RESEARCH ARTICLE

Effects of chronic anthropogenic disturbance and rainfall on the specialization of ant–plant mutualistic networks in the Caatinga, a Brazilian dry forest

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Abstract
1. Anthropogenic disturbance and climate change might negatively affect the ecosystem services provided by mutualistic networks. However, the effects of such forces remain poorly characterized. They may be especially important in dry forests, which (1) experience chronic anthropogenic disturbances (CADs) as human populations exploit forest resources, and (2) are predicted to face a 22% decline in rainfall under climate change.

2. In this study, we investigated the separate and combined effects of CADs and rainfall levels on the specialization of mutualistic networks in the Caatinga, a seasonally dry tropical forest typical of north-eastern Brazil. More specifically, we examined interactions between plants bearing extrafloral nectaries (EFNs) and ants. We analysed whether differences in network specialization could arise from environmentally mediated variation in the species composition, namely via the replacement of specialist by generalist species.

3. We characterized these ant–plant networks in 15 plots (20 × 20 m) that varied in CAD intensity and mean annual rainfall. We quantified CAD intensity by calculating three indices related to the main sources of disturbance in the Caatinga: livestock grazing (LG), wood extraction (WE) and miscellaneous resource use (MU). We determined the degree of ant–plant network specialization using four metrics: generality, vulnerability, interaction evenness and $H'_2$.

4. Our results indicate that CADs differentially influenced network specialization: we observed positive, negative, and neutral responses along LG, MU and WE gradients, respectively. The pattern was most pronounced with LG. Rainfall also shaped network specialization, markedly increasing it. While LG and rainfall were associated with changes in network species composition, this trend was not related to the degree of species specialization. This result suggests that shifts in network specialization might be related to changes in species behaviour, not species composition.

5. Our study highlights the vulnerability of such dry forest ant–plant networks to climate change. Moreover, dry forests experience highly heterogeneous
anthropogenic disturbances, creating a geographic mosaic of selective forces that may shape the co-evolution of interactions between ants and EFN-bearing plants.

**KEYWORDS**

anthropogenic disturbance, anti-herbivore defence, climate change, extrafloral nectaries, mutualistic network, plant-animal interactions, seasonally dry tropical forest, specialization

### 1 | INTRODUCTION

While specialization of mutualistic networks plays a central role in species coexistence and, possibly, speciation (Dyer et al., 2007; Dynesius & Jansson, 2000), it has received relatively little attention in conservation biology. However, it is widely accepted that anthropogenic disturbances are major drivers of specialist-generalist replacement (Clavel, Julliard, & Devictor, 2011; McKinney & Lockwood, 1999; Tabarelli, Peres, & Melo, 2012), which can lead to biotic homogenization (Devictor et al., 2010) and loss of functionality (Girão, Lopes, Tabarelli, & Bruna, 2007; Lopes, Girão, Santos, Peres, & Tabarelli, 2009). The root cause is that specialists have a narrower breadth of resource use than do generalists, which means they tend to be more sensitive to changes in habitat, food availability and food quality (Devictor et al., 2010; Futuyama & Moreno, 1988).

Thus, if species form specialized mutualisms (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007), the disturbance-related extinction or decline of one partner could threaten the other (Weiner, Werner, Lisemnair, & Blüthgen, 2014). Therefore, even though a species may survive a disturbance event, the resulting changes in resource availability could have detrimental effects on specialist populations. Species' responses to environmental change might thus be tightly linked to the degree of specialization within mutualisms (Vázquez & Simberloff, 2002). Moreover, disturbance could leave species abundance unaffected but change behavioural interactions in an environmentally dependent fashion (Brose et al., 2005; Tylianakis, Tscharntke, & Lewis, 2007).

