dispersal distance, with increasing disturbance.

Materials and methods

Study area

The Caatinga is a mosaic of xerophytic, deciduous, semi-arid thorn scrubs and seasonally dry forests occupying 884,453 km² of north-eastern Brazil (Pennington et al. 2000; Prado 2003), and is one of the world's most diverse dry ecosystems (MMA 2011). It was first colonized by European settlers in the mid sixteenth century, and 45 % of its area has since been transformed to croplands, pastures and human settlements (MMA 2011). Almost all remaining Caatinga vegetation experiences chronic human disturbance associated with relatively low-intensity resource extraction (MMA 2011), such as grazing and browsing by goats and cattle, firewood harvesting, and hunting (Leal et al. 2005). Although such disturbance does not markedly change vegetation physiognomy (Toledo et al. 1994), it can have important ecological impacts (Singh 1998; Gunderson 2000) and therefore seriously threatens Caatinga conservation.

Our study was conducted in a continuous patch of Caatinga vegetation near Parnamirim city (8°5'S; 39°34'W; 393 m a. s. l.) in Pernambuco state. The climate is semi-arid with most of the 550 mm mean annual rainfall falling between January and May (IBGE 1985). The wet season is highly variable in its length, with the dry season lasting for 7–11 months (Nimer 1972; Prado 2003). Soils are predominantly non-calcic brown soils, regosols and planosols (IBGE 1985).

We established 24 study sites (each 50 × 20 m; separated by at least 2 km) over an area of approximately 150 km², with 13 sites on regosols and 11 on non-calcic brown soils. The study sites were selected to represent a range of intensity of anthropogenic pressure, as indicated by proximity to human settlements. Areas that had experienced acute rather than chronic disturbance, such as slash and burn agriculture, were not included.

Myrmecochorous species

Euphorbiaceae is a dominant plant family in Caatinga vegetation and represents the largest group of myrmecochorous plants in this ecosystem. In other ecosystems around the world, myrmecochory is a syndrome commonly associated

with short plants (Giladi 2006). However, approximately 60 % of all Caatinga euphorbs are diplochorous tall shrubs or small trees (I. R. Leal, unpublished data), with ballistic discharge of seeds from explosive dehiscent capsules followed by myrmecochory (Leal et al. 2007). The seeds of all these myrmecochores have a caruncle-type elaiosome that attracts ant dispersers (Gorb and Gorb 2003). The diaspores are differentially attractive to high-quality disperser ants, which preferentially remove diaspores with a high proportional biomass of the elaiosome (Leal 2010). We thus used two contrasting diaspores: those of *Croton sonderianus* Müll. Arg. (hereafter referred to as ‘*Croton*’), with a tiny elaiosome (3 % of total diaspore mass), and *Jatropha mollissima* (Pohl.) Baill. (hereafter referred to as ‘*Jatropha*’), with a large elaiosome (20 % of total diaspore mass). Both species are tall shrubs, up to 4 and 3 m in height, respectively.

Measurement of anthropogenic disturbance

The habitat structure of Caatinga vegetation (especially the lack of a well-developed ground layer) combined with the chronic rather than acute nature of disturbance (see below), meant that reliable quantification of the level of disturbance based on habitat characteristics was not possible. Instead, we used surrogates of intensity of resource use, based on 34 semi-structured interviews with local people, to characterise levels of anthropogenic disturbance at each of our 24 study sites. The major disturbances were identified as grazing by stock (goats and cattle), firewood collection, and hunting (K. F. Rito, unpublished data). All these disturbances affect ants indirectly, through changes in habitat structure. Their intensity was inversely related to proximity to rural properties or to the city of Parnamirim (L. C. Leal, unpublished data). Through the interviews, we collected information on the number of people living in, and the number of stock managed by, each property.

We used five metrics to characterize the level of anthropogenic disturbance in each study area: distance to Parnamirim, distance to nearest farm, distance to nearest road, number of stock (goats and cattle combined) managed by farms within 2 km, and number of people living in farms within 2 km. All spatial analyses were conducted using satellite imagery and ARCGIS software, with distances measured from the centres of sites. For each of the five metrics, we classified sites into four categories, each with six sites. For the three distance metrics, categories ranged from one (highest distances values) to four (lowest distance values), and, for numbers of stock and people, from one (lowest) to four (highest). We summed the values of each metric to obtain an overall disturbance score for each site, with the higher the score, the higher the disturbance. We used breakpoints in the frequency distribution of disturbance scores to

classify sites into four categories of level of anthropogenic disturbance: low (four sites), moderate (nine sites), high (six sites), and very high (seven sites).

Seed dispersal

At each site, we established two 40-m transects (one for each diaspore species) separated by 20 m for diaspore-removal experiments. Five observation stations with 10-m spacing were established along each transect. At each observation station, ten seeds were placed on white filter paper cards (6 cm × 6 cm). The use of such cards facilitates observations, and does not affect ant dispersal behaviour (Byrne and Levey 1993). We placed seeds at stations at 0700 hours, and monitored them at 30-min intervals from 0800 hours to 1800 hours to make observations on disperser ant species. Removed diaspores were not replaced. This was done for 1 day for each site, between March and June 2011.

