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Plant protection services mediated by extrafloral nectaries decline with aridity but are not influenced by chronic anthropogenic disturbance in Brazilian Caatinga

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Abstract

1. Most terrestrial species occur in human-modified landscapes that are experiencing climate change. In addition to direct impacts on species, both anthropogenic disturbance and climate change can have important effects through changes in species interactions, including the disruption of ecological services provided by them.
2. Here we investigate how chronic anthropogenic disturbance (CAD) and aridity affect the effectiveness of plant protection services provided by ants to plants bearing extrafloral nectaries (EFNs).
3. The study was conducted across 13 01-ha plots distributed along CAD and aridity gradients in Caatinga vegetation of northeastern Brazil. We focused on *Pityrocarpa moniliformis*, the most abundant and widely distributed EFN-bearing tree species occurring in our study area, and we used experimental attack rates on termites as a measure of effectiveness of ant protection services. We investigated the relative roles of nectar production (volume and concentration) and ant species composition in mediating the effects of CAD and aridity on the effectiveness of protection services.
4. Attack rates by ants declined with increasing aridity but were not related to CAD. The volume of extrafloral nectar declined with increasing CAD but was not affected by aridity, whereas the concentration was not related to either CAD or aridity. The composition of attendant ant species varied with aridity but not with CAD.

5. *Synthesis*: Our findings suggest that CAD does not affect plant-protection services mediated by EFNs in Brazilian Caatinga. However, ant-protection services declined with increased aridity, and this occurred through changes in the composition of attendant ant species rather than by changes in the production of extrafloral nectar. Such a response to increasing aridity highlights the vulnerability of EFN-bearing plants to climate change through decreased predation of herbivores.

Keywords: anti-herbivore defense, human disturbance, climate change, extrafloral nectaries, plant-animal interactions, tropical dry forest.

Introduction

Chronic anthropogenic disturbance (CAD; *sensu* Singh 1998) is one of the main threats to biodiversity in developing countries, especially in the semi-arid tropics that support a high density of rural populations depending on forest resources for their livelihoods (Singh et al. 1997, Ribeiro et al. 2015). CAD is characterized by a continuous removal of small portions of forest biomass due to activities such as livestock grazing, wood extraction and collection of non-timber products (Singh 1998). At the regional scale it can have as great an impact on biodiversity as do acute disturbances such as deforestation and forest fragmentation (Martorell and Peters 2005, Barlow et al. 2016, Ribeiro et al. 2015, 2016, Schulz et al. 2016, Sfair et al. 2018, Arnan et al. 2018a). Furthermore, most regions in the semi-arid tropics are threatened by declining rainfall and increasing temperatures due to climate change (Magrin et al. 2014), which can mediate and intensify the effects of anthropogenic disturbance (Gibb et al. 2015, Frishkoff et al. 2016, Rito et al. 2017, Arnan et al. 2018a).

Biodiversity loss due to disturbance and climate change can have broader ecological impacts through its cascading effects on species interactions (Tylianakis et al. 2008, Kiers et al. 2010, Aizen et al. 2012). These interactions mediate many aspects of ecosystem functioning (Valiente-Banuet et al. 2015, Dias et al. 2013). For instance, mutualisms play a key role in the functioning of ecosystems by providing services such as pollination, seed dispersal, plant protection and nutrient transfer (Terborgh et al. 2008, Wilson et al. 2009, Potts et al. 2010), and are strongly affected by both anthropogenic disturbances and climate change (Tylianakis et al. 2008, Kiers et al. 2010, Vilela et al. 2018), either through changes in species composition (Jones et al. 2008, Winfree et al. 2009, Potts et al. 2010, Leal et al. 2014), and/or in species behaviour (Brose et al. 2005, Tylianakis et al. 2007, Câmara et al. 2018).

This study addresses the effects of CAD and aridity on the effectiveness of protection services provided by ants that are mediated by extrafloral nectaries (EFNs). EFNs are produced by at least 4,000 plant species throughout the world (Weber and Keeler 2013). Their nectar functions to attract ants (Bentley 1977), which then repel or kill insect herbivores (Rosumek et al. 2009, Heil 2015, Del-Claro et al. 2016), potentially reducing plant herbivory and increasing plant growth and reproductive success (Fiala 1994, Nascimento and Del-Claro 2010, Marazzi et al. 2012).

Extrafloral nectar can be of particular value as a food resource for ants, with important implications for the structure and composition of ant communities and for multitrophic ant-plant-