To date, anthropogenic disturbances have been found to have contrasting effects on the specialization of mutualistic networks. While some studies have shown that disturbance decreases specialization in plant–pollinator (Aizen, Sabatiano, & Tylianakis, 2012), plant–frugivore (Menke, Böhning-Gaese, & Schleuning, 2012) and ant–plant networks (Emer, Venticinque, & Fonseca, 2013), others have found no effects at all (plant–frugivore network, Schleuning et al., 2011; Dáttillo, Aguiar, Quesada, & Dirzo, 2015; ant–plant network, Falcão, Dáttillo, Díaz-Castelazo, & Rico-Gray, 2017). Disturbance type appears to matter. For instance, network specialization may be affected by habitat fragmentation (Aizen et al., 2012) but not necessarily by land-use change (Weiner et al., 2014) or by the introduction of exotic species (Emer, Memmott, Vaughan, Montoya, & Tylianakis, 2016). Such patterns could result from different anthropogenic disturbances having different effects on resource availability and quality. Furthermore, there may be interactions between disturbances and climatic conditions. For example, plant–hummingbird networks are more specialized in regions with high precipitation and low temperatures (Abrahamamczyk & Kessler, 2010; Dalsgaard et al., 2011), but the opposite is true for plant–insect pollinator networks (Dalsgaard et al., 2009). In general, theory predicts that biotic specialization should be favoured as precipitation and temperature increase because of the opportunities afforded by high levels of productivity (Schemske, 2002; Srivastava & Lawton, 1998).

Seasonally dry tropical forests (SDTFs) harbour a great diversity of mutualistic species networks (Leal, Lopes, Machado, & Tabarelli, 2018; Machado & Lopes, 2004), which contribute to multiple ecosystem functions by driving processes as diverse as pollination, dispersal, plant defence and nutrient transfer (Kiers, Palmer, Ives, Bruno, & Bronstein, 2010). However, SDTFs are the most threatened type of major tropical forest (Miles et al., 2006). The dry tropics are home to large human populations that depend on natural resources for subsistence (Singh, Rawat, & Garkoti, 1997). These populations continuously remove small quantities of forest biomass via livestock grazing, firewood collection and the exploitation of miscellaneous resources (e.g. the exploitation of non-timber products such as medicinal plants and hunting), which each leads to chronic anthropogenic disturbance (CAD; sensu Singh, 1998). The consequence is the emergence of heterogeneous landscapes of resource use (Martorell & Peters, 2005; Ribeiro, Arroyo-Rodriguez, Santos, Tabarelli, & Leal, 2015). Although the effects of CADs have only recently started to be evaluated, some studies have already revealed they are significant for plants (Hernández-Oria, Chavez, & Sánchez, 2006; Ribeiro et al., 2015; Ribeiro et al. 2016; Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli, 2017), animals (Oliveira, Ribeiro-Neto, Andersen, & Leal, 2017; Ribeiro-Neto, Arnan, Tabarelli, & Leal, 2016) and plant–animal interactions (Leal, Andersen, & Leal, 2014, 2015). Moreover, in the dry tropics, it has been predicted that climate change will increase temperatures and decrease precipitation by 2100 (Magrin et al., 2014), which will threaten natural biota (Feng, Porporato, & Rodriguez-Iturbe, 2013; Miles et al., 2006). There is particular concern that climate change could aggravate CAD effects on biodiversity in the dry tropics (Frishkoff et al., 2016; Gibb et al., 2015; Hirota, Holmgren, Van Nels, & Scheffer, 2011).

In this study, we focused on the facultative mutualistic networks established between plants bearing extrafloral nectaries (EFN) and the ants that attend them. EFN-bearing plants produce carbohydrate-rich resources, which attract ants that often then protect the plants against herbivores (Bentley, 1977; Fagundes, Dáttillo,
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Although such networks occur in many different ecosystems (Rico-Gray & Oliveira, 2007), the protection provided by ants to EFN-bearing plants appears to be particularly effective in arid environments (Leal & Peixoto, 2016). However, arid environments usually experience significant anthropogenic disturbance (Miles et al., 2006), which can lead to declines in the abundance of specialist EFN-bearing plants (Leal et al., 2015), the abundance of specialist arboreal ants (Oliveira et al., 2017) and ant visitation rates (Leal et al., 2015).