We recorded the number of diaspores removed at each site at the end of our observation period (1800 hours). We acknowledge that diaspore removal from a single observation station may not be an independent event due to the recruitment behaviour of many ant species. However, only 12 % of our diaspores were removed by ants with recruitment behaviour, and, in the few cases that all ten diaspores were removed from a station, removal was done by the non-recruiting species *Dinoponera quadriceps*. For statistical purposes we therefore treat each removal event as independent, and use the mean percentage of diaspore removed per site as a measure of rate of diaspore removal. We also recorded, collected and identified all ant species interacting with diaspores, and recorded the distance (displacement) of removal for all removals >1 cm.

Our observations on ant morphological and behavioural traits revealed that all species interacting with seeds could be readily classified into either of two disperser guilds. One consisted of medium- to large-bodied (>5 mm total length), solitary foraging ants that readily collected diaspores and transported them to their nests, which were sometimes many metres away. We classified these as high-quality dispersers. The other consisted of small-bodied (<5 mm), recruit-foraging ants, which often fed on elaiosomes in situ, and typically removed seeds short distances. We classified these as low-quality dispersers.

Data analysis

We used two-way ANOVA to analyse variation in ant disperser richness in relation to level of anthropogenic disturbance and soil type, and three-way ANOVA (with disturbance, soil and plant species as factors) to examine variation in mean rates of diaspore removal, mean removal

distance, and fate (nest or dropped en route) of diaspores removed by high-quality dispersers. We then used χ^2 -tests to examine the effects of disturbance on the frequency of long-distance (>2 and >5 m) dispersal events. We selected thresholds of 2 and 5 m because the former will result in transport of diaspores beyond the parent canopy of our study species (Leal et al. 2007), and the latter has been considered to be important for distance dispersal by ants (Andersen 1988; Gomez and Espadaler 1998). Analysis of long-distance removal was conducted on two datasets, one with sites classified into the four disturbance categories, and the other using just two categories: low and all higher levels (moderate, high and very highly disturbed sites) combined in order to provide a stronger contrast. In all cases, disturbance was nested under soil type, and, when required, we used a posteriori Tukey tests for comparisons among disturbance categories and plant species. Normality of the residuals and homogeneity of variances verified through Shapiro–Wilk and Levene tests, respectively. Data that did not meet homoscedastic criteria were $\log_{(10)}$ transformed or arcsine-square root transformed in the case of percentage data.

We performed a partial canonical correspondence analysis (CCA) to analyse the effects of disturbance on the composition of ant disperser species, controlling for possible effects of soil type. This analysis was conducted on ant abundance data, as measured by the number of interactions with diaspores (combining results from both transects for each site). Finally, we used two-way ANOVA to test the effect of disturbance on the number of removals by high-quality disperser ant species. All ANOVA and χ^2 analyses were conducted with STATISTICA 8.0 (Statsoft, Tulsa, OK), and multivariate analysis was conducted using PRIMER.

Results

Of the 1,200 diaspores from each plant species offered across the sites, 44.7 % of *Jatropha* and 34.4 % of *Croton* diaspores were removed. There was a significant interaction between disturbance and diaspore species for rates of removal ($F_{2,35} = 2.75$; $df = 5$; $p = 0.03$). Removal rates did not vary with disturbance for *Croton*, but declined with increasing disturbance for *Jatropha*, where it was twice as high at low compared with more highly disturbed sites (Fig. 1).

In total, we observed 1,168 ant-diaspore interactions, involving 22 ant species. Diaspores were removed in 72 % of these interactions, involving 11 ant species (Table 1); in the remaining cases ants were observed consuming the elaiosome in situ, without diaspore removal. We were able to observe and identify ant disperser species in almost

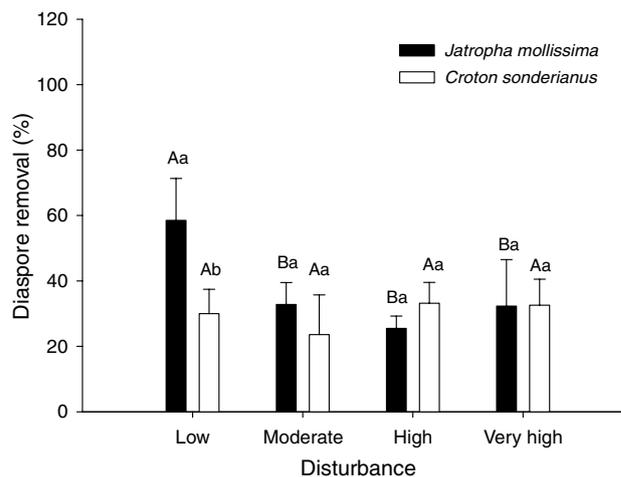


Fig. 1 Overall percentage of diaspores from two euphorb species ($n = 50$ per species) removed by ants in habitats under different levels of chronic anthropogenic disturbance ($n = 24$). Bars represent SEs. Different capital letters indicate significant differences among disturbance categories and different lower-case letters indicate significant differences among plant species, according to two-way ANOVA

60 % of all removals. Two ant species, *Dinoponera quadriceps* and *Ectatomma muticum*, were responsible for 72 % of all observed removals (Table 1). *D. quadriceps* was a particularly dominant remover of *Jatropha* diaspores, being responsible for 56 % of removals for this species, compared with only 2 % for *Croton*. On four occasions, the dung beetle *Canthon carbonarius* was observed removing diaspores for 2, 4, 27 and 65 cm, respectively, in three different sites (see Iannuzzi et al. 2013). Crickets were also observed consuming *Croton sonderianus* elaiosomes in situ in two of our sites.