herbivore interactions (Blüthgen and Fiedler 2004, Lange et al 2013, 2017; Dáttilo et al 2015, Díaz-Castelazo et al. 2017). For example, a reduction in nectar production can reduce the frequency and change the identity of ants attending plants (Fagundes et al. 2017, Lange et al. 2017), and consequently reduce the effectiveness of plant protection services by ants (Kost and Heil 2005, Fagundes et al. 2017). However, the outcome of these interactions can vary with both abiotic and biotic conditions across space and time (Kersch and Fonseca 2005, Rudgers and Strauss 2004) because it depends not only on extrafloral nectar secretion, but also on the abundance and identity of attendant ants (Di Giusto et al. 2001, Del-Claro et al. 2016, Fagundes et al. 2017) and on the identity and abundance of herbivores (Barton 1986, Pringle et al. 2013). Both CAD and climatic change can lead to changes in the secretion of extrafloral nectar, which can have cascading effects on the composition or behaviour of attendant ants and consequently on plant protection services (Díaz-Castelazo et al. 2017, Câmara et al. 2018). For example, disturbance can reduce nectar production due to reduced resource availability (Hernández-Villanueva 2010, Chavarro-Rodríguez et al. 2013), which could lead to lower visitation by ants (Leal et al. 2015, Díaz-Castelazo et al 2017). Similarly, EFN activity is sensitive to declining rainfall because stressful conditions reduce nectar secretions (Nichol and Hall 1988, Rico-Gray et al. 1998, Lange et al. 2013). On the other hand, the protection provided by ants to EFN-bearing plants might be more effective in arid environments due to higher carbon stress and herbivory pressure, which lead trees to increase the concentration of carbohydrates when water is scarce to insure themselves against extreme herbivory (Pringle et al. 2013). CAD and climate change are also important drivers of ant assemblages (Diamond et al. 2016, Arnan et al. 2018a, Câmara et al. 2018) and so can affect attendant ants directly rather than through the production of extrafloral nectar (Rudgers and Strauss 2004). For example, Leal and Peixoto (2017) have shown that the effectiveness of plant protection services by ants to EFN-bearing plants is higher in more arid environments due to a higher abundance of aggressive ants.

Almost all studies of the effects of CAD and a changing climate on ant protection services mediated by EFNs have taken an indirect approach, measuring either extrafloral nectar secretion (Hernández-Villanueva 2010, Chavarro-Rodríguez et al. 2013) or the activity of attendant ants (Rico-Gray et al. 1998, Fernández-Martínez and Díaz-Castelazo 2009, Leal et al. 2015, Câmara et al. 2018; Alves-Silva et al. 2020) rather than protection services directly. Our study takes such a direct approach in the Caatinga dry forest of semi-arid, northeastern Brazil. Caatinga is an ideal study system for this purpose because a large proportion of its flora has EFNs (Câmara et al.

2018), the region suffers from high levels of CAD (Ribeiro et al 2015, Rito et al. 2017, Tomasella et al. 2018), and rainfall is forecast to decrease by more than 20% by 2100 (Magrin et al. 2014). Our study address two key questions. First, how do CAD and aridity influence ant predatory activity as a direct measure of the effectiveness of protection services provided by ants? Second, what are the relative roles of nectar production and ant species composition in mediating the effects of CAD and aridity on the effectiveness of protection services provided by ants? In order to avoid confounding effects of variation in plant species composition, we focus on a single plant species, *Pityrocarpa moniliformis* (Benth.) Luckow & R. W. Jobson (Fabaceae), which is the most abundant and widely distributed EFN-tree in our study system, and it attracts a variety of ants (Câmara et al. 2018).

Materials and Methods

Study area

Our study was conducted in Catimbau National Park (8°24'00" and 8°36'35" S; 37°0'30" and 37°1'40" W), located in Pernambuco State, north-eastern Brazil (Figs. 1 and 2). The Park covers an area of nearly 640 km², where annual rainfall varies markedly because of topographic influences, from 480 mm to 1100 mm per year, while the mean annual temperature is 23°C (Rito et al. 2017). Nutrient-poor, quartzite sandy soils are predominant in the Park (covering approximately 70% of its area), and support a relatively open, low-stature vegetation in which Fabaceae, Euphorbiaceae and Cactaceae are the dominant families (Rito et al. 2017; Fig. 2). The EFN-bearing plants belong primarily to Fabaceae and Euphorbiaceae, and represent nearly 30% of the total woody flora in the Park (Câmara et al. 2018).

The Park remains occupied by low-income rural populations that depend on natural resources for their livelihoods, resulting in a mosaic of different levels of CAD (Rito et al. 2017). The main activities are raising of livestock (goats and cattle), firewood collection and exploitation of non-timber forest products (Arnan et al. 2018b, Câmara et al. 2018, Sfair et al. 2018).

We selected thirteen 50 m × 20 m plots from the 20 permanent plots of the Catimbau ILTER (International Long Term Ecological Research) project (<https://www.peldcatimbau.org>) where our focal plant species occur (Câmara et al. 2018, Rito et al. 2017). These plots cover a wide range of CAD and rainfall (Fig. 1). All plots were on sandy soil, on flat terrain, and supported old-growth vegetation. Plots were separated by a minimum of 2 km, and they all occurred within an area of 215 km² (Rito et al. 2017).

Characterization of CAD and aridity gradients

We characterized the intensity of CAD in each plot by computing a global multimetric index as proposed by Martorell & Peters (2005, 2009). We integrated five disturbance metrics related to the three main sources of CAD in Caatinga vegetation: livestock grazing, wood extraction and exploitation of non-timber forest products (Ribeiro et al. 2015, Rito et al. 2017, Arnan et al. 2018b). To measure livestock grazing, we computed the length of goat trails and counted goat and cattle dung. We combined the two measures of goat activity (trail length and dung frequency) to obtain a single measure for goats. Our measures of wood extraction considered both live stems and coarse woody debris (Arnan et al. 2018b). We used four measures of accessibility to people as surrogates of intensity of harvesting of non-timber products (e.g., medicinal plants, animal and human foods): proximity to the nearest house, proximity to the nearest village, proximity to the nearest road and number of people living in the houses with influence in the plots. These four measures were integrated into single disturbance metric representing human pressure. Data from our five disturbance indicators (cattle, goats, live-wood extraction, coarse woody debris extraction, and human pressure) were integrated into a single CAD index (for methodological details, see Arnan et al. 2018b). The index ranges from 2 (lowest intensity) to 58 (highest intensity) among our 13 plots.