We aimed to investigate the separate and combined influences of different CADs and rainfall levels on the specialization of networks formed by ants and EFN-bearing plants in the Caatinga, a SDTF typical of north-eastern Brazil. The Caatinga biome is found in the world’s most populated semi-arid region and sustains over 27 million people (Gariglio, Sampaio, Cestaro, & Kageyama, 2010). The rainfall gradient within the Caatinga is broad (Sampaio, 1995), and the biome supports a high diversity of mutualisms (Leal et al., 2018). Increasingly, though, the Caatinga is being exposed to different CADs (livestock grazing, wood extraction and miscellaneous resource use). It thus represents an excellent study system for examining the influences of CADs and climate change on the specialization of ant–plant mutualisms in SDTFs. We tested the following hypotheses: (1) the level of network specialization will decrease with increasing CAD intensity and decreasing rainfall, (2) networks will become less specialized due to the interactive effects of increased CAD intensity and decreased rainfall, and (3) decreases in network specialization will largely arise from changes in the species composition of networks, as a result of specialist-generalist replacement in dry highly disturbed areas.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our study in Catimbau National Park (State of Pernambuco, north-eastern Brazil, 8°24′00″ and 8°36′25″ S; 37°09′30″ and 37°09′30″ W), a natural reserve covering nearly 64,000 ha. The climate is hot; annual rainfall varies from 480 to 1,100 mm; and the mean annual temperature is 23°C (Sociedade Nordestina de Ecologia, 2002). Deep sandy soils predominate (quartzite sand: 70% of area), but planosols (15% of area) and lithosols (15% of area) are also present (Sociedade Nordestina de Ecologia, 2002). Catimbau contains typical Caatinga taxa: the shrubs and trees mostly belong to the families Fabaceae, Euphorbiaceae, Boraginaceae and Burseraceae, while the herbaceous understorey plants are largely in the Cactaceae and Bromeliaceae (Rito et al., 2017). There are many EFN-bearing plants—those in Fabaceae and Euphorbiaceae are the most common (Reis, 2016). Catimbau became a national park in 2002, but it is still inhabited by rural populations that rely on its natural resources for subsistence (Rito et al., 2017). Their main activities include livestock farming (mainly goats and cattle), firewood collection and the harvesting of miscellaneous forest resources (e.g. medicinal plants, edible fruit or animal game; Rito et al., 2017).

2.2 | Characterizing chronic anthropogenic disturbance and rainfall

We established 15 plots (20 × 20 m; separated by at least 2 km) across 214.3 km². The study area was dominated by old-growth vegetation, and the plots experienced different CAD intensities and rainfall levels (Figure 1).
2.2.1 Chronic anthropogenic disturbance

We characterized disturbance intensity by calculating three different indices that corresponded to the main sources of CADs within the Caatinga and particularly in Catimbau: (1) livestock grazing (LG)—consumption of vegetation, trampling and other physical damage caused by goats and cattle, (2) wood extraction (WE)—the extraction of dead and live wood for fuel, fence construction and artisanal production, and (3) miscellaneous resource use (MU)—the use of non-wood resources by humans (e.g. medicinal plants, animal game; Leal et al., 2014, 2015; Ribeiro et al., 2015). Index values were calculated using the following formula:

\[ I = \frac{\sum_{i=1}^{n} (y_i - y_{\text{min}})}{(y_{\text{max}} - y_{\text{min}})} \times 100, \]

where \( I \) is disturbance intensity; \( y_i \) is the observed value for a given disturbance metric in plot \( i \); \( y_{\text{min}} \) is the minimum observed value for the disturbance metric across all plots; \( y_{\text{max}} \) is the maximum observed value for the disturbance metric across all plots; and \( n \) is the number of individual disturbance metrics incorporated in the index. This formula thus standardizes the metrics (sometimes of different units) to take on a value between 0 and 1, allowing them to be combined in the same index. Index values ranged from 0 to 100 (from no disturbance to maximum-intensity disturbance). Both the LG and WE indices quantified disturbances that were directly measured in the field. For the LG index, we estimated grazing levels by measuring the length of goat trails and the frequency of goat and cattle dung (see Appendix S1 for details). Then, we combined the two estimates of goat grazing (trail length and dung frequency) by means of PCA. Both measures were highly positively correlated \((r > .90)\) with the first PCA axis, which explained 88% of variance. We therefore used its coordinates to obtain a single measure of goat grazing. The LG index was then calculated by inputting measures of goat grazing and cattle dung frequency into the formula above. For the WE index, we estimated the extraction of live wood and the collection of firewood (Appendix S1) and plugged them directly into the formula above. Finally, the MU index was determined using three indirect variables that are proxies for local anthropogenic pressure and habitat accessibility. More specifically, we determined two relevant geographic distances—plot proximity to the nearest house and plot proximity to the nearest road (using satellite imagery and \textsc{arcgis} 10.1 software)—as well as a socioecological variable—the number of people living in the area that influence the plot (Appendix S1). Then, the values of these metrics were inputted into the formula above to obtain the MU index. The three indices were not highly correlated (LG vs. WE: \( r = .05 \), LG vs. MU: \( r = .65 \) and MU vs. WE: \( r = .003 \)), which underscores that they are independent and measure different forms of anthropogenic disturbance.