Three ant species were classified as high-quality dispersers: *D. quadriceps*, *E. muticum* and *Camponotus crassus*, which together accounted for 75 % of all observed diaspore removals (Table 1). Mean body size of these species ranged from approximately 4 mm in *C. crassus* to 22 mm in *D. quadriceps*. *C. crassus* contributed only 4 % of all ant-diaspore interactions and less than 1 % of all diaspore removals; we therefore consider only *D. quadriceps* and *E. muticum* as high-quality dispersers for statistical analysis, and refer to them simply as ‘*Dinoponera*’ and ‘*Ectatomma*’, respectively. Low-quality dispersers comprised species of *Pheidole*, *Solenopsis*, *Acromyrmex* and *Crematogaster* (Table 1), all with body size <4 mm and in almost all cases <2 mm.

The number of ant disperser species ranged from one to eight per site, and did not vary with level of disturbance ($F_{4,17} = 2.25$; $df = 4$; $p = 0.11$; Fig. 2a). However, overall ant disperser composition varied significantly with disturbance (CCA, $F = 2.5$; $df = 1$; $p < 0.001$; Fig. 3). A range of low-quality disperser species were positively associated

Table 1 Number of removals and mean removal distance (\pm SD) per ant species removing myrmecochorous diaspores from two Euphorbiaceae species at sites experiencing different levels of chronic anthropogenic disturbance

	Chronic disturbance level				Total of removed seeds	Mean removal distance (cm)
	Low	Moderate	High	Very high		
High-quality dispersers						
<i>Dinoponera quadriceps</i> (Din)	71	62	32	21	186	563.97 \pm 444.22
<i>Ectatomma muticum</i> (Ect)	4	34	93	16	148	26.82 \pm 57.52
<i>Camponotus crassus</i> (Ca1)	6	0	4	0	10	16.70 \pm 21.90
Low-quality dispersers						
<i>Pheidole</i> sp.1 (Ph1)	12	0	9	28	49	19.03 \pm 32.05
<i>Pheidole</i> sp.2 (Ph2)	0	0	2	7	9	10.50 \pm 6.76
<i>Pheidole</i> sp.3 (Ph3)	0	0	9	0	9	17.86 \pm 2.45
<i>Acromyrmex rugosus</i> (Ac)	0	0	7	0	7	55.00 \pm 3.45
<i>Crematogaster</i> sp. (Cr)	0	0	2	0	2	2.50 \pm 1.00
<i>Solenopsis</i> sp.1 (So1)	14	4	0	3	21	94.11 \pm 257.44
<i>Solenopsis</i> sp.2 (So2)	16	1	0	0	17	179.45 \pm 62.45
<i>Solenopsis</i> sp.3 (So3)	0	0	3	0	3	3.00 \pm 0.00

Codes for each ant species are given in parentheses

with disturbance, whereas several other species, notably *Dinoponera*, were negatively associated with disturbance (Fig. 3).

The numbers of interactions by high-quality ant disperser species were significantly affected by disturbance. In particular, the number of diaspore interactions with *Dinoponera* declined systematically with increasing disturbance ($F_{4,16} = 9.02$; $df = 4$; $p < 0.001$), and was more than tenfold higher in low compared with very highly disturbed sites (Fig. 2b). The number of diaspore interactions with *Ectatomma* was highest at intermediate levels of disturbance ($F_{4,16} = 7.20$; $df = 4$; $p < 0.01$; Fig. 2b).

Diaspores were removed up to 18 m, with a mean removal distance of 118.2 ± 286.7 cm (\pm SD). *Jatropha* diaspores were removed on average 175.41 ± 154.8 cm, more than fivefold farther than *Croton* diaspores [12.7 ± 18.7 ($F_{1,42} = 10.46$; $df = 1$; $p < 0.001$)]. Mean removal distance by high-quality dispersers was 319.52 ± 285.2 cm, more than 20-fold further than by low-quality dispersers ($F_{1,42} = 16.1$; $df = 1$; $p < 0.001$). The high mean removal distance by high-quality dispersers was due primarily to *Dinoponera* (563.97 ± 444.2 , compared with 26.82 ± 57.52 cm for *Ectatomma*; $F_{1,19} = 29.019$; $df = 1$; $p < 0.001$). *Dinoponera* was also responsible for 94 % of removals >2 m, and all removals >5 m. Mean removal distance for *Ectatomma* was not affected by disturbance, but decreased with disturbance for *Dinoponera* ($F_{3,30} = 2.83$; $df = 3$; $p = 0.04$; Fig. 4a). Comparing the fate of diaspores removed by *Dinoponera* and *Ectatomma*, 76 and 8 % of diaspores removed by them reached the nest, respectively. However, the proportion of diaspores removed

by both species that reached the nest was not affected by disturbance ($F_{3,24} = 0.95$; $df = 3$; $p = 0.34$).