We used the aridity gradient at Catimbau to assess the effects of a changing climate.

Contemporary climatic gradients are powerful tools for studying future climate change (Caddy-Retalic et al. 2017) through a space-for-time substitution approach (Blois et al. 2013), and we used such an approach for assessing impacts of future increases in aridity. To characterize the aridity gradient, mean annual rainfall within each plot was obtained from the WorldClim database (www.worldclim.org) at a spatial resolution of 1 km extracted using the package *maptolls* (Bivand and Lewin-Koh 2015) in the R software (R Core Team 2016). Mean annual rainfall in our plots ranged from 940 mm to 510 mm, over a small geographic area. Catimbau is thus an ideal study system for analysing ecological responses to variation in aridity. We also computed a global aridity index ranging from 0.33 to 0.65 per plot (Appendix S1), which represent areas of moderate to high susceptibility to desertification (Matallo Jr 1999, MMA 2007). Since the aridity index was highly correlated ($r = 0.98$, $p < 0.001$) with rainfall we retain rainfall as our measure of aridity because it is more commonly used in diversity studies (Hawkins et al. 2003, Dunn et al. 2009, Rito

et al. 2017). The CAD and aridity indices were not significantly correlated with each other ($r = 0.35$, $p = 0.24$), and therefore the gradients were statistically independent.

Study species

Pityrocarpa moniliformis (Benth.) Luckow & R. W. Jobson (Fabaceae) (Fig. 2) is the most abundant and widely distributed EFN-bearing tree species occurring in Catimbau NP (Câmara et al. 2018, Rito et al. 2017). It is endemic to Brazil, occurring primarily in Caatinga but also in Atlantic Forest (Morim 2015). Its EFNs are an enclosed-concave type, located singly on the rachis between the first pair of pinnae (Melo et al. 2010; Fig. 2c).

Sampling

We selected 10 adult (height 1-2 m, and diameter basal height ≥ 3 cm) plants per plot, all with similar size and architecture to control for possible ontogenic effects on EFN activation and nectar production (Villamil et al. 2013). Plants were separated from each other by a minimum of 10 m to ensure that most, if not all, attendant ants on different plants were from different colonies (Agosti and Alonso 2000).

Predatory activity by ants: For all the 10 focal plants per plot, we selected one apical branch to conduct experimental observations of attack rates by ants during the day (7:00-10:00 a.m.). For each plant, we counted the initial abundance of ants on the selected branch before the experiment started. Following previous studies (Oliveira et al. 1987, Fagundes et al. 2017), we used live termites (*Syntermes* sp.) as simulated herbivores. Five termites were glued onto the branch by the dorsum, each one in the middle of the foliole from different leaves as far distant as possible from each other. We observed ant behaviour (attack or no attack) in response to termite-baits during 10 min, and measured the time taken by each ant species to attack after termites were placed on the plant. Our observation period was limited to 10 min to enable us to maximize the number of plants sampled while minimizing temporal variability between samples (we avoided sampling during the midday heat), and to ensure that the termites remained alive throughout our observations (Leal et al. 2015, Câmara et al. 2018). We considered that the attack succeeded when ants captured the termites. We used two measures of ant predatory activity: (1) attack rate (proportion of termites attacked out of the total of five termites) and (2) mean time taken to attack the termites. If a termite was not attacked over the 10 mins, time was excluded from our analyses. Additionally, we

used an index of protection effectiveness (PE) for each ant species using the formula (modified from Fagundes et al. 2017):

$$PE_i = n(t^{-1} r)$$

where n is mean of the number of workers of ant species i initially observed on the branch, t is the mean time taken to attack, and r is the ratio between the mean number of attacks and the mean number of interactions between ants and EFN-bearing plants (see below). We also calculated the protection effectiveness index for each plot (PE_p) using the weighted mean of the PE_i index of all ant species that occurred there.

Extrafloral nectar secretion: For each of three focal plants per plot, we selected three apical branches with completely expanded leaves per plant and collected nectar from one EFN per branch (i.e. three EFNs per plant). We first cleaned the EFNs with distilled water and dried them with a paper towel. EFNs were then isolated from nectar-feeding insects by covering the leaves with a standard-size bag of nonwoven fabric, and applying Tanglefoot® (Tanglefoot Company, Grand Rapids, Michigan USA) around each plant branch (Blüthgen et al. 2004, Bixenman et al. 2011). After 24 hrs, nectar volume was sampled with a 10 μ l Hamilton micro syringe. Due to low nectar volume not allowing direct measurement of concentration, a known amount of distilled water was applied to each EFN and the nectar concentration of this mixture was measured using a Kasvi K52-032 portable Brix refractometer 0-32%. The concentration of the original nectar was then estimated following Díaz-Castelazo et al. (2005) [$C1 = (V2*C2)/V1$]. Extrafloral nectar was collected during the day (07:00-10:00 a.m.) in nine plots from May to July 2016 and in the remaining four plots in May 2017. To avoid any confounding effects of sampling year, both sampling periods included plots representing a range of variation in CAD and rainfall.

Attendant ants: During the same day that we conducted experimental observations of attack rates by ants, ant sampling was carried out on another apical branch of the same 10 focal plants for up to 5 min as described by Leal et al. (2015) during the day (07:00-10:00 a.m.) between May and July 2017. For each sample, we recorded the identity of ants that contacted their mouthparts with EFNs. Ant species that could not be identified in the field were collected, placed in 70% ethanol, and brought to the lab. Ants were identified to species, or to morphospecies when species identification was not possible. Interactions were defined by the frequency of occurrence of ant species interacting with EFN-bearing plants, regardless of the total number of ant workers (Cámara et al. 2018).