2.2.2 Rainfall

Mean annual rainfall was obtained for each plot using the WorldClim database (Rito et al., 2017), which contains spatial climate data from 1950 to 2000. Spatial resolution was 1 km, and mean annual rainfall was extracted using \textsc{arcgis}. Values ranged from 510 mm to 940 mm, indicating the presence of a steep rainfall gradient in Catimbau.

2.3 Characterizing interactions between ants and EFN-bearing plants

We characterized interactions between ants and EFN-bearing plants in 2014 and 2016 during the wet season (March–July), when EFN activity is high (TC, personal observation). To determine which plant species bear EFNs and to identify study plants, we carried out preliminary observations of all the plants in a given plot in early 2014 (Table S1). Then, once in 2014 and once in 2016, we carried out a census of all the EFN-bearing plants with a height \( \leq 1 \) m and a diameter at breast height (DBH) \( \geq 3 \) cm that were found within the plots (\( M \pm SD: 35.9 \pm 15.1 \) plants per plot). Each plant was observed for at least 10 min in each of the two censuses. They were considered to be attended by ants when the ants’ mouthparts came in contact with the EFNs. All observations occurred between 6:00 a.m. and 10:00 a.m., that is during the period of maximum daytime ant activity in the study area (T. Câmara, pers. obs.). During each census, we noted all interacting ant and EFN-bearing plant species (Tables S1 and S2). We attempted to identify all the species involved. However, when this was not possible in the field, samples were collected and brought to the laboratory for identification. Samples that could not be identified to species were classified to morphospecies.

2.4 Characterizing network specialization

For each plot, we built a matrix using all the interactions observed between EFN-bearing plants and attendant ants in 2014 and 2016. More specifically, we used the number of interactions between individual EFN-bearing plants and attendant ant species; the total number of ant workers involved was ignored. To characterize network specialization, we used four complementary quantitative metrics: (1) weighted generality (Gw), which expresses the degree of specialization at the highest trophic level and is defined as the mean effective number of EFN-bearing plants visited by each ant species weighted by ant species interaction frequency, (2) weighted vulnerability (Vw), which expresses the degree of specialization at the lowest trophic level and is defined as the mean effective number of ants per EFN-bearing plant species weighted by EFN-bearing plant species interaction frequency, (3) interaction evenness (IE), which measures whole-network specialization by quantifying the equity of interaction frequencies between EFN-bearing plant species and attendant ant species, and (4) the network specialization index \( H_G^c \), which measures whole-network specialization by determining the difference between realized and expected interaction frequencies (Blüthgen, Menzel, & Blüthgen, 2006). For more details, see Appendix S2 and Dormann, Fründ, Blüthgen, and Greuber (2009). In summary, low values of Gw, Vw and interaction evenness indicate that networks are highly specialized; Gw and Vw reveal the relative specialization of the ant species and plant species, respectively. In contrast, larger values of \( H_G^c \) (range: 0–1) indicate greater network specialization.
As metric values could be influenced by sampling effects (i.e. interaction number and network size [the sum of EFN-bearing plant species and attendant ant species]), we also calculated specialization metrics using data from null models (Dalsgaard et al., 2017). We generated 10,000 randomized matrices for each observed matrix using the Patefield algorithm, which constrains both interaction number and network size and assumes that all network partners have the same probability of interacting with each other (Blüthgen, Fründ, Vázquez, & Menzel, 2008). We used the following Z-transformation formula:

\[ Z = \frac{x_i - \mu}{\sigma}, \]

where \( x_i \) is the observed value of a given metric for given plot \( i \), \( \mu \) is the mean metric value obtained from the 10,000 randomized matrices for a given plot \( i \), and \( \sigma \) is the metric’s standard deviation from the 10,000 randomized matrices for a given plot \( i \). We calculated observed and null-model metric values using the bipartite package (Dormann et al., 2009) in R (Development Core Team 2016).