There was a significant interaction between diaspore species and disturbance for removal distance ($F_{1,35} = 5.88$; $df = 1$; $p = 0.02$). Removal distances of *Croton* diaspores were uniformly short across all disturbance levels, whereas mean removal distance declined systematically with increasing disturbance for *Jatropha*, being fourfold higher in low compared with very highly disturbed sites (Fig. 4b). Disturbance had a marked effect on the shape of the dispersal curve, increasing the incidence of very short removal distances and decreasing the incidence of long-distance removals (Fig. 5). At sites with low disturbance, 87 % of all removals were >2 m, compared with only 8–18 % at more highly disturbed sites ($\chi^2 = 39.65$; $df = 3$; $p < 0.001$). Similarly, 34 % of all seed removal events were >5 m at sites with low disturbance, compared with only 1.20, 4.4 and 0 % respectively at sites with medium, high and very high disturbance ($\chi^2 = 37.63$; $df = 3$; $p < 0.001$; Fig. 5).

Discussion

The species richness of diaspore-remover ants was not significantly affected by chronic anthropogenic disturbance in our study system. However, overall ant disperser composition and notably the number of removals by both our key high-quality disperser ants varied markedly with disturbance. Removals by *Dinoponera* declined systematically with disturbance, while those by *Ectatomma* were highest at intermediate disturbance levels. Ant abundance was not measured directly, but we attribute these responses to the

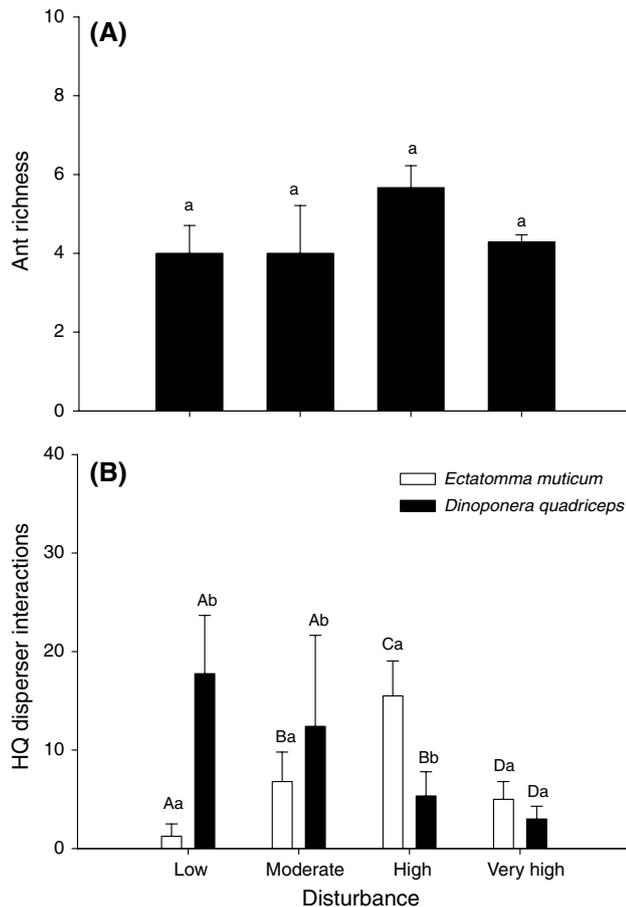


Fig. 2 Mean richness of ant disperser species (a) and frequency of interaction of two high-quality disperser ant species (HQ) with diaspores ($n = 100$) (b) from two euphorb species in habitats under different levels of chronic anthropogenic disturbance ($n = 24$). Bars represent SEs. Different capital letters indicate significant differences among disturbance categories and different lower-case letters indicate significant differences among plant species, according to two-way ANOVA

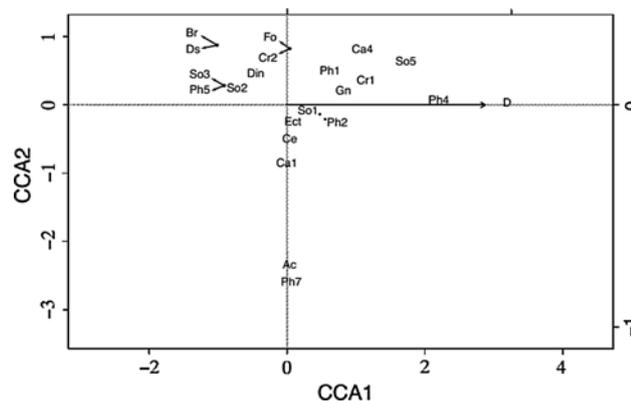


Fig. 3 Canonical correlation analysis biplot of ant disperser species (see Table 1 for species' codes) in relation to disturbance (arrow). Lines joining species to dots indicate the location of multiple species at a single point