Statistical analyses

We used a generalized linear mixed model (GLMM) with a Binomial error distribution to evaluate the effects of CAD and rainfall on ant attack rate, and GLMMs with a Gaussian error distribution to evaluate the effects of CAD and rainfall on the mean time taken to attack per plant, and on the protection effectiveness per plot (PE_p). For the first two models, we included the initial abundance of ants before the experimental observations of attack rates per plant as a covariate, since ant abundance is likely to influence the probability of ant attack and attack time. Plot was included in the models as a random factor to account for the hierarchical data structure of trees nested within plots.

We used GLMMs with a Gaussian error distribution to evaluate the effects of CAD and rainfall on the mean volume and concentration of extrafloral nectar per plant, and on the number of interactions between EFNs and ants. Plot and year of sampling were included in the models as random factors to control for spatial and temporal clustering, respectively. Data that did not obey homoscedastic criteria (mean volume and concentration of extrafloral nectar) were $\log(x) + 1$ transformed. We did not include the interaction between CAD and rainfall in the models due the relatively low number of plots. To allow direct comparison of the predictors, we standardized CAD and aridity data by subtracting the respective mean and dividing by the respective standard deviation. We used *lme4* version 1.1-7 package (Bates et al. 2014) to build general and generalized mixed models in R.

The effects of CAD and rainfall on the composition of attendant-ant species were evaluated by canonical correspondence analysis (CCA) of sites based on ant species composition, using *vegan* version 2.3 package (Oksanen et al 2015) in R. For this analysis, we considered the frequency with which each ant species attended EFN-bearing plants per plot. We performed a randomization test (10000 permutations) to obtain the statistical significance of CAD and rainfall as explanatory variables (Legendre et al. 2011).

Results

We observed 238 interactions involving 16 ant species attending *P. moniliformis* EFNs.

Camponotus crassus occurred in all plots, and *C. crassus* and *Cephalotes pusillus* were the most frequent ant species attending EFNs, involved in 40.7% of all interactions (Table 2). The mean number of interactions between ants and *P. moniliformis* per plot was strongly related to rainfall,

ranging from 3.8 ± 0.44 (mean \pm SE) in the least arid plot to 1.1 ± 0.18 in the most arid plot (Table 1, Fig. 3a). It was not related to CAD (Table 1).

Eight (half) of the attendant ant species were observed attacking termites (Table 1). *Camponotus crassus* and *Crematogaster* nr. *evallans* were responsible for 41.6% and 30.5% of all attacks, respectively (Table 2). The overall rate of termite attack was only 5.5% (Table 2). Attack rate per plot decreased with decreasing rainfall, ranging from 0.21 ± 0.06 (mean \pm SE) in the least arid plot to zero in the most arid plot (Fig. 3b), and was positively correlated with the number of interactions between ants and EFNs observed during observations of attendant ants (Spearman's $r = 0.46$, $p < 0.01$). Attack rate did not vary with CAD (Table 1). Considering only those plots that had attacks, ants took on average 1.1 ± 0.27 minutes (mean \pm SE) to attack termites in the least arid plot and 3.8 ± 0.40 minutes in the most arid plot (Fig. 2c). The mean time taken to attack decreased with increasing rainfall (Table 1, Fig. 3c), and it was negatively correlated with the number of interactions (Spearman's $r = 0.38$, $p = 0.03$). There was no relationship between attack time and CAD (Table 1). *Crematogaster crinosa* and *Camponotus cingulatus* were the quickest ant species to attack (Table 2). *Azteca* sp. A had by far the highest PE_i , followed by *Crematogaster* nr. *evallans* and *Camponotus cingulatus* (Table 2). PE_p was related to rainfall, ranging from zero in the least arid plot to 0.44 ± 0.20 (mean \pm SE) in the most arid plot (Table 1, Fig. 3d). It was not related to CAD (Table 1).

The mean nectar volume of *Pityrocarpa moniliformis* decreased significantly with increasing CAD (Table 1), from 1.7 ± 0.22 μ l (mean \pm SE) in the least disturbed plot to 0.19 ± 0.11 μ l in the most disturbed plot (Table 1, Fig. 4). The mean nectar volume was not related to mean annual rainfall (Table 1). The mean nectar concentration ranged from 0.31 ± 0.01 Brix to 15.26 ± 0.41 Brix (mean \pm SE), but did not significantly vary with either CAD or rainfall (Table 1).

The first and second axes of the CCA of the composition of attendant ant species explained 25.5% and 7.9% respectively of the variation (Fig. 5), and only the first axis was significant (Table 3).

The composition of attendant ant species varied significantly with rainfall but not with CAD (Table 3, Fig. 5). The main ant species that attacked termites and the ant species with higher PE_i (*Azteca* sp. A, *Crematogaster* nr. *evallans* and *Camponotus cingulatus*; Table 2) were associated with higher rainfall, whereas *Cephalotes* nr. *cordatus* and *Camponotus blandus* were associated with lower rainfall (Fig. 5).