For both plants and ants, we characterized species-specific levels of specialization in each plot using \( d_i^t \), which expresses the exclusivity of partnerships between particular EFN-bearing plant species and attendant ant species (Blüthgen et al., 2006). Then, we calculated the weighted per-plot mean of \( d_i^t \) (by determining species \( i \)’s number of interactions in a given plot compared to its total interactions across all plots) (Tables S1 and S2). As for \( H_s^t \), higher values of \( d_i^t \) (range: 0–1) indicate greater specialization.

2.5 | Statistical analyses

We used general linear models to test the separate and combined effects of the CADs (LG, WE and MU) on the network specialization metrics. For each analysis, we started with a full model that included LG, WE, MU, and rainfall as the main independent variables and the interactions between each disturbance index and rainfall (LG x rainfall, WE x rainfall and MU x rainfall). The response variables were the metrics calculated from the observed and null-model data. Then, we used a backward-selection procedure to choose the best-fit model (a single model containing a maximum of three terms, excluding the intercept). The best-fit models were those with the lowest Akaike information criterion values (\( \Delta AIC_c < 2 \); Burnham & Anderson, 2002). We then applied model averaging to make inferences about how CADs and rainfall influenced ant–plant network specialization. First, for each variable, we averaged coefficients and 95% confidence intervals across the best-fit models. Second, we considered variables to be significant when the 95% confidence intervals did not include 0. Model selection and averaging were carried out using the muMin package in R.

We also tested the effects of the CADs and rainfall on community composition (separately for the plants and the ants) using canonical correspondence analysis (CCA), implemented with the vegan package in R. In these analyses, we used the abundance of EFN-bearing species (i.e. plant species observed interacting with attendant ants) and the frequencies of attendant ant species (i.e. ant species observed attending EFN-bearing plants). Plant and ant species with frequencies of less than five were excluded from the analysis to prevent bias introduced by rare species (Russildi, Arroyo-Rodriguez, Hernández-Ordóñez, Pineda, & Reynoso, 2016).

The species-specific CCA scores associated with significant CCA axes were taken to be the environmental responses of the plant and ant species to CADs or rainfall. To test whether these responses were dependent on species specialization, we carried out separate Spearman rank correlations between the CCA scores and the \( d_i^t \) values for the plants, the ants and each significant CCA axis.

3 | RESULTS

We recorded 555 interactions between 23 EFN-bearing plant species and 33 attendant ant species. There were between two and nine EFN-bearing plant species per plot. Eight were rare (recorded in just one plot), while two were common (Cenostigma microphylla: eight plots; Tacinga palmadora: 10 plots). Ptyrocarpa moniliformis, C. microphylla and T. palmadora accounted for encompassed most of the interactions (47.6%) (Figure 1). There were between 5 and 13 attendant ant species per plot. Eleven were rare (recorded in just one plot), while one was extremely common (Camponotus crassus: all plots). C. crassus and Cephalotes pusillus accounted for most of the interactions (53.3%; Figure 1).

Overall, the best-fit models indicated that network specialization was indeed influenced by CADs and rainfall. However, results differed for the different metrics (Table 1). In the analyses based on the observed data, LG and MU were retained in the best-fit models for Vw and \( H_s^t \) but were only significant in the latter case (Tables 1 and S3). While \( H_s^t \) increased with increasing LG (Figure 2a), it declined with increasing MU (Figure 2b). Rainfall was retained in the best-fit models for Gw and \( H_s^t \) but was only significant in the latter case (Table S3). \( H_s^t \) increased with increasing rainfall (Figure 2c).

In the analyses based on the null-model data, LG and rainfall were retained in the best-fit models for all the metrics (Table 1). Both Gw and IE were significantly negatively associated with LG (Figure 3a,b) and rainfall (Figure 3c,d). LG, WE and rainfall were retained in the best-fit model for Vw, but only rainfall was significant (Figure 3e and Table S3). Although LG, WE, MU, rainfall and the LP x rainfall interaction were retained in the best-fit model for \( H_s^t \), none were significant (Tables 1 and S3).

