



Disturbance Winners or Losers? Plants Bearing Extrafloral Nectaries in Brazilian Caatinga

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ABSTRACT

Plants bearing extrafloral nectaries (EFNs) often have traits typical of pioneer species, and may be expected to proliferate in disturbed habitats. However, a negative effect of disturbance on visitation by attendant ants could prevent EFN-bearing plants from acting as disturbance winners. Here, we address the effects of chronic anthropogenic disturbance on the abundance of EFN-bearing plants and their interactions with attendant ants in Caatinga vegetation of northeastern Brazil. We recorded the abundance of EFN-bearing plants, proportion of plants visited by ants and composition of ant attendant species at 24 sites varying in levels of disturbance. EFN-bearing plants as a whole did not behave as a disturbance winner group. The responses of the 13 species to increasing disturbance were highly variable, with three species declining in abundance (loser species). The richness of ant species attending EFNs did not vary with disturbance, but species composition did. The overall proportion of EFN-bearing plants attended by ants per 5-min period was not affected by disturbance. However, for the three loser species, attendance decreased from about 50 percent with low and moderate disturbance to half that with very high disturbance. We hypothesize that disturbed sites are more stressful for loser species compared with other EFN-bearing plants, with physiological stress resulting in lower production of EFN secretions and reduced attraction of ants. This would make such species double losers, with physiological stress at disturbed sites not only directly influencing their performance but also indirectly affecting it through the disruption of a key mutualism.

Key words: anthropogenic disturbance; ant–plant interaction; Caatinga; facultative mutualism; nectar; semi-arid vegetation.

HABITAT MODIFICATION IS A PRIMARY CAUSE OF GLOBAL BIODIVERSITY DECLINE (Sala *et al.* 2000), and understanding the mechanisms driving ecological degradation in disturbed habitats remains one of the most important challenges for ecologists. One important step is to understand how disturbance affects different functional groups of plants and animals (Luque *et al.* 2013). Most studies of disturbance have focused on its negative effects on species. Such disturbance ‘losers’ are often specialized taxa that are characteristic of climax vegetation (Tabarelli *et al.* 2012). However, many species actually benefit from habitat disturbance (Lewis *et al.* 2009). These disturbance winners often have wide geographical ranges and exhibit r-strategist behavior that allows them to take advantage of the open sites and release of resources that are associated with the decline of loser species in disturbed habitats (McKinney & Lockwood 1999, Tabarelli *et al.* 2012).

Winner–loser replacement involving a proliferation of native, disturbance-tolerant species has been well-documented for plants in tropical forests (Santos *et al.* 2008, 2010, Tabarelli *et al.* 2010a,

b, Lobo *et al.* 2011). In these ecosystems, disturbance drives the replacement of shade tolerant, old growth species by native pioneer species (Laurance *et al.* 2006, Tabarelli *et al.* 2008, Aguiar & Tabarelli 2010). These replacements result in an impoverishment of local vegetation not only in terms of taxonomic and phylogenetic composition but also of plant functional traits (Santos *et al.* 2008, 2010, but see Hernández-Ruedas *et al.* 2014). Such changes in plant functional traits can have important implications for resource availability for animal species (Melo *et al.* 2006, Girão *et al.* 2007). Hence, winner–loser replacements also may result in shifts in plant–animal interactions, with cascading effects on ecological structure and function of local and regional communities (Aguilar *et al.* 2006, Tabarelli *et al.* 2010a,b).