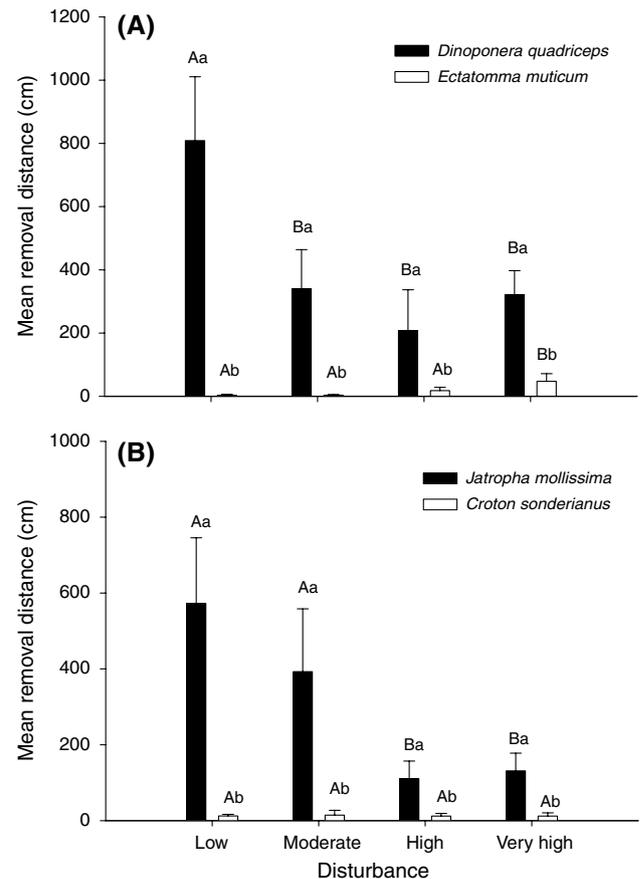


Fig. 4 Mean removal distance of diaspores from two euphorb species by two high-quality disperser ant species (a) and by all ant species combined (b) in habitats under different levels of chronic anthropogenic disturbance ($n = 24$). Bars represent SEs. Different capital letters indicate significant differences among disturbance categories and different lower-case letters indicate significant differences among plant species, according to two-way ANOVA

effects of disturbance on species' abundances. The responses of ant species to disturbance are highly variable among ecosystems and are strongly dependent on species' functional traits (Hoffmann and Andersen 2003; Phillpott et al. 2010). The unavailability of direct measurements of habitat disturbance means that a mechanistic analysis of how disturbance affected our ant species is not possible. However, according to ant functional-group classification based on global-scale responses to environmental stress and disturbance (Andersen 1995), most Caatinga disperser ants are either Opportunists or Generalised Myrmicinae, which tend to have high tolerances of habitat disturbance (Hoffmann and Andersen 2003). In particular, *Ectatomma* is functionally very similar to the fellow ectatommine and Opportunist *Rhytidoponera*, which is the dominant disperser ant genus in Australia (Andersen and Morrison 1998; Gove et al. 2007) and likewise is favoured by moderate disturbance (Hoffmann and Andersen 2003 and references therein).

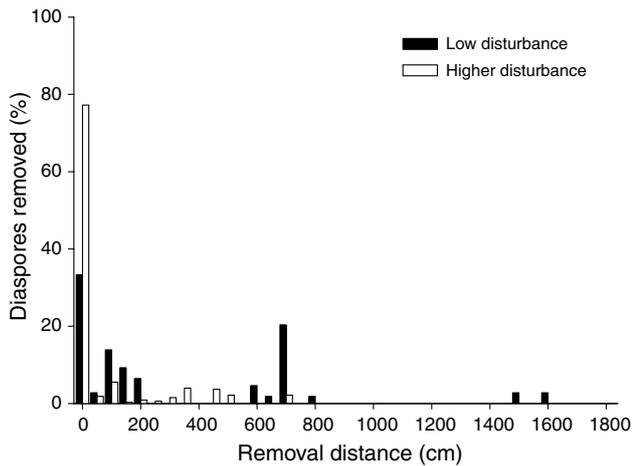


Fig. 5 Seed-dispersal curves generated by ants (all species combined) removing myrmecochorous diaspores from two euphorb species in habitats under low (low + moderately disturbed sites) and higher (high + very highly disturbed sites) levels of disturbance ($n = x$ and y , respectively)

In contrast to *Ectatomma*, *Dinoponera* was highly sensitive to disturbance. The frequent removal of myrmecochorous diaspores by *Dinoponera* is highly unusual for a ponerine ant genus (however see Pizo and Oliveira 1998, 2000; Passos and Oliveira 2002, 2003), as most ponerine species are specialist predators. Our study species (*Dinoponera quadriceps*) is primarily carnivorous (Araújo and Rodrigues 2006), as appears to be typical for the genus (Fourcassié and Oliveira 2002). Specialist predators are typically among the ants most sensitive to disturbance (Hoffmann and Andersen 2003; Leal et al. 2012; Senior et al. 2013), and *Dinoponera* showed such a response in our study. *Dinoponera* was the dominant disperser ant in that it was responsible for a substantial proportion (37 %) of all seed removals, and 97 % of all removals >2 m. Its response to disturbance therefore had important implications for the effects of disturbance on seed dispersal.

Disturbance also affected the composition of low-quality disperser ants, with several such species being positively associated with disturbance. These species typically feed on elaiosomes in situ, without effective dispersal, and so can be considered mutualism cheaters. Disturbance therefore not only reduces removal by the highest-quality seed disperser (*Dinoponera*), but favours cheater species.

Removal rates of *Jatropha* diaspores at more highly disturbed sites were about half that at sites with low disturbance, whereas removal rates of *Croton* diaspores were not affected by disturbance. *Jatropha* diaspores are known to be more attractive to, and dependent on, high-quality seed-disperser ants than are those of *Croton* (Leal 2010). In our study, high-quality disperser ants were responsible for almost 90 % of all observed *Jatropha* diaspore removals,

compared with only 31 % for *Croton*. *Dinoponera* was responsible for 92 % of all removals of *Jatropha* diaspores, and so the lower removal rates at more highly disturbed sites can be directly attributed to reduced removals by *Dinoponera*.