In the plant-specific CCA, the first and second axes explained 41% and 28% of the variation in species composition, respectively (Figure 4a); however, only the first axis was significant (Table S4). Both WE and rainfall were significant (Table 2). Axis 1 differentiated plant communities that were favoured by wood extraction and increased rainfall from plant communities that were harmed by wood extraction and decreased rainfall. For example, Cenostigma pyramidalis was more abundant in plots with higher levels of wood extraction, while Senna velutina...
was more abundant in plots with higher rainfall (Figure 4a). In the ant-specific CCA, the first and second axes were significant, explaining 40% and 36% of the variation in community composition, respectively (Figure 4b). Both LG and rainfall were significant (Table 2) and associated with axis 1; rainfall was also associated with axis 2. *Dolichoderus quadricincticulatus* and

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**TABLE 1** Results of the best-fit models ($\Delta AIC_c < 2$) examining the separate and combined influences of chronic anthropogenic disturbances (livestock grazing, LG; wood extraction, WE; and miscellaneous resource use, MU) and rainfall levels on the specialization of networks formed by ants and EFN-bearing plants. The network specialization metrics were weighted generality ($G_w$), weighted vulnerability ($V_w$), interaction evenness ($I_E$) and $H'_2$. Each metric was calculated twice, once using observed data (obs) and once using data from null models (null). For each variable retained in the best-fit model, we have indicated the mean coefficient ($\beta$), the unconditional standard error ($SE$), the 95% confidence intervals (95% CI), the p-value and relative variable importance (RVI). Significant variables (according to 95% confidence intervals) are in bold. Observed IE does not appear because no variables were retained in its best-fit model.

**FIGURE 2** Influence of (a) livestock grazing, (b) miscellaneous resource use and (c) mean annual rainfall on the observed network specialization index $H'_2$. The metric values and 95% confidence intervals (in grey) were calculated by averaging estimates across the best-fit models ($\Delta AIC_c < 2$).
Crematogaster crinosa were common in plots with high LG levels, while Pheidole radoskowiskii was common in plots with low LG levels. Pseudomyrmex elongatus and Azteca sp. A were common in wetter plots, while Brachymyrmex sp. A and Cephalotes pr. cordatus were common in drier plots (Figure 4b).

For EFN-bearing plant species, there was no relationship between the response to WE and rainfall (i.e. CCA1 scores) and specialization (mean $d' \pm$ SD: $0.17 \pm 0.09$; Spearman $r_s = -.27$, $p = .284$). Similarly, in attendant ant species, neither the response to LG and rainfall (i.e. CCA1 scores) (Spearman $r_s = .27$, $p = .314$) nor the response to rainfall only (i.e. CCA2 scores; Spearman $r_s = .4822$, $p = .071$) was correlated with specialization ($d' = 0.21 \pm 0.22$).

4 | DISCUSSION

We found that CADs and rainfall separately influenced the degree of specialization in ant-plant networks in the Caatinga. Livestock grazing and, in particular, rainfall were most strongly associated with increased specialization. To a lesser degree, miscellaneous resource use was associated with declines in specialization. There was no relationship between wood extraction and specialization. The composition of plant and ant communities varied with disturbance and rainfall. However, such changes were not related to the degree of species specialization, which means that the pattern cannot be explained by specialist–generalist replacement. Furthermore, these changes were not due to CAD-related effects on species richness and/or the abundance of EFN-bearing plants and ant attendants as results were consistent using both the observed and null model-based metrics.

Previous research has shown that, along gradients of anthropogenic disturbance, the degree of specialization in mutualistic plant-animal networks can either decrease (plant-frugivore networks: Menke et al., 2012; plant-pollinator networks: Alzen et al., 2012) or remain unaffected (plant-frugivore networks: Schleuning et al., 2011; plant-pollinator networks: Weiner et al., 2014). However, most of these studies were focused on acute disturbances such as forest fragmentation (Albrecht et al., 2013), logging (Menke et al., 2012; Schleuning et al., 2011) and land-use change (Weiner et al., 2014). Here, we demonstrate that chronic disturbances (sensu Singh, 1998) may also influence the degree of specialization in mutualistic networks. More interestingly, we have shown that different forms of anthropogenic disturbance occurring within the same landscape may have contrasting effects on network specialization. For example, the relationship was strongly positive for livestock grazing, slightly negative for miscellaneous resource use and non-existent for wood extraction.