Plants bearing extrafloral nectaries (EFNs) exemplify a plant functional group that can benefit from habitat disturbance and subsequently change the pool of resources available for its faunal attendants. EFNs are not related to pollination, but rather attract aggressive insects (particularly ants) that help protect the plant from its insect herbivores (Rico-Gray & Oliveira 2007 and references therein). EFNs have evolved independently many times (Barrera & Nobel 2004, Nogueira *et al.* 2012), occurring in more

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than 700 genera representing more than 108 families (Marazzi *et al.* 2013). EFNs are especially prevalent in plants with high growth rates and affinity for full-light habitats, which are common traits of pioneer species (Schupp & Feener 1991, Bluthgen & Reinferath 2003). EFN-bearing plants might therefore be expected to be disturbance winners. However, if disturbance negatively affects attendant ants and reduces rates of visitation by ant mutualists, this might prevent EFN-bearing plants from fully exploiting disturbed habitats. Indeed, several ant–plant mutualistic systems have been negatively affected by human disturbance through the replacement of specialist ants by generalist species that provide poorer plant-protection services (*e.g.*, Zelikova & Breed 2008, Leal *et al.* 2014).

Here, we address the effects of disturbance on EFN-bearing plants and their attendant ants in Caatinga vegetation of north-eastern Brazil. We specifically examine the effects of chronic anthropogenic disturbance (*sensu* Singh 1998) on the (1) abundance of EFN-bearing plants, (2) proportion of EFN plants visited by ants, and (3) composition of EFN-attending ant species. We hypothesize that the density of EFN-bearing plants will increase with disturbance, but that rates of EFN visitation will decline because of changes in the composition of EFN-attending ant species.

METHODS

STUDY SITES.—Caatinga vegetation is a mosaic of xerophytic, deciduous thorn scrubs, and seasonally dry forests covering nearly 900,000 km² of northeastern Brazil (Pennington *et al.* 2009). Nearly, half of its area has been transformed to croplands, pastures, and human settlements since European colonization (MMA 2011), and almost all remaining Caatinga vegetation experiences chronic disturbance associated with grazing and browsing by goats and cattle, firewood harvesting, and hunting (Leal *et al.* 2005). Chronic disturbance is characterized by the removal of small amounts of natural resources over time (Singh 1998). It does not dramatically alter overall vegetation structure, but can have ecological consequences that seriously threaten Caatinga conservation (Singh 1998).

The study took place in a continuous area of Caatinga vegetation near Parnamirim city (8°5'S; 39°34'W and 393 m a.s.l.) in Pernambuco state, northeastern Brazil. The climate is semi-arid, with most of the 550 mm mean annual rainfall arriving between January and May (IBGE - Instituto Nacional de Geografia e Estatística 1985). However, the length of wet season is highly variable, with dry seasons commonly lasting >7 months (Nimer 1972, Prado 2003). Soils are predominantly non-calcic brown soils (clay soil), regosols and planosols (sandy soils) (IBGE - Instituto Nacional de Geografia e Estatística 1985). We established 24 study sites (each 50 m × 20 m; separated by at least 2 km) over an area of approximately 152 km², with 13 on regosols and 11 on non-calcic brown soils.

The natural habitat structure of Caatinga vegetation (especially the lack of a well-developed ground layer) combined with the chronic rather than acute nature of disturbance prevented the

quantification of level of disturbance based on habitat characteristics. Instead, we characterized different levels of chronic disturbance using surrogates of intensity of human activity and resource use (adapted from Martorel & Peters 2005, for more details see Leal *et al.* 2014). A range of studies have used this method to assess levels of chronic disturbance (see Martorel & Peters 2005 and references therein). Areas experiencing acute (such as slash and burn agriculture) rather than chronic disturbance in the last 50 years were not included.

