

Effects of increasing aridity and chronic anthropogenic disturbance on seed dispersal by ants in Brazilian Caatinga

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Abstract

1. Anthropogenic disturbance and climate change are the main drivers of biodiversity loss and ecological services around the globe. There is concern that climate change will exacerbate the impacts of disturbance and thereby promote biotic homogenization, but its consequences for ecological services are unknown.
2. We investigated the individual and interactive effects of increasing chronic anthropogenic disturbance (CAD) and aridity on seed dispersal services provided by ants in Caatinga vegetation of north-eastern Brazil.
3. The study was conducted in Catimbau National Park, Pernambuco, Brazil. Within an area of 214 km², we established nineteen 50 × 20 m plots that encompassed gradients of both CAD and aridity. We offered diaspores of six plant species, three myrmecochorous diaspores and three fleshy fruits that are secondarily dispersed by ants. We then quantified the number of interactions, seed removal rate and dispersal distances, and noted the identities of interacting ant species. Finally, we used pitfall trap data to quantify the abundances of ant disperser species in each plot.
4. Our results show that overall composition of ant disperser species varied along the gradients of CAD and aridity, but the composition of high-quality dispersers varied only with aridity. The total number of interactions, rates of removal and mean distance of removal all declined with increasing aridity, but they were not related to CAD. These same patterns were found when considering only high-quality disperser species, driven by the responses of the dominant disperser *Dinoponera quadriceps*. We found little evidence of interactive effects of CAD and aridity on seed dispersal services by ants.
5. Our study indicates that CAD and aridity act independently on ant-mediated seed dispersal services in Caatinga, such that the impacts of anthropogenic disturbance are unlikely to change under the forecast climate of increased aridity. However, our findings highlight the vulnerability of seed dispersal services provided by ants

in Caatinga under an increasingly arid climate due to low functional redundancy in high-quality disperser species. Given the large number of plant species dependent on ants for seed dispersal, this has important implications for future plant recruitment and, consequently, for the composition of Caatinga plant communities.

KEYWORDS

ant–plant mutualism, biotic interactions, climate change, human disturbance, seasonally dry tropical forest

1 | INTRODUCTION

Both anthropogenic disturbance and climate change are primary conservation threats in virtually all ecosystems (Sala et al., 2000), having the potential to rearrange species assemblages, with cascading effects on biotic interactions such as the disruption of mutualisms and the reduction of the provision of ecological services provided by these interactions (Kiers, Palmer, Ives, Bruno, & Bronstein, 2010; Tylianakis, Didham, Bascompte, & Wardle, 2008). It has been suggested that anthropogenic disturbance and climate change may favour the same set of species, triggering a process of biotic homogenization (i.e. the reduction of multiple species assemblages into one overall simpler assemblage) that could make drier ecosystems similar to highly disturbed ones (Frishkoff et al., 2016). Such homogenization is likely to reduce ecosystem resilience (Hirota, Holmgren, Van Nes, & Scheffer, 2011) following the loss of key ecological services such as pollination and seed dispersal (Hegland, Nielsen, Lázaro, Bjerknes, & Totland, 2008; Memmott, Craze, Waser, & Price, 2007; Tylianakis et al., 2008). Moreover, there is increasing concern that climate change might exacerbate the effects of anthropogenic disturbance by imposing an additional strong environmental filter in disturbed areas (Hirota et al., 2011; Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017). However, the combined and interactive effects on biodiversity of anthropogenic disturbance and climate change remain poorly understood (Sirami et al., 2017; but see Brook, Sodhi, & Bradshaw, 2008; Gibb et al., 2015; Frishkoff et al., 2016) and their consequences for ecological services are unknown.