It has been reported that EFN-bearing plants experiencing high levels of herbivory produce more nectar, thus attracting more ants (Hernandez-Cumplido, Forter, Moreira, & Benrey, 2016; Huang, Siemann, Carillo, & Ding, 2015)—a strategy that better defends the plants against herbivores. Indeed, in savannas, large herbivores shape ant-plant interactions. Palmer et al. (2008) showed that, in areas from which large herbivores had been excluded for 10 years, nectar production declined and colonization by less aggressive ants increased, triggering higher tree mortality. The Caatinga has no native large herbivores—they are believed to have gone extinct more than 11,000 years ago (De Vivo & Carmignotto, 2004). However, non-native large herbivores, such as goats and cattle, were
introduced into the Caatinga at the time of European colonization, in the 16th century (MMA, 2017); they might currently be serving similar functional roles to the extinct species. As extrafloral nectar production is an induced defence response (Huang et al., 2015), herbivory might activate EFNs and thus strengthen interactions with particular ant species. However, wood extraction and miscellaneous resource use probably do not modify resource availability (i.e. nectar availability) in a manner that mediates this mutualism. That said, miscellaneous resource use might alter the interaction behaviour of either plants or ants; it was not associated with community composition changes.

Some studies have already shown that current climatic conditions are shaping the degree of specialization in mutualistic networks of pollinators and seed dispersers across the globe (Dalsgaard et al., 2011; Schleuning et al., 2012). We found some support for our first hypothesis: rainfall levels were associated with specialization in networks of EFN-bearing plants and attendant ants within a Caatinga forest. Other studies have found that intra-annual variation in rainfall might also influence such networks (Lange, Dáttilo, & Del-Claro, 2013; Rico-Gray, Díaz-Castelazo, Ramírez-Hernandez, Guimarães, & Holland, 2012). The mechanism could be water availability, which could affect nectar secretion (Rico-Gray et al., 1998) and, subsequently, network structure. In the Caatinga, productivity is highest where rainfall is highest (Sampaio, 2003), and higher productivity might generate more opportunities for species to specialize (Schemske, 2002; Srivastava & Lawton, 1998).

As far as we know, our study is the first to look for evidence that anthropogenic disturbance and rainfall act in tandem to influence the specialization of mutualistic networks, our second hypothesis. We found no support for this idea. Several recent studies have

**FIGURE 4**  Results of the canonical correspondence analyses examining the associations between three chronic anthropogenic disturbances (LG, WE and MU), rainfall and the species composition of (a) EFN-bearing plant communities and (b) attendant ant communities in Catimbau National Park, Brazil. The abbreviations for the EFN-bearing plant species are as follows: Cfol = Chloroleucon foliolosum, Chel = Croton heliotropifolius, Cmic = Centostigma microphylla, Cnep = Croton nepetifolius, Cpyr = Centostigma pyramidalis, Ctri = Croton tricolor, Cffe = Cynophalla flexuosa, Ptub = Pilosocereus tuberculatus, Psti = Piptadenia stipulacea, Pmon = Pityrocarpa moniliformis, Sgla = Sapium glandulosum, Sbah = Senegalia bahiensis, Spia = Senegalia piahuiensis, Ssp = Senegalia sp., Sriz = Senna rizzii, Sspl = Senna splendidia, Svel = Senna velutina, Tpal = Tacinga palmadora and Vcur = Varronia curassavica. The abbreviations for the attendant ant species are as follows: AztA = Azteca sp. A, BraA = Brachymyrmex sp. A, BraC = Brachymyrmex sp. C, Ccra = Camponotus crassus, Ccor = Cephalotes pr. cordatus, Cpus = Cephalotes pusillus, Ccri = Crematogaster crinosa, Ceva = Crematogaster pr. evallans, Cobs = Crematogaster pr. obscurata, Dqua = Dolichoderus quadridenticulatus, Dtho = Dorymyrmex thoracicus, Prad = Pheidole radoskowiskii, Paca = Pseudomyrmex acanthobius, Pelo = Pseudomyrmex elongatus, Pgra = Pseudomyrmex gracilis and Svir = Solenopsis virulens.
TABLE 2 Results of the canonical correspondence analyses (CCAs) used to test the influence of livestock grazing (LG), wood extraction (WE), miscellaneous resource use (MU) and rainfall on the species composition of EFN-bearing plant communities and attendant ant communities. Significant values are in bold.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>(\chi^2)</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>EFN-bearing plant species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LG</td>
<td>1</td>
<td>0.248</td>
<td>1.245</td>
<td>.254</td>
</tr>
<tr>
<td>WE</td>
<td>1</td>
<td>0.376</td>
<td>1.886</td>
<td>.021</td>
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<tr>
<td>MU</td>
<td>1</td>
<td>0.200</td>
<td>1.001</td>
<td>.501</td>
</tr>
<tr>
<td>Rainfall</td>
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<td>1.660</td>
<td>.038</td>
</tr>
<tr>
<td>Residual</td>
<td>10</td>
<td>1.996</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Attendant ant species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LG</td>
<td>1</td>
<td>0.176</td>
<td>1.745</td>
<td>.047</td>
</tr>
<tr>
<td>WE</td>
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<td>0.126</td>
<td>1.243</td>
<td>.253</td>
</tr>
<tr>
<td>MU</td>
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<td>1.745</td>
<td>.150</td>
</tr>
<tr>
<td>Rainfall</td>
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</tr>
<tr>
<td>Residual</td>
<td>10</td>
<td>1.010</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Wealthsome consider that disturbance intensity and climatic variation interact to modulate biodiversity responses (Frishkoff et al., 2016; Gibb et al., 2015; Rito et al., 2017). However, most of these studies were conducted at much larger spatial scales than that of our study (but see Rito et al., 2017 for the same study area).