Discussion

Our study investigated the effects of CAD and aridity on the effectiveness of plant protection services provided by ants to EFN-bearing *Pityrocarpa moniliformis* in Brazilian Caatinga, which experiences high levels of subsistence resource use and is forecast to receive substantial reductions in rainfall over coming decades. Unlike most previous studies on ant-EFN interactions, we used experimental observations of predatory activity to measure protection services provided by ants. We found that the effectiveness of ant protection services was highly sensitive to aridity, declining markedly with decreasing rainfall. This was consistent with the negative relationship that we found between aridity and the mean number of ant-EFN interactions, which is often used as a surrogate of the protection services provided (Bronstein 1998; Di Giusto et al. 2001, Rico-Gray and Oliveira, 2007). This could be expected to result in stronger herbivore pressure on plants in more arid areas, which is consistent with recent studies in our study area showing that rates of leaf herbivory by insects increase with increasing aridity (Andrade et al. 2020, Alencar et al. unpublished data). Since these studies also include plants without EFNs, our findings suggest that decreased effectiveness of EFNs exacerbates a more general trend of increased herbivory with increased aridity. However, other studies elsewhere have shown a reverse pattern, either because nectar concentration increases with water limitation (Pringle et al. 2013) or because arid sites have more-aggressive ants (Leal and Peixoto 2017). Meanwhile, we found no effect of CAD on anti-herbivory protection, and this was consistent with a lack of relationship between CAD and the number of ant-EFN interactions.

We also evaluated the role of nectar production and ant species composition in mediating the effectiveness of protection service provided by ants. Neither mean EFN concentration nor volume were related to aridity. This was unexpected given that most previous studies have shown that both nectar concentration and volume decline with decreasing water availability (Yamawo et al. 2012, Newman and Wagner 2013, Chavarro-Rodríguez et al. 2013, Lange et al. 2013). However, none of these studies were of natural aridity gradients, but rather involved soil watering (Yamawo et al. 2012, Newman and Wagner 2013) or temporal variation during the day (Lange et al. 2013) or between seasons (Chavarro-Rodríguez et al. 2013). Further research is required to test the extent to which the lack of response of nectar production by *P. moniliformis* to increased aridity is typical of widely distributed EFN-bearing plants.

In contrast to the effects of aridity, we found that the mean nectar volume declined with increasing CAD, as has been shown in previous studies (Hernández-Villanueva 2010, Chavarro-Rodríguez et al. 2013). Such a decline has been attributed to reduced water availability due to higher

transpiration in disturbed areas (Chavarro-Rodríguez et al. 2013). However, this is unlikely to be the mechanism in our study given that we found no relationship between nectar secretion (volume and concentration) and aridity, or between nectar concentration and CAD. The reduction of mean nectar volume with increasing CAD independently of changes in nectar concentration suggests that reduced nectar production in disturbed areas is not caused by higher transpiration. An alternative factor influencing nectar production is herbivory pressure (Huang et al. 2015), and herbivory by goats was a key component of our CAD index (Arnan et al. 2018b) that strongly affects plants, ants and their interactions in Catimbau NP (Arnan et al. 2018a, Câmara et al. 2018, Sfair et al. 2018). Some studies have suggested that nectar production increases under increasing herbivory pressure (Palmer et al. 2008, Huang et al. 2015, Hernandez-Cumplido et al. 2016). However, plants can adopt different strategies to deal with herbivory (Strauss and Agrawal 1999) under different resource conditions (Hawkes and Sullivan 2010), including compensatory growth (McNaughton 1983) and reduced investment in carbon-based defences (Scogings et al. 2011). *Pityrocarpa moniliformis* shows functional responses to high levels of herbivory by livestock in the form of a higher number of branches and higher leaf mass (Sfair et al. 2018), and its reduced nectar production with increased CAD might similarly be related to herbivory by livestock. Notably, the decline in nectar production did not result in reduced predatory activity by ants and therefore the protection services provided by them. This shows that variation in the protection service that ants provide to EFN-bearing plants can be independent of the quantity or quality of nectar produced (Rudgers and Strauss 2004). The composition of ant species attending EFNs varied markedly with aridity, but, in contrast to the study of Leal and Peixoto (2017) who found higher abundance of aggressive ants in the most arid areas, the most aggressive ants according to our experiments (*Azteca* sp. A, *Crematogaster* nr. *evallans* and *Camponotus cingullatus*) were most abundant at least arid sites at Catimbau NP. This explains the declining protective services with increased aridity as measured by attack on termites, and it reinforces the highly facultative nature of this mutualism (Bronstein 1998, Rico-Gray and Oliveira 2007, Rosumek et al. 2009), such that the frequency and identity of ant partners are highly variable (Del-Claro et al. 2016). Since mean nectar production in *P. moniliformis* was not related to aridity, the variation in species composition with aridity was therefore due to other factors, such as differential resistance to desiccation (Arnan and Bluthgen 2015, Bujan et al. 2016).

Unlike the case for aridity, the composition of attendant ant species on *P. moniliformis* did not vary significantly with CAD in our study. The composition of EFN-attendant ants does vary with CAD for EFN-bearing plant species more generally (Câmara et al. 2018; Alves-Silva et al. 2020); however, in Caatinga this apparently applies only to plants whose abundances decline at disturbed sites (Leal et al. 2015), which is not the case for *P. moniliformis* (Rito et al. 2017). Moreover, a recent study carried out in Catimbau showed that some ant species may not change their abundance along the disturbance gradient, but instead shift their microhabitat use from foraging in sun-exposed microhabitats to foraging in shaded microhabitats in the most disturbed areas (Silva et al. 2019). This absence of CAD effects on the composition of EFN-attendant ants may explain the lack of effects on the protective services along the CAD gradient.