Ants are providers of key ecological services in most terrestrial ecosystems (Del Toro, Ribbons, & Pelini, 2012). The impacts of disturbance on ant communities act primarily through habitat change (Andersen, 2018), and an important determinant of species responses is body size (Gibb et al., 2018). Given that climate variables such as temperature and rainfall play major roles in shaping ant communities (Dunn et al., 2009; Kaspari, O'Donnell, & Kercher, 2000), climate change can be expected to interact with disturbance in complex ways, including mediation or intensification of disturbance effects on ant communities and the ecological service ants provide (Gibb et al., 2015). One such service is myrmecochory, a globally important seed dispersal syndrome found among 11,000 angiosperm species from 77 plant families (Lengyel, Gove, Latimer, Majer, & Dunn, 2009), whose diaspores possess a lipid-rich appendage (elaiosome) for attracting and aiding transport by ants (Beattie,

1985). Ants typically transfer the diaspores to their nests, remove the elaiosome and discard the intact seed in nest galleries or outside refuse piles (Beattie, 1985) where they can germinate and establish (Hughes & Westoby, 1992a; Manzaneda & Rey, 2012). The effects of anthropogenic disturbance on myrmecochory can be highly variable. Although some studies have shown negative effects (i.e. decreasing removal rate and dispersal distance; Almeida, Mayhé-Nunes, & Queiroz, 2013; Leal, Andersen, & Leal, 2014; Rocha-Ortega, Bartimachi, Neves, Bruna, & Valsconcelos, 2017), others have shown effects to be positive (i.e. increasing removal rate and dispersal distance; Parr, Andersen, Chastagnol, & Duffaud, 2007; Dominguez-Haydar & Armbrrecht, 2011; Beaumont, Mackay, & Whalen, 2013) or neutral (Ness, 2004).

Changes in the quality of seed dispersal services provided by ants are usually related to changes in composition of ant disperser species. Highest quality seed dispersal services are typically provided by large-bodied ant species because they readily collect seeds and transport them over large distances (Andersen & Morrison, 1998; Leal, Correia Neto Lima, Oliveira, Andersen, & Leal, 2014). Large ant species are especially sensitive to disturbance (Gibb et al., 2018; Leal, Andersen, & Leal, 2014), and this can result in severe reductions in the quality of seed dispersal services in disturbed habitats (Almeida et al., 2013; Gove, Majer, & Dunn, 2007; Leal, Andersen, & Leal, 2014; Ness, Bronstein, Andersen, & Holland, 2004). Although smaller insects are considered more sensitive to high temperatures through desiccation (Baudier, Mudd, Erickson, & O'Donnell, 2015; Kühnel, Brückner, Schmelzle, Heethoff, & Blüthgen, 2017), recent studies have found that the most sensitive ants to climate change are in fact the largest (Andrew, Miller, Hall, Hemmings, & Oliver, 2019; Gibb et al., 2018). This might be because large ants require more resources and take longer to mature, thus reducing their adaptive capacity (Gibb et al., 2018; McCain & King, 2014; Savage, Gillooly, Brown, West, & Charnov, 2004). The sensitivity of large-bodied ants to disturbance might therefore be exacerbated under climate change, further reducing the loss of seed dispersal services provided by ants.

Seed dispersal by ants is not restricted to myrmecochorous plants, as ants can opportunistically disperse a wide variety of fleshy fruits (or seeds from them) after being attracted by the pulp (Böhning-Gaese, Gaese, & Rabemanantsoa, 1999; Passos & Oliveira, 2004; Pizo & Oliveira, 2006). By secondarily dispersing fleshy fruits, ants can positively affect seed fate and germination of diaspores primarily adapted

for vertebrate dispersal (Christianini, Mayhé-Nunes, & Oliveira, 2007; Levey & Byrne, 1993; Passos & Oliveira, 2004). Given that anthropogenic disturbance often has a particularly severe impact on vertebrate species (Dirzo et al., 2014) and consequently on the seed dispersal services provided by them (Estes et al., 2011), the dispersal of fleshy fruits by ants might be especially important at disturbed sites (Christianini, Oliveira, Bruna, & Vasconcelos, 2014). Both fleshy fruits and elaiosomes are attractive to omnivorous ants, and so it could be expected that ants providing high-quality services to myrmecochorous plants (i.e. large-bodied species with large foraging ranges) would do likewise to plants producing fleshy fruits. If so, then CAD and aridity would have the same effects on both dispersal types, and therefore have a broader impact on plant communities. However, all this remains to be investigated.