Grazing by stock (goats and cattle), firewood collection, and hunting are the main sources of disturbance in our study area, and their intensity is inversely related to proximity to rural properties and to the city of Parnamirim (Ribeiro *et al.* 2015). We classified our 24 sites according to four disturbance levels based on five metrics: distance to Parnamirim, distance to nearest farm, distance to nearest road, number of stock (goats and cattles combined) managed by farms within 2 km, and number of people living in farms within 2 km, as outlined in Leal *et al.* (2014). For each of the five metrics, we classified sites into four categories, each with six sites. For the three distance metrics (measured using satellite imagery), categories ranged from 1 (highest distance values) to 4 (lowest distance values). For numbers of stock and people, categories ranged from 1 (lowest) to 4 (highest). We summed the values of each metric to obtain an overall disturbance score for each site, with a higher score indicating higher levels of disturbance. We did not ascribe differential weight to any particular disturbance surrogate as there was no basis for doing so. The frequency distribution of disturbance scores showed four clear categories of level of anthropogenic disturbance, rather than continuous variation (Fig. S1), and these categories were used to classify our sites as experiencing low (five sites), moderate (six sites), high (six sites), and very high (seven sites) disturbance.

SAMPLING.—We conducted our field observations during the wet season (February and May of 2012), when the EFNs were most active. In each of the 24 study sites, we counted all woody plant species with basal diameter >3 cm. To determine which species bear EFNs, we checked all plants for the presence of visible non-floral nectar glands or nectar accumulation. We used available taxonomic lists and previous reports for EFN-bearing plants in Caatinga (Melo *et al.* 2010a,b) to confirm our field observations and to ensure that we included EFN-bearing plants for which we did not observe EFNs in the field.

We selected the 20 study sites with the highest abundances of EFN-bearing plants to examine ant visitation. In each site, we inspected one branch on each EFN-bearing plant for up to 5 min, and considered the plant to be attended by ants when we observed ants feeding on at least one extrafloral nectary gland during that period. A 5-min observation per plant gave us only a snapshot of EFN attendance by ants, but our aim was to obtain comparative data across sites rather than to document comprehensively all ants attending any particular plant. We made all observations between 0700 and 1700 h, avoiding the hottest period of the day (1100–1300 h) when ant activity and EFN attendance is reduced (Oliveira *et al.* 1999 and pers. obs.). Our

sampling protocol did not cover nocturnal activity. We collected ants that could not be readily identified in the field for identification in the laboratory.

DATA ANALYSIS.—We used one-way ANOVA to evaluate differences in relation to level of disturbance in the density (number per plot) and relative abundance (percentage of total plants) of EFN-bearing plants, the density of non EFN-bearing plants, the percentage of EFN-bearing plants attended by ants, and the richness of EFN-attending ants. We arcsine-square root-transformed percentage data and verified the normality of the residuals and homogeneity of variances through Shapiro–Wilk and Levene tests, respectively. We log-transformed data that did not meet homoscedasticity criteria. We constructed Bray–Curtis similarity matrices based on the frequency of EFN-attending ant species, and used pair-wise ANOSIM to test for the effects of disturbance (nested under soil type) on species composition. We used similarities of percentage (SIMPER) to determine which ant species contributed most to any similarities among disturbance levels. We conducted all ANOVAs with STATISTICA 8.0 (Statsoft, Inc, Tulsa, U.S.A.) and multivariate analysis using PRIMER.

Interpretations of ANOVA results are potentially constrained by the fact that some disturbance categories were represented by sites from only one soil type (all the ‘low’ sites used to observe ant visitation were located on non-calcic brown soils, whereas all ‘high’ sites were on regosols), and so there is potential confounding of disturbance with soil type. However, there is no systematic bias in soil type along the disturbance gradient (Table 1). To account for the effects of soil type, whenever we found a statistically significant effect of disturbance we re-analyzed the data using residuals from an analysis of the effect of soil type. In all cases, the effects of disturbance still proved to be statistically significant, and we present results only from the original analyses.