Some studies have found that CADs and rainfall influence plant (Ribeiro et al., 2015; Ribeiro et al. 2016; Rito et al., 2017) and ant (Oliveira et al., 2017; Ribeiro-Neto et al., 2016) community structure and composition in the Caatinga. We also observed that CADs and rainfall levels were associated with changes in the compositions of EFN-bearing plant communities and attendant ant communities, supporting part of our third hypothesis. Plant community composition varied with wood extraction intensity; ant community composition varied with livestock grazing intensity; and both plant and ant community composition varied with rainfall levels. However, contrary to the other part of our third hypothesis, we did not find a correlation between the environmental responses of plants or ants and their degree of specialization, suggesting that compositional changes are not behind the changes in network specialization. One explanation may be that ant–plant interactions involving extraguild nectaries are often generalized and facultative (Blüthgen et al., 2007; Heil & McKey, 2003; Rico-Gray & Oliveira, 2007). Studies that focused on more specialized mutualisms, such as those between plants and frugivores (Albrecht et al., 2013) and plants and pollinators (Weiner et al., 2014), found that, in disturbed habitats, specialist frugivores and pollinators were more negatively affected than were generalist frugivores and pollinators. Here, the two ant species that accounted for more than 50% of the interactions (C. crassus and C. pusillus) did not respond to the environmental factors we studied. Another explanation might be that same ant species behave differently in different environments (Brose et al., 2005; Tylianakis et al., 2007). Unfortunately, there were not enough commonly occurring ant species to test this hypothesis.

Our main finding—that different CADs and rainfall levels are associated with different levels of specialization in mutualisms involving ants and EFN-bearing plants—has various implications. First, and according to the specialist–generalist evolutionary paradigm (Devictor et al., 2010; Levins, 1968), human activities can compromise the quality of plant protection services in SDTFs. According to this paradigm, specialist species are good at a few services, while generalists are mediocre at many services. However, a recent study on the plant protection services provided by ants showed that the most protective ant species might be the most generalist as well (Fagundes et al., 2017). Unfortunately, this study examined protection against non-natural plant enemies, and we still need to learn more about the effectiveness of mutualisms protecting against natural enemies before making predictions about how protection services change depending on environmental conditions. Second, the large heterogeneity in anthropogenic disturbance and rainfall levels in Catimbau National Park has created a mosaic of ant–plant interactions—and the degree of specialization differs, as do interaction identity, interaction strength and plant protection quality. This mosaic may result in different selective forces that operate on the co-evolution of species involved in these mutualisms, especially in dry environments. Although we lack information on the effects of such variation on the success of plant protection services, we can imagine that the scenario is one in which a human-driven selection mosaic exists (Thompson, 2005) and in which the local adaptive responses of plants might arise because of local variation in community composition and function. Finally, despite great spatial variation in specialization responses, the strong influence of rainfall suggests that the predicted 22% decline in precipitation in the Caatinga by 2100 (Magrin et al., 2014) could trigger the loss of the most specialized ant–plant networks, which would have implications for related ecosystem services.

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AUTHORS’ CONTRIBUTIONS

T.C., X.A. and I.R.L. conceived the ideas and designed the experiments. T.C., F.M.P.O. and R.T.Q. collected the data. N.B. contributed to the network analysis. T.C. 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 ACCESSIBILITY

The data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.g7m7c70 (Câmara et al., 2018).

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