In conclusion, we found no evidence of CAD affecting EFN-mediated plant protection services provided by ants to *P. moniliformis*. Despite mean nectar volume declining with increasing CAD, this did not affect the number of interactions between ants and EFN-bearing plants or the composition of attendant ant species. In contrast, we found a negative impact of aridity on the protection services provided by ants, mediated by changes in the composition of attendant ant species rather than by variation in extrafloral nectar. This suggests that changes in ant species composition under the forecast climate-change scenario of increasing aridity are likely to result in reduced ant protection services to *P. moniliformis* and consequently reduced benefits in relation to plant growth and reproductive success (Nascimento and Del-Claro 2010, Marazzi et al. 2012).

Pityrocarpa moniliformis is responsible for most EFN-ant interactions in our study system, and the ant species providing protection services to this species probably also provide services to other EFN-bearing plants (Leal et al. 2015, Câmara et al. 2018). This implies that the high vulnerability of ant-mediated plant protection services under an increasingly arid climate is likely to apply more generally to Caatinga vegetation given that such a large proportion of Caatinga plants have extrafloral nectaries (Leal et al. 2017).

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Author’s contributions

FMPO, ANA and IRL originally conceived the ideas and designed the experiments. FMPO, TC and JIFD collected the ant-plant interaction data, while CLSO and EMSR collected the extrafloral nectar data. XA contributed to the development of the methodology and statistical analyses. FMPO conducted the analyses and coordinated the writing of the manuscript. All the authors significantly contributed to the manuscript drafts and gave their final approval for submission.

Data Availability

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0rxwdbx3> (Oliveira et al. 2020).

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Table 1 – Effects of chronic anthropogenic disturbance (CAD) and rainfall on nectar secretion and volume, ant predatory activity, and ant protection effectiveness (PE) for *Pityrocarpa moniliformis* in Catimbau National Park, Pernambuco, Brazil. PE was calculated from data on attack rate and time spent to attack termites. Initial ant abundance was used as a covariate in the models of attack rate, time spent to attack and PE. R² represents the conditional coefficient of determination of the whole statistical model.

Response variables	Explanatory variables	R ²	DF	F	P
Number of interactions	CAD	0.58	1	0.30	0.58
	Rainfall		1	11.91	< 0.01
	Residuals		128		
Attack rate	CAD	0.29	1	0.80	0.38
	Rainfall		1	21.82	< 0.01
	Ant abundance		1	0.20	0.88
	Residuals		127		
Time spent to attack	CAD	0.26	1	0.40	0.51
	Rainfall		1	15.60	< 0.01
	Ant abundance		1	0.13	0.76
	Residuals		33		
Protection effectiveness	CAD	0.20	1	14.76	< 0.01
	Rainfall		1	3.28	0.07
	Residuals		33		
Extrafloral nectar volume	CAD	0.60	1	4.56	0.03
	Rainfall		1	2.34	0.09
	Residuals		37		
Extrafloral nectar concentration	CAD	0.18	1	0.35	0.55
	Rainfall		1	0.16	0.60
	Residuals		27		

Table 2 – Ant species interacting with and attacking termites on *Pityrocarpa moniliformis* over the gradients of chronic anthropogenic disturbance (CAD) and rainfall gradients at Catimbau National Park, Pernambuco, Brazil. PE is the index of protection effectiveness.

Ant species	Number of plots	Number of interactions	Number of attacks	Mean time \pm SD (min)	PE
<i>Azteca</i> sp. A	2	6	3	1.41 \pm 1.1	4.25
<i>Brachymyrmex</i> sp. A	2	4	0	0	0
<i>Camponotus blandus</i> (Smith, 1858)	1	3	0	0	0
<i>Camponotus cingulatus</i> (Mayr, 1862)	1	1	1	1 \pm 0	1
<i>Camponotus crassus</i> (Mayr, 1862)	13	67	15	3.5 \pm 3.2	0.19
<i>Camponotus fastigatus</i> (Roger, 1863)	6	20	0	0	0
<i>Camponotus</i> sp. D	1	1	0	0	0
<i>Camponotus vittatus</i> (Forel, 1904)	3	9	2	2.5 \pm 1.5	0.09
<i>Cephalotes</i> nr. <i>cordatus</i>	4	10	0	0	0
<i>Cephalotes pusillus</i> (Klug, 1824)	7	30	1	3 \pm 0	0.01
<i>Crematogaster crinosa</i> (Mayr, 1862)	3	7	2	1.66 \pm 1.3	0.51
<i>Crematogaster</i> nr. <i>evallans</i>	8	22	11	2.0 \pm 1.5	2
<i>Dorymyrmex thoracicus</i> (Gallardo, 1916)	4	17	0	0	0
<i>Ectatomma muticum</i> (Mayr, 1870)	2	2	1	5 \pm 0	0.1
<i>Pseudomyrmex acanthobius</i> (Emery, 1896)	5	19	0	0	0
<i>Pseudomyrmex gracilis</i> (Fabricius, 1804)	6	20	0	0	0

Table 3 – Results of canonical correspondence analysis (CCA) testing the influence of chronic anthropogenic disturbance (CAD) and rainfall on the composition of ant species attending extrafloral nectaries of *Pityrocarpa moniliformis* at Catimbau National Park, Pernambuco, Brazil. Significant values are in bold.

Source of variation	DF	χ^2	F	P
<i>Axis</i>				
CCA1	1	0.30	3.19	<0.01
CCA2	1	0.07	0.83	0.55
<i>Variables</i>				
CAD	1	0.08	0.90	0.42
Rainfall	1	0.28	2.04	0.04
Residual	11	1.23		

Figure Legends

Figure 1 - Maps showing Caatinga dry forest in Brazil (A), Catimbau National Park in Pernambuco State (B), and the distribution of the thirteen 50 m × 20 m plots (circles) over the gradients of chronic anthropogenic disturbance (CAD) and rainfall. The amount of black in the circles reflects intensity of CAD within the plot, with an increasing amount representing increasing CAD.