RESULTS

In total, we observed 5396 plants (mean of 224.8 per 50 m × 20 m site) belonging to 13 EFN-bearing species across all sites (Table 2). *Croton sonderianus* (Euphorbiaceae) was the most abundant species, with 3267 individuals (61% of total) across all plots. The Fabaceae had the highest number of EFN-bearing species (nine) followed by the Euphorbiaceae (four). The overall densities of EFN-bearing plants ($F_{(3,21)} = 0.86$; $P = 0.46$; Fig. 1) and non-EFN plants ($F_{(3,21)} = 1.51$; $P = 0.25$; Fig. 1) were not affected by disturbance level, similar to the dominant *C. sonderianus*

(Table 2). However, other species showed contrasting responses. Densities of *Bauhinia cheilantha*, *Poincianella pyramidalis*, and *Senna macranthera* (all Fabaceae) decreased with increasing disturbance (and are hereafter referred to as loser species), whereas *Anadenanthera colubrina* and *Mimosa tenuiflora* (both Fabaceae) were most common at intermediate levels of disturbance (Table 2 winner species). *Poincianella pyramidalis* showed a bimodal density pattern in relation to disturbance (Table 2), but we consider it a loser species because it was substantially less abundant under moderate and high disturbance compared with low.

We observed a total of 14 ant species attending EFN-bearing plants (Table 3). *Camponotus crassus* was the most frequent ant species attending EFNs, representing 81 percent of all ant-attendance observations. The richness of EFN-attending ant species was not affected by disturbance ($F_{(3,16)} = 0.655$; $P = 0.60$). However, ant species composition varied with disturbance level (ANOSIM, Global R = 0.7, $P = 0.04$). *Camponotus crassus* and *Camponotus* sp. 2 together contributed 31 percent (very high vs. high disturbance) to 54 percent (very high vs. low) of dissimilarities between disturbance classes. The proportion of plants attended by particular ant species was not affected by disturbance (*C. crassus*: $F_{(3,16)} = 1.26$; $df = 3$; $P = 0.32$; *Camponotus* sp. 2: $F_{(3,16)} = 1.26$; $df = 3$; $P = 0.33$; *Cephalotes* sp.1: $F_{(3,16)} = 1.72$; $df = 3$; $P = 0.21$; other species combined: $F_{(3,16)} = 0.43$; $df = 3$; $P = 0.74$). Ants visiting *Croton sonderianus* nectaries represented 47 percent of all interactions and 77 percent of the interactions observed in plant species that did not respond to disturbance. We separately analyzed changes in composition of ant species visiting *Croton sonderianus* and found it was not affected by disturbance (ANOSIM; Global R = 0.07; $P = 0.22$).

We observed 1220 EFN-bearing plants attended by ants, representing 22.6 percent of the total EFN-bearing plants (Table 2). The rate of ant attendance per 5-min period varied markedly between EFN-bearing plants, ranging from 9 percent in *Croton sonderianus* to 90 percent in *Croton adamantinus* (Table 2). The total proportion of plants attended by ants was not affected by disturbance ($F_{(3,16)} = 0.572$, $df = 3$, $P = 0.641$; Table 2). However, this varied among plant species according to their functional responses to disturbance (Fig. 2). For loser species, the rate of ant attendance also decreased with disturbance, from about 50 percent with low and moderate disturbance, to half that with very high disturbance ($F_{(3,16)} = 4.03$; $df = 3$; $P = 0.026$; Fig. 2). By contrast, there was no variation in rate of ant attendance for the other plant functional types (Fig. 2). The variation in ant attendance was not related to variation in total density of EFN-bearing plants (Pearson’s correlation index = -0.28). We also separately analyzed the proportion of attended individuals, and it was not affected by disturbance (ANOVA; $F_{(3,14)} = 0.28$; $P = 0.60$).

DISCUSSION

Contrary to our hypothesis, EFN-bearing plants as a whole did not behave as disturbance winners by showing increased

TABLE 1. Distribution of study sites according to disturbance level and soil type in Caatinga vegetation near Parnamirim city, Northeast Brazil.