Given the dominant role played by *Dinoponera* in long-distance removals, its reduced removal rates with increasing disturbance would be expected to have a major impact on patterns of distance dispersal. Indeed, mean removal distance of *Jatropha* diaspores was fourfold higher in low compared with very high disturbance, and no removals further than 5 m were observed in highly disturbed sites. In general, myrmecochory generates short dispersal distances when compared with dispersal by other animal species. However, some diaspores can reach relatively long distances when they are removed by large-bodied ants with large foraging ranges (Gomez and Espadaler 1998). Myrmecochorous plants are often of very small stature, and so relatively short dispersal distances are enough to remove diaspores away from parental influence and provide escape from parental competition (Leal et al. 2007). However, myrmecochorous Euphorbiaceae in Caatinga are taller than most other myrmecochorous plants around the world (I. R. Leal, unpublished data), and diaspores therefore need to be removed further for effective distance dispersal. Our findings show that the incidence of removals >2 m is dramatically reduced by disturbance in Caatinga, suggesting that dispersal services are severely compromised at highly disturbed sites. Given that myrmecochorous Euphorbiaceae species are a dominant component of the Caatinga flora (Rodal and Nascimento 2006), this may significantly limit vegetation recovery after disturbance.

In conclusion, despite a high diversity of seed-dispersing ant species, our Caatinga system has only a very limited number of high-quality seed dispersers, and these are functionally very different in terms of distance dispersal and response to chronic anthropogenic disturbance. In particular, the species responsible for most long-distance dispersals is highly sensitive to disturbance, and so distance dispersal decreases markedly with increasing disturbance. Despite high overall diversity there is therefore very limited functional redundancy in disperser ant species, resulting in low disperser resilience in relation to disturbance. This is likely to have important longer-term implications for recruitment by myrmecochorous plants, and therefore on vegetation composition and structure, at sites subject to high anthropogenic disturbance.

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Conflict of interest The authors declare that they have no conflict of interest.