Figure 2 - Study area and species: (A) a landscape view of Catimbau National Park showing part of the aridity gradient, (B) an individual of *Pityrocarpa moniliformis*, (C) detail of the extrafloral nectary, and (D) *Dorymyrmex thoracicus* worker feeding on extrafloral nectar.

Figure 3 - Mean (\pm SE) and model-fitted lines of number of interactions between ants and extrafloral nectaries (a), attack rates (b) and time taken to attack (c) by ants, and the protection effectiveness index (PE) (d) for *Pityrocarpa moniliformis* along the gradients of chronic anthropogenic disturbance (CAD) and rainfall in Catimbau National Park, Pernambuco, Brazil.

Figure 4 - Mean (\pm SE) and model-fitted lines of extrafloral nectar volume of *Pityrocarpa moniliformis* along the gradients of chronic anthropogenic disturbance (CAD) and rainfall in Catimbau National Park, Pernambuco, Brazil.

Figure 5 - Representation of attendant ant species and gradients of chronic anthropogenic disturbance (CAD) and rainfall in Catimbau National Park, on the first two axes of the canonical correspondence analysis (CCA). Abbreviations: AztA, *Azteca* sp. A; BraA, *Brachymyrmex* sp. A; Cbla, *Camponotus blandus*; Ccin, *Camponotus cingulatus*; Ccra, *Camponotus crassus*; Cfas, *Camponotus fastigatus*; CamD, *Camponotus* sp. D; Cvit, *Camponotus vittatus*; Ccor, *Cephalotes* nr. *cordatus*; Cpus, *Cephalotes pusillus*; Ccri, *Crematogaster crinosa*; Ceva, *Crematogaster* nr. *evallans*; Dtho, *Dorymyrmex thoracicus*; Emut, *Ectatomma muticum*; Paca, *Pseudomyrmex acanthobius*; Pgra, *Pseudomyrmex gracilis*. Asterisks indicate ant species that attacked termites.