Our study aims to investigate how anthropogenic disturbance and increasing aridity interact to influence ant-mediated seed dispersal (both myrmecochory and non-myrmecochory) in Caatinga, the largest and most diverse of the world's seasonally dry tropical forest (Silva, Leal, & Tabarelli, 2017) that is recognized as a global hotspot for myrmecochory (Leal, Leal, Oliveira, Arcoverde, & Andersen, 2017; Leal, Wirth, & Tabarelli, 2007; Leal, Andersen, & Leal, 2014; Leal, Correia Neto Lima et al., 2014). Anthropogenic disturbance has been previously shown to reduce the quality of ant-mediated seed dispersal services for myrmecochorous diaspores at one Caatinga site (Leal, Andersen, & Leal, 2014). However, it is unclear how representative this is of Caatinga, given the marked variation in soils, rainfall and vegetation within the biome (Moro et al., 2015). We specifically tested three hypotheses. Our first hypothesis is that ant species providing high-quality dispersal services for myrmecochorous plants will also provide high-quality dispersal services for fleshy fruits. We predict that the same ant species that most rapidly remove myrmecochorous seeds and transport them the furthest distances will do likewise for fleshy fruits. Our second hypothesis is that increasing anthropogenic disturbance has similar effects as increasing aridity on seed dispersal by ants. We predict that both increasing anthropogenic disturbance and aridity will reduce the number of interactions between diaspores and ants as well as the quality of seed dispersal services (i.e. seed removal rate and seed dispersal distance). We also predict that these effects are due to changes in ant disperser species composition, particularly a reduction in the abundance of high-quality seed dispersers. Our third hypothesis is that there are also interactive effects of anthropogenic disturbance and aridity, such that the effects of disturbance are contingent on the level of aridity. We predict that disturbance has a greater impact in more arid sites, due to the lower primary productivity conferring lower resilience to ant communities and, consequently, to seed dispersal services by ants.

2 | MATERIALS AND METHODS

2.1 | Study area

Caatinga is a mosaic of seasonally dry tropical forests and scrub vegetation (Pennington, Lavin, & Oliveira-Filho, 2009) that covers

912,529 km² of north-eastern Brazil (Silva et al., 2017) (Supporting Information Figure S1). It is considered one of the most endangered ecosystems in Brazil due to extensive conversion to agriculture (45% of its area has been deforested; Silva et al., 2017). In addition, remaining vegetation is exploited by high densities of people (26 inhabitants/km²) who are highly dependent on forest resources for their livelihoods and therefore exert high levels of chronic anthropogenic disturbance (CAD; sensu Singh, 1998; Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal, 2015; Rito et al., 2017). Under future climate change, the Caatinga region is projected to receive about 22% less rainfall than it currently does (Magrin et al., 2014).

Our study was conducted in Catimbau National Park, Pernambuco State (8°24'00" and 8°36'35"S; 37°0'30" and 37°1'40"W, Supporting Information Figure S1). Mean annual rainfall varies markedly in Catimbau, from 1,100 mm in the south-east to 480 mm in the north-west, and the mean temperature is 23°C (Rito et al., 2017). Approximately 70% of its 607 km² is covered by quartzite sandy soils supporting low-stature Caatinga vegetation (Rito et al., 2017). The park was created in 2002, and low-income rural populations still live in the park, using it for grazing and browsing by livestock, collection of living and dead wood, harvesting of non-timber forest products and hunting (Rito et al., 2017).

We selected nineteen 20 m × 50 m plots to cover a wide range of disturbance and annual rainfall based on RapidEye satellite imagery and field observations (Supporting Information Figure S1). All plots were on sandy soil, had similar slope and supported old-growth vegetation that had not experienced slash-and-burn agriculture for at least 50 years. Plots were separated by a minimum of 2 km and occurred within an area of 214.3 km² (Rito et al., 2017).