	Low	Moderate	High	Very high
Regosols	1	4	6	4
Non-calcic brown	4	2	0	3

TABLE 2. Relative abundance, mean density, and disturbance response of EFN-bearing plants in habitats under different levels of chronic anthropogenic disturbance in Caatinga vegetation near Parnamirim city, Northeast Brazil. Values in parentheses represent percentage of each species attended by ants at sites under different disturbance level. Disturbance responses reflect changes in abundance in relation to disturbance; winner-highest relative abundance at intermediate levels of disturbance; loser-relative abundance declining with increasing level of disturbance. P values are from ANOVA; NS = not significantly affected by disturbance.

EFN-bearing species	Relative (%) abundance	Density (%)				Disturbance response	P value
		Low	Moderate	High	Very high		
<i>Anadenanthera colubrina</i>	1.9	13.5 (50)	65.4 (29)	16.3 (0)	4.8 (0)	Winner	0.031
<i>Bauhinia cheilantha</i>	1.4	87.3 (2)	5.1 (75)	0.0 (0)	8.9 (0)	Loser	0.003
<i>Croton sonderianus</i>	60.5	24.2 (4)	18.9 (31.6)	19.7 (10.2)	33.1 (19)	NS	0.753
<i>Croton adamantinus</i>	8.4	13.2 (31.4)	22.8 (13.5)	43.0 (42)	19.5 (17)	NS	0.513
<i>Piptadenia stipulacea</i>	3.0	44.0 (25)	96.0 (13.5)	12.0 (33)	12.0 (25)	NS	0.068
<i>Poincianella pyramidalis</i>	9.8	46.2 (41.6)	0.7 (46)	13.8 (37)	32.6 (25)	Loser	0.004
<i>Poincianella microphylla</i>	1.6	47.7 (0)	9.1 (0)	29.5 (5)	13.6 (50)	NS	0.538
<i>Senegalia pollyphylla</i>	2.1	1.9 (0)	31.9 (16.2)	17.9 (0)	50.0 (8)	NS	0.463
<i>Senna macranthera</i>	1.6	71.4 (50)	19.0 (18.7)	7.1 (5)	2.3 (0)	Loser	<0.001
<i>Sapium glandulosum</i>	1.9	2.8 (0)	11.6 (4.2)	23.6 (37.5)	50.9 (11)	NS	0.573
<i>Cnidocolus quercifolius</i>	4.0	18.7 (65)	14.6 (22)	26.5 (50)	33.3 (44.4)	NS	0.356
<i>Mimosa tenuiflora</i>	1.7	16.0 (16.7)	70.2 (3)	1.3 (0)	12.8 (0)	Winner	0.02
Other species	1.6						

TABLE 3. Number of EFN-bearing plant species visited and percentage of total observed EFN-ant interactions for each ant species observed attending EFNs in Caatinga vegetation near Parnamirim city, Northeast Brazil.

Ant Species	Number of plant species	Percent total interactions
Myrmicinae		
<i>Cephalotes chypeatus</i>	1	0.08
<i>Cephalotes pusillus</i>	5	0.82
<i>Cephalotes</i> sp.	11	3.37
<i>Crematogaster</i> sp.1	4	0.68
<i>Crematogaster</i> sp.2	1	0.08
<i>Pheidole fallax</i>	2	0.16
Formicinae		
<i>Camponotus crassus</i>	13	80.95
<i>Camponotus (Taenomyrmex)</i> sp.1	1	0.08
<i>Camponotus</i> sp.2	12	9.35
<i>Camponotus</i> sp.3	4	1.44
Ectatomminae		
<i>Gnamptogenys</i> sp.1	4	0.49
Pseudomyrmicinae		
<i>Pseudomyrmex</i> sp.1	8	1.93
<i>Pseudomyrmex</i> sp.2	6	0.49
Dolichoderinae		
<i>Dorymyrmex spurius</i>	1	0.08

abundance at disturbed sites. The density of some species did indeed appear to be promoted by moderate disturbance, given that it was highest at intermediate levels of disturbance. How-

ever, the abundance of other EFN-bearing species declined with increasing disturbance, and so can be considered as disturbance losers. Such variable responses might be expected because of the very high phylogenetic diversity (and consequently independent evolutionary histories) of EFN-bearing plants (Barrera & Nobel 2004, Nogueira *et al.* 2012).