Figure 1

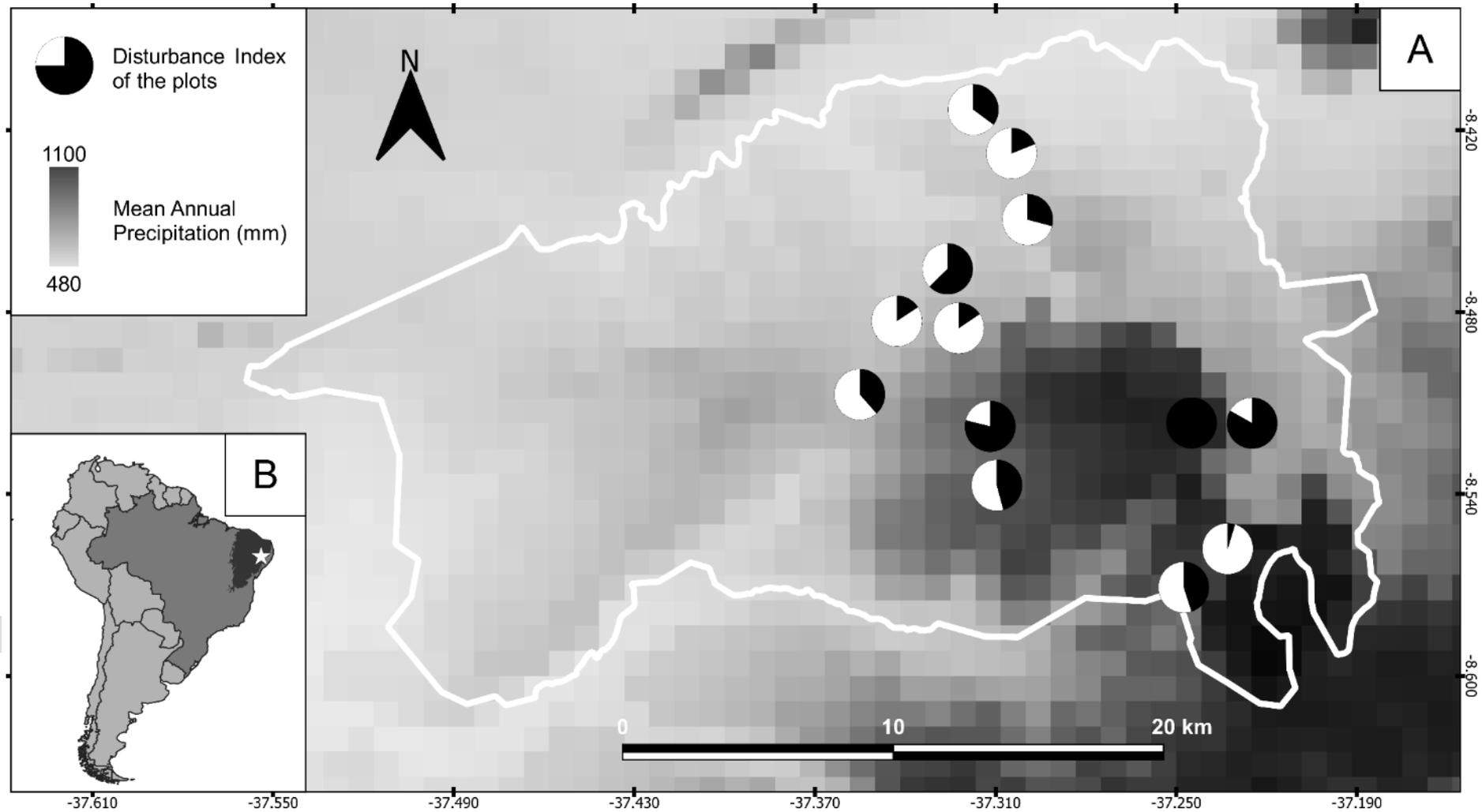


Figure 2



Figure 3

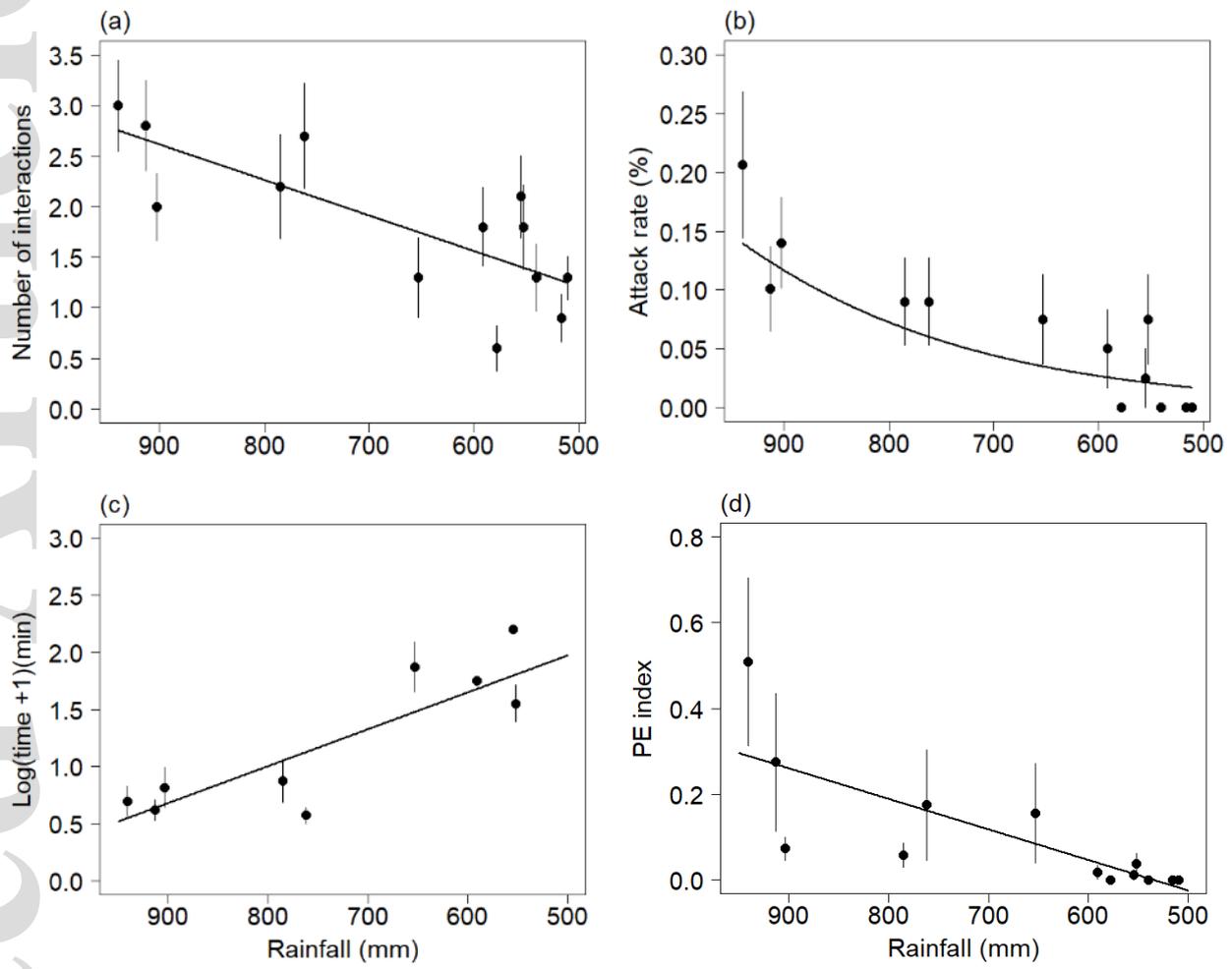


Figure 4

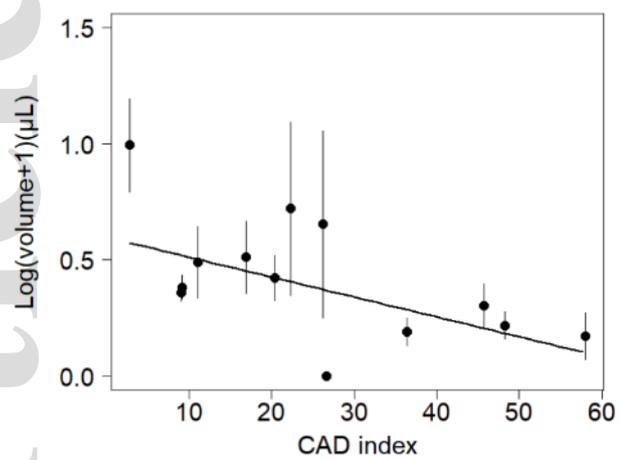


Figure 5