2.2 | Measurement of CAD and aridity

To characterize the level of CAD in the 19 plots, we computed a global multi-metric index that integrates eight disturbance indicators related to the three main sources of CAD in Catimbau (see Appendix S1 and Arnan et al., 2018, for more details of how to calculate the global multi-metric index): livestock pressure (herbivory by goats and cattle), wood extraction (live and dead wood) and extraction of non-timber forest products (medicinal plants, food items for humans, hunting and livestock fodder). These CAD indicators were measured using three approaches: (a) *Geographic distances based on remote sensing*: two distances were measured, proximity to the nearest house and proximity to the nearest road, using satellite imagery and ArcGIS 10.1 software. Since distance is inversely related to level of disturbance, we used the inverse of distance as our metric; (b) *Interviews with local inhabitants*: we identified the nearest village to each plot using GIS and then conducted informal and semistructured interviews to assess the number of people in each village, which we weighted by distance from the plots; and (c) *Measures of disturbance in the field*: we conducted field assessments of goat trail length, goat dung, cattle dung, alive wood extraction (stem cuts) and coarse woody debris extraction (litter) within each plot (see Arnan et al.,

2018, for more details). The index ranges from 2 to 58 (from the lowest to the highest disturbance intensity) among the plots.

To characterize the aridity gradient, data on mean annual precipitation were acquired from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). We downloaded the dataset at 30 arc-second resolution (<http://www.worldclim.org>), and the value of mean annual precipitation at each plot was extracted using package *maptolls* (Bivand & Lewin-Koh, 2015) in the R software (R Core Team, 2016). Mean annual precipitation in our plots ranged from 940 mm to 510 mm. Such a large range in mean annual rainfall within a small geographic area makes Catimbau an ideal study system for analysing ecological responses to variation in aridity. Aridity is usually considered as the ratio of mean annual precipitation to potential evapotranspiration (Armas, Rodríguez-Echeverría, & Pugnaire, 2011); we also computed a global aridity index, but since it was very highly correlated with precipitation ($r = 0.98$; see Appendix S2 for more details), we retain precipitation as our measure of aridity because it is more commonly used in diversity studies (Dunn et al., 2009; Hawkins et al., 2003; Rito et al., 2017). The aridity and CAD gradient were not significantly correlated ($r = 0.23$, $p > 0.05$) and therefore were statistically independent.

2.3 | Seed dispersal by ants

To quantify ant-mediated seed dispersal services, we used diaspores from six locally abundant plant species that represent the morphological range of diaspores dispersed by ants in the region: three myrmecochores (*Jatropha mutabilis*, *Jatropha ribifolia* and *Croton nepetaefolius*) and three fleshy-fruited (*Simaba ferruginea*, *Sideroxylon obtusifolium* and *Melocactus bahiensis*) (Supporting Information Table S1). Diaspores were collected earlier in the rainy season when our experiments were conducted, and were stored in paper bags at -20°C prior to use. We observed ant–diaspore interactions at six stations separated by 10 m along each of two parallel 50-m transects (separated by 20 m) established in each plot. At each station, five conspecific diaspores were placed on a white filter paper card (6 cm \times 6 cm) as described in Leal, Andersen, & Leal, (2014). During each observation period, all diaspores on a transect were from the same species, and the two transects within a plot had different species, one a myrmecochore and the other not. There were three observation periods (two between March and May 2015 and one in April 2016) such that all six diaspore species were observed once in each plot. Stations were monitored at 15-min intervals from 06:00 hr to 18:00 hr over one day for each monitoring period, and removed diaspores were not replaced. Any ant contact with a diaspore for the apparent purpose of feeding (i.e. ants manipulating the diaspores try to collect part of them) was considered as an interaction (Leal et al., 2007), and different ant species could interact more than once with a diaspore (i.e. more than one interaction event for each diaspore). For each observed interaction, we recorded the identity of the ant species, whether or not the diaspore was removed (we considered a removal event when a diaspore was moved ≥ 5 cm), and the distance

of any removal (defined as the displacement from the station to where the diaspore was either dropped or taken into an ant nest).

We classified interacting ant species as either high- or low-quality dispersers following Leal, Andersen, & Leal, (2014); Leal, Correia Neto Lima et al., (2014). High-quality seed dispersers comprised medium to large (body length >5.0 mm) ants that transport diaspores over relatively long (>2 m) distances and deposit them isolated or in small groups in nests or in nest refuse piles. Low-quality seed dispersers were small ants (<5.0 mm) that feed on the diaspores in situ without diaspore removal or transport diaspores over short distances (<2 m) and deposit them in large groups in nest refuse piles (Leal, Andersen, & Leal, 2014; Leal, Correia Neto Lima et al., 2014). Leaf-cutting ants were also classified as low-quality dispersers despite their relatively large body size and ability to transport seeds over long distances, because they usually cut or bury all seedlings growing on or near their nests (Leal et al., 2017).