References

- Aizen M, Sabatino M, Tylianakis JM (2012) Specialization and rarity predict non-random loss of interactions from mutualistic networks. *Science* 335:1486–1489. doi:10.1126/science.1215320
- Andersen AN (1988) Dispersal distance as a benefit of myrmecochory. *Oecologia* 75:507–511. doi:10.1007/BF00776412
- Andersen AN (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J Biogeogr* 22:15–29. doi:10.2307/2846070
- Andersen AN, Morrison SC (1998) Myrmecochory in Australia’s seasonal tropics: effects of disturbance on distance dispersal. *Aust J Ecol* 23:483–491. doi:10.1111/j.1442-9993.1998.tb00756.x
- Araújo A, Rodrigues Z (2006) Foraging behavior of the queenless ant *Dinoponera quadriceps* Santschi (Hymenoptera: Formicidae). *Neotrop Entomol* 35:159–164. doi:10.1590/S1519-566X2006000200002
- Bascompte J, Jordano P (2007) Plant-animal mutualistic network: The architecture of biodiversity. *Annu Rev Ecol Evol Syst* 38:567–593. doi:10.1146/annurev.ecolsys.38.091206.095818
- Beattie AJ (1985) The evolutionary ecology of ant-plant mutualisms, 1st edn. Cambridge University Press, Cambridge
- Bond WJ (1995) Assessing the risk of extinction due to pollinator and disperser failure. In: Lawton JH, May M (eds) *Extinction rate*. Oxford University Press, New York, pp 131–146
- Bossard CC (1991) The role of habitat disturbance, seed predation and ant dispersal on establishment of the exotic shrub *Cytisus scoparius* in California. *Am Midl Nat* 126:1–13
- Brunn HH, Lundgren R, Phillip M (2008) Enhancement of local species richness in tundra by seed dispersal through guts of muskox and barnacle goose. *Oecologia* 155:101–110. doi:10.1007/s00442-007-0892-y
- Byrne MM, Levey DJ (1993) Removal of seeds from frugivore defecation by ants in a Costa Rica forest. *Vegetatio* 107(108):367–374. doi:10.1007/BF00052235
- Colles A, Liow JH, Prizing A (2009) Are specialists at risk under environmental changes? Neocological, paleoecological and phylogenetic approaches. *Ecol Lett* 12:849–863. doi:10.1111/j.1461-0248.2009.01336.x
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Syst* 34:487–515. doi:10.1146/annurev.ecolsys.34.011802.132419
- Farwig N, Berens DG (2012) Imagine a world without seed dispersers: a review of threats, consequences and future directions. *Basic Appl Ecol* 13:109–115. doi:10.1016/j.baee.2012.02.006
- Filgueiras BKC, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in Atlantic forest. *Biol Conserv* 144:362–369. doi:10.1016/j.biocon.2010.09.013
- Fourcassié V, Oliveira PS (2002) Foraging ecology of the giant Amazonian ant *Dinoponera gigantea* (Hymenoptera, Formicidae, Ponerinae): activity schedule, diet and spatial foraging patterns. *J Nat Hist* 36:2211–2227. doi:10.1080/00222930110097149
- Giladi I (2006) Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* 112:481–492. doi:10.1111/j.0030-1299.2006.14258.x
- Gomez C, Espadaler X (1998) Myrmecochorous dispersal distances: a world survey. *J Biogeogr* 25:573–580. doi:10.1046/j.1365-2699.1998.2530573.x
- Gorb E, Gorb SN (2003) *Seeds dispersal by ants in a decidual forest ecosystem. Mechanisms, strategies, adaptations*, 1st edn. Kluwer, Dordrecht
- Gove AD, Majer JD, Dunn RR (2007) A keystone ant species promotes seed dispersal in a “diffuse” mutualism. *Oecologia* 153:687–697. doi:10.1007/s00442-007-0756-5
- Gunderson LH (2000) Ecological resilience—in theory and application. *Annu Rev Ecol Evol Syst* 31:425–439. doi:10.1146/annurev.ecolsys.31.1.425
- Hanna L, Carr JL, Lankerani A (1995) Human disturbance and natural habitat: a biome level analysis of a global dataset. *Biodivers Conserv* 4:128–155. doi:10.1007/BF00137781
- Hoffmann BD, Andersen AN (2003) Responses of ants to disturbance in Australia with particular reference to functional groups. *Austral Ecol* 28:444–464. doi:10.1046/j.1442-9993.2003.01301.x
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35. doi:10.1890/04-0922
- Iannuzzi L, Leal LC, Meiado MV, Ribeiro SC, Salomão RP (2013) First record of myrmecochorous diaspores removal by dung beetles in the Caatinga vegetation, a Brazilian semi-arid ecosystem. *J Arid Environ* 88:1–3. doi:10.1016/j.jaridenv.2012.08.001
- IBGE (1985) *Atlas Nacional do Brasil: Região Nordeste*. IBGE, Rio de Janeiro
- Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. *Annu Rev Ecol Syst* 29:83–112. doi:10.1146/annurev.ecolsys.29.1.83
- Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, Leubhn G, Minckley R, Packer L, Potts SG, Roulston T, Steffan-Dewenter I, Vazquez DP, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein AM, Regetz J, Ricketts TH (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol Lett* 10:299–314. doi:10.1111/j.1461-0248.2007.01018.x
- Laliberté E, Wells JA, DeClerk F, Metcalfe DJ, Catterall CP, Queiroz C, Aubin I, Bonser SP, Ding Y, Fraterrigo JM, McNamara S, Worgan JW, Merlos DS, Vesik PA, Mayfield MM (2009) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol Lett* 12:1–11. doi:10.1111/j.1461-0248.2009.01403.x
- Leal LC (2010) Características dos elaiossomos de sementes de Euphorbiaceae e suas influências na atividade dos agentes dispersores no semi-árido nordestino. Master thesis, Botany Department, Universidade Federal de Pernambuco, Brazil
- Leal IR, Silva JMC, Tabarelli M, Lacher TE (2005) Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil. *Conserv Biol* 19:701–706. doi:10.1111/j.1523-1739.2005.00703.x
- Leal IR, Wirth R, Tabarelli M (2007) Seed dispersal by ants in the semi-arid Caatinga of north-east Brazil. *Ann Bot* 99:885–894. doi:10.1093/aob/mcm017
- Leal IR, Filgueiras BKC, Gomes JP, Andersen AN (2012) Effects of habitat fragmentation on ant richness and functional composition in Atlantic forest of northeastern Brazil. *Biodivers Conserv* 21:1687–1701. doi:10.1007/s10531-012-0271-9
- Lengyel S, Gove A, Latimer AM, Majer JD, Dunn RR (2010) Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. *Perspect Plant Ecol Evol Syst* 12:43–55. doi:10.1016/j.ppees.2009.08.001
- Marini L, Bruun HH, Heikkinen RK, Helm A, Honnay O, Krauss J, Kuhn I, Lindborg R, Partel M, Bommarco R (2012) Traits related