The species composition of ant attendants varied between low/moderately disturbed sites on the one hand, and high/very highly disturbed sites on the other, mainly due to differences in the frequency of occurrence of the two primary attendant species, *Camponotus crassus* and *Camponotus* sp. 2. The quality of antiherbivore services provided by EFN-attending ants varies markedly between species (Ness *et al.* 2009), and changes in the composition of ant attendants can have important consequences for EFN-bearing plants. The species composition of ants attending EFNs varied with disturbance, but the relative quality of services offered by these species is unknown, so we cannot assess the direct implications of such compositional change. However, the services provided by attendant ants are clearly influenced by rates of visitation, and we can assume that any reductions in rates of attendance by ants represent reductions in the services provided.

The overall proportion of EFN-bearing plants attended by ants was not affected by disturbance, but this varied between plant species. In particular, rates of ant attendance declined with increasing disturbance for loser species. This response was shown only by loser species, and so cannot be explained by a general influence of disturbance on attendant ants. Rather, it indicates that disturbance reduced the ability of loser plant

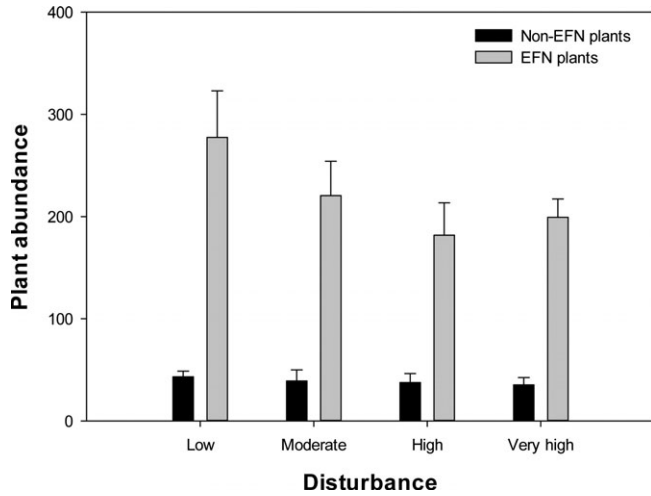


FIGURE 1. Total abundance of non-EFN and EFN-bearing woody plants in relation to disturbance in Caatinga vegetation near Parnamirim city, Northeast Brazil. Bars represent standard errors. No significant differences in relation to disturbance were found.

species to attract ants. This could be due to a range of factors, such as reduction in the number or change in location of EFNs, or, more likely, to a change in the quantity or quality of nectar produced by them. Although EFN production is

considered to be physiologically ‘cheap’ for plants, it still requires resources that could be allocated to other plant functions, and plants consequently regulate nectar production according to environmental conditions (Simms 1992, Heil *et al.* 2000, Strauss *et al.* 2002). In particular, extrafloral nectar secretion can be negatively affected when plants experience low water supply or high temperatures; both conditions commonly observed in disturbed habitats (see Murcia 1995). Plants under water stress close their stomata to avoid water loss, and, given that EFN glands are often modified stomata (Heil 2011), any factor affecting stomatal function will also affect EFN secretion. Furthermore, under stressful conditions plants produce respiration-reducing hormones that also reduce the biosynthesis of nectar sugars and nectar secretion (Nichol & Hall 1988). Therefore, the decline in ant attendance of loser plants could be related to a reduction in EFN secretions at disturbed sites due to physiological stress.

In conclusion, we hypothesize that disturbed sites are more stressful for the loser species compared with other EFN-bearing plants, with physiological stress resulting in lower production of EFN secretions and therefore reduced attraction of ants. In other words, reduced physiological performance at disturbed sites may result in a reduction in antiherbivore services for loser plant species. Thus, abiotic stress at disturbed sites would affect loser species not only directly but also indirectly through disrupting their mutualism with ants.