2.4 | Abundance of seed-disperser ants

We used results from a survey of ants using 20 pitfall traps operated for 48 hrs in each plot during March 2015 (Arcoverde et al., unpublished data) for data on the abundances of seed-dispersing ants. This survey recorded 17 of the 20 ant disperser species observed during our study; the other three species (*Pheidole fera*, *Pheidole pr. fracticeps* and *Pheidole* sp. A) were responsible for $< 1\%$ of total removal events (see Table 1) and were not considered in analyses of the species composition of disperser ants.

2.5 | Data analyses

Unless otherwise specified, our unit of analysis was observation station for analyses of seed dispersal and plot for analysis of pitfall data. We used generalized linear mixed models (hereafter GLMM) to evaluate the effect of the diaspores type (myrmecochorous seeds or fleshy fruits) on removal rate (proportion of observed diaspore removals out of five diaspores offered per station) and mean removal distances by high-quality dispersers. For these models, we used plot and diaspore species as random factors.

To evaluate the effects of CAD, precipitation and their interaction on the composition of ant seed-disperser species at the plot level (based on pitfall data), we conducted a canonical correspondence analysis (CCA) using the frequency of occurrence of species as a measure of species abundance. We performed a randomization test (1,000 aleatorizations) to obtain the statistical significance of explanatory variables. Further, we performed Spearman's correlations between the abundance of each ant disperser species and the CCA axes significantly associated with the CAD and aridity gradients considering the first two axes.

We used GLMMs with Poisson error distribution to analyse the effects of CAD, precipitation and their interaction on the total number of interactions between ants and diaspores, and on the number of interactions performed by low- and high-quality dispersers separately. We also used GLMMs to evaluate the effects of CAD,

TABLE 1 Total removed diaspores and mean removal distance for each ant species removing myrmecochorous seeds (M) and fleshy fruits (F) along the rainfall and chronic anthropogenic disturbance gradients at Catimbau National Park, Pernambuco, Brazil. Ant species were classified in low-quality dispersers and high-quality dispersers following Leal et al. (2017). Mean Weber's length values are considered an indicative of worker body size and were obtained from another work conducted in the same study area (Arnan et al., 2018)

Ant species	Mean (\pm SD) Weber's length (mm)	Number of removed seeds		Mean removal distance (cm)	
		M	F	M	F
High-quality dispersers					
<i>Dinoponera quadriceps</i>	8.8 \pm 0.28	134	206	708.8 \pm 483.6	826.5 \pm 426.7
<i>Ectatomma muticum</i>	3.6 \pm 0.30	47	10	200.1 \pm 121.7	224 \pm 138.5
Low-quality dispersers					
<i>Acromyrmex rugosus</i>	1.7 \pm 0.31	1	0	5.0 \pm 0.0	-
<i>Atta sexdens</i>	2.0 \pm 0.35	4	6	281.0 \pm 0.0	20.5 \pm 13.7
<i>Dorymyrmex thoracicus</i>	1.3 \pm 0.07	9	0	6.1 \pm 3.9	-
<i>Pheidole fera</i>	0.9 \pm 0.0	1	0	9.0 \pm 0.0	-
<i>Pheidole pr. fracticeps</i>	0.6 \pm 0.09	1	0	5.0 \pm 0.0	-
<i>Pheidole radoskowskii</i>	0.8 \pm 0.04	99	3	15.1 \pm 23.7	4.7 \pm 0.7
<i>Pheidole</i> sp. A	0.8 \pm 0.12	1	0	8.0 \pm 0.0	-
<i>Pheidole</i> sp. B	0.6 \pm 0.09	14	0	9.1 \pm 4.6	-
<i>Pheidole</i> sp. C	0.6 \pm 0.03	19	1	17.1 \pm 35.0	5.0 \pm 0.0
<i>Pheidole</i> sp. D	0.8 \pm 0.06	13	3	7.6 \pm 6.0	6.3 \pm 3.7
<i>Pheidole</i> sp. E	0.6 \pm 0.06	27	1	12.0 \pm 11.9	5.0 \pm 0.0
<i>Pheidole</i> sp. P	0.7 \pm 0.03	4	0	9.1 \pm 7.3	-
<i>Pheidole triconstricta</i>	0.9 \pm 0.03	2	0	6.0 \pm 1.0	-
<i>Solenopsis</i> sp. B	0.8 \pm 0.05	2	0	10.0 \pm 5.6	-
<i>Solenopsis</i> sp. C	0.7 \pm 0.07	3	0	5.3 \pm 2.8	-
<i>Solenopsis tridens</i>	0.4 \pm 0.04	55	0	10.8 \pm 12.9	-
<i>Solenopsis virullens</i>	0.4 \pm 0.07	22	0	16.4 \pm 20.7	-
<i>Tetramorium</i> sp. A	0.4 \pm 0.05	1	0	40.0 \pm 0.0	-