- to species persistence and dispersal explain changes in plant communities subjected to habitat loss. *Divers Distrib* 18:890–908. doi:[10.1111/j.1472-4642.2012.00893.x](https://doi.org/10.1111/j.1472-4642.2012.00893.x)
- Markl JS, Scheleuning M, Forget PM, Jordano P, Lambert JE, Traveset A, Wright SJ, Böhning-Gaese K (2012) Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conserv Biol* 26:1072–1081. doi:[10.1111/j.1523-1739.2012.01927.x](https://doi.org/10.1111/j.1523-1739.2012.01927.x)
- Martorrel C, Peters EM (2005) The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. *Biol Conserv* 124:199–207. doi:[10.1016/j.biocon.2005.01.025](https://doi.org/10.1016/j.biocon.2005.01.025)
- MMA (Ministério do Meio Ambiente) (2011) Caatinga. <http://www.mma.gov.br/biomass/caatinga>. Accessed December 2011
- Murcia C (1995) Edge effects in fragmented forest: implications for conservation. *Trends Ecol Evol* 10:58–62. doi:[10.1016/S0169-5347\(00\)88977-6](https://doi.org/10.1016/S0169-5347(00)88977-6)
- Ness JH, Bronstein J, Andersen AN, Holland JN (2004) Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions. *Ecology* 85:1244–1250
- Ness JH, Morin F, Giladi I (2009) Uncommon specialization in mutualism between a temperate herbaceous plant guild and the ant: are Aphaenogaster ants keystone mutualists? *Oikos* 118:1793–1804. doi:[10.1111/j.1600-0706.2009.17430.x](https://doi.org/10.1111/j.1600-0706.2009.17430.x)
- Nimer E (1972) Climatologia da região sudeste do Brasil. *Rev Bras Geol* 34:3–48
- Palmer TM, Stanton ML, Young TP, Goheen JR, Pringle RM, Karban R (2008) Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. *Science* 11:192–195. doi:[10.1126/science.1151579](https://doi.org/10.1126/science.1151579)
- Passos L, Oliveira PS (2002) Ants affect the distribution and performance of *Clusia criuva* seedlings, a primary bird-dispersed rainforest tree. *J Ecol* 90:517–528. doi:[10.1046/j.1365-2745.2002.00687.x](https://doi.org/10.1046/j.1365-2745.2002.00687.x)
- Passos L, Oliveira PS (2003) Interaction between ants, fruits and seeds in a restinga forest in southeastern Brazil. *J Trop Ecol* 19:261–270. doi:[10.1017/S0266467403003298](https://doi.org/10.1017/S0266467403003298)
- Pennington RT, Prado DA, Pendry C (2000) Neotropical seasonally dry forests and Pleistocene vegetation changes. *J Biogeogr* 27:261–273. doi:[10.1046/j.1365-2699.2000.00397.x](https://doi.org/10.1046/j.1365-2699.2000.00397.x)
- Phillpott SM, Perfecto I, Ambrecht I, Parr C (2010) Ant diversity and function in disturbed and changing habitats. In: Lach L, Parr C, Abbott K (eds) *Ant ecology*. Oxford University Press, New York, pp 137–157
- Pizo MA, Oliveira PS (1998) Interaction between ants and seeds of a nonmyrmecochorous neotropical tree, *Cabrlea canjerana* (Meliaceae), in the Atlantic forest of southeast Brazil. *Am J Bot* 85:885–894
- Pizo MA, Oliveira PS (2000) The use of fruits and seeds by ants in the Atlantic forest of southeast Brazil. *Biotropica* 32:851–861. doi:[10.1111/j.1744-7429.2000.tb00623.x](https://doi.org/10.1111/j.1744-7429.2000.tb00623.x)
- Prado DE (2003) As Caatingas das Américas do Sul. In: Leal IR, Almeida-Cortez J, Santos JC, Tabarelli M (eds) *Ecologia e Conservação da Caatinga*, 1st edn. Editora Universitária da UFPE, Recife, pp 3–73
- Restrepo C, Gomez N (1998) Responses of understory birds to anthropogenic edges in a Neotropical montane forest. *Ecol Appl* 8:170–183. doi:[10.1890/1051-0761\(1998\)008\[0170:ROUBTA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)008[0170:ROUBTA]2.0.CO;2)
- Riutta T, Slade EM, Bebbler DP, Taylor ME, Malhi Y, Riordan P, MacDonald DW, Morecroft MD (2012) Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. *Soil Biol Biochem* 49:124–131. doi:[10.1016/j.soilbio.2012.02.028](https://doi.org/10.1016/j.soilbio.2012.02.028)
- Rodal MJN, Nascimento LM (2006) The arboreal component of a dry forest in northeastern Brazil. *Braz J Biol* 66:479–491. doi:[10.1590/S1519-69842006000300014](https://doi.org/10.1590/S1519-69842006000300014)
- Santos BA, Arroyo-Rodriguez V, Moreno CE, Tabarelli M (2010) Edge-related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. *PLoS ONE*. doi:[10.1371/journal.pone.0012625](https://doi.org/10.1371/journal.pone.0012625)
- Senior MJM, Hamer KC, Bottrell S, Edwards DP, Fayle TM, Lucey JM, Mayhew PJ, Newton R, Peh KSH, Sheldon FH, Stewart C, Styring AR, Thom MDF, Woodcock P, Hill JK (2013) Trait-dependence declines of species following conversion of rain forest to oil palm plantations. *Biodivers Conserv* 22:253–268. doi:[10.1007/s10531-012-0419-7](https://doi.org/10.1007/s10531-012-0419-7)
- Singh SP (1998) Chronic disturbance, a principal cause of environmental degradation in developing countries. *Environ Conserv* 25:1–2. doi:[10.1017/S0376892998000010](https://doi.org/10.1017/S0376892998000010)
- Swihart RK, Gehring TM, Kolozsvary MB, Nupp TU (2003) Responses of ‘resistant’ vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Divers Distrib* 9:1–18. doi:[10.1046/j.1472-4642.2003.00158.x](https://doi.org/10.1046/j.1472-4642.2003.00158.x)
- Toledo VM, Ortíz B, Medellín-Morales S (1994) Biodiversity islands in a sea of pasturelands: indigenous resources management in the humid tropics of Mexico. *Etnoecológica* 2:37–50
- Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini-review. *Ecol Res* 17:229–239. doi:[10.1046/j.1440-1703.2002.00482.x](https://doi.org/10.1046/j.1440-1703.2002.00482.x)
- Woodcock P, Edwards DP, Fayle TM, Newton RB, Khen CV, Bottrell SH, Hamer KC (2011) The conservation value of South East Asia’s highly degraded forests: evidence from leaf-litter ants. *Philos Trans R Soc B* 366:3256–3264. doi:[10.1098/rstb.2011.0031](https://doi.org/10.1098/rstb.2011.0031)