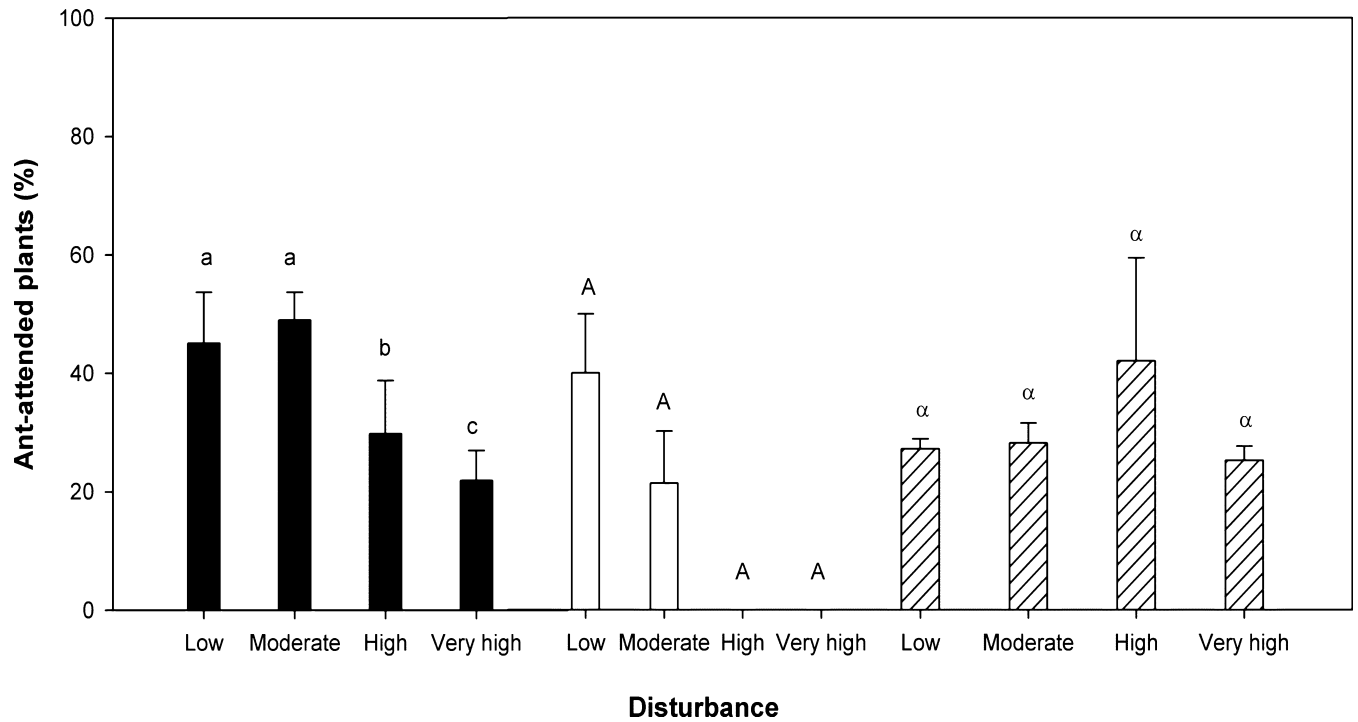


FIGURE 2. Variation in percentage of EFN-bearing plants attended by ants in relation to disturbance, with plant species classified into three groups: losers (black bars); most abundant at intermediate disturbance (empty bars), and species unaffected by disturbance (shaded bars) in Caatinga vegetation near Parnamirim city, Northeast Brazil. Bars represent standard errors. Lowercase, uppercase, and Greek letters indicate significant differences among disturbance categories.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. Frequency distribution of human disturbance scores of the 26 study plots, obtained through surrogates of intensity of human activity and resource use.

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