precipitation and their interaction on removal rates and mean removal distances, considering all ant disperser species and high- and low-quality dispersers separately. For all these models, we used plot and diaspore species as random factors. Additionally, we built GLMMs to evaluate the effects of CAD, precipitation and their interaction on removal rates and mean removal distances for each diaspore species individually (using plot as a random factor), as well as for the four most common ant species removing the diaspores (using plot and diaspore species as random factors).

For all the removal rate models, we used a binomial error distribution, and for the removal distance models, we used a Gaussian error distribution. Analyses were performed in R. We checked residuals for normality and homoscedasticity in all models. Data that did not meet homoscedastic criteria were $\log(x) + 1$ transformed. We also checked for overdispersion in all models. When detected, we fitted a Poisson-lognormal model (Harrison, 2014). We used the packages *vegan* version 2.3 (Oksanen et al., 2015) for CCA analysis and *lme4* version 1.1-7 (Bates et al., 2014) to build the GLMM models.

We repeated our analyses by using the three individual disturbance pressure indices (livestock pressure, wood extraction and extraction of non-timber products) instead of the global multi-metric measure of CAD. They all showed the same results as those from the global measure and so are not reported here.

3 | RESULTS

3.1 | Seed-disperser ants

We observed 1469 ant-diaspore interactions involving 33 ant species, with 65.4% of these interactions involving myrmecochorous seeds. Diaspores were removed in 59% of the interactions (68.4% for myrmecochorous seeds), involving 20 ant species (Table 1). Two ant species were classified as high-quality dispersers: *Dinoponera quadriceps* and *Ectatomma muticum*, and they were responsible for 49.5% of all removals (48.5% for myrmecochorous seeds and 51.5% for fleshy fruits). Low-quality dispersers were species of *Dorymyrmex*, *Pheidole*, *Solenopsis* and *Tetramorium* (Table 1). The abundance of high-quality dispersers (*D. quadriceps* and *E. muticum*) based on pit-fall catches was positively correlated with the removal rates from observation stations for myrmecochorous seeds (Spearman's $r = 0.35$, $p = 0.05$), fleshy fruits ($r = 0.45$, $p = 0.04$) and all diaspores ($r = 0.53$, $p = 0.02$). It was also positively correlated with mean dispersal distance for myrmecochorous seeds (Spearman's $r = 0.61$, $p < 0.01$), fleshy fruits ($r = 0.34$, $p = 0.05$) and all diaspores ($r = 0.52$, $p = 0.02$). Removal rates by high-quality dispersers did not vary with diaspore type (GLMM: $F = 3.67$, $p = 0.19$), and this same pattern was found for mean removal distance (GLMM: $F = 4.03$, $p = 0.18$).

According to our CCA, the composition of ant disperser species varied significantly with precipitation ($F_{1,15} = 1.96$, $p = 0.03$, Figure 1) and CAD ($F_{1,15} = 1.91$, $p = 0.04$, Figure 1), but not with their interaction ($F_{1,15} = 1.44$, $p = 0.19$, see Supporting Information Table S2 for more details on CCA results). Precipitation was associated with axis 1, while CAD was associated with axis 2. The abundance of *D. quadriceps* increased with increasing precipitation (Spearman's $r = 0.74$, $p < 0.01$), but that of *E. muticum* decreased (Spearman's $r = -0.48$, $p = 0.04$). However, CAD had no effect on the abundance of either ant species (Spearman's $r = -0.05$, $p = 0.82$; and Spearman's $r = 0.14$, $p = 0.56$ for *D. quadriceps* and *E. muticum*, respectively). The responses of the abundance of low-quality dispersers were highly variable among species. For example, CAD was negatively related to the abundance of *Solenopsis* sp. 1 (Spearman's $r = -0.47$, $p = 0.04$), but positively to that of *Acromyrmex rugosus* (Spearman's $r = 0.50$, $p = 0.03$). Similarly, increasing precipitation was negatively related to the abundance of *Solenopsis virullens* (Spearman's $r = -0.51$, $p = 0.02$), but positively for *Dorymyrmex thoracicus* (Spearman's $r = 0.54$, $p = 0.01$) and *Pheidole* sp. C (Spearman's $r = 0.59$, $p < 0.01$, Supporting Information Table S3).

3.2 | Seed dispersal

The number of interactions per plot ranged from 28 to 152. It increased with increasing precipitation (GLMM: $\chi^2 = 5.94$, $df = 678$,

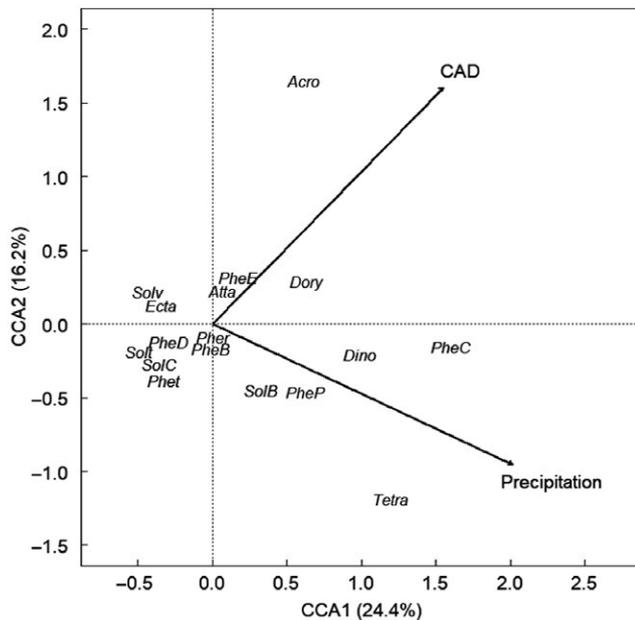


FIGURE 1 Representation of ant species and environmental gradients (precipitation and chronic anthropogenic disturbance – CAD) affecting ant disperser community composition at Catimbau National Park, on the first two axes of the canonical correspondence analysis (CCA). Abbreviations: *Acro*, *Acromyrmex rugosus*; *Atta*, *Atta sexdens*; *Dino*, *Dinoponera quadriceps*; *Dory*, *Dorymyrmex thoracicus*; *Ecta*, *Ectatomma muticum*; *Pheir*, *Pheidole radoskowskii*; *Pheit*, *Pheidole triconstricta*; *PheB*, *Pheidole* sp. B; *PheC*, *Pheidole* sp. C; *PheD*, *Pheidole* sp. D; *PheE*, *Pheidole* sp. E; *PheIP*, *Pheidole* sp. P; *Solt*, *Solenopsis tridens*; *Solv*, *Solenopsis virullens*; *SolB*, *Solenopsis* sp. B; *SolC*, *Solenopsis* sp. C; *Tetra*, *Tetramorium* sp. 1

$p = 0.01$; Figure 2a), but did not vary with CAD ($\chi^2 = 0.16$, $p = 0.69$) nor with the interaction between precipitation and CAD ($\chi^2 = 1.13$, $p = 0.28$). The number of interactions by high-quality dispersers likewise increased with increasing precipitation (GLMM: $\chi^2 = 4.17$, $df = 678$, $p = 0.04$, Figure 2b) and did not vary with CAD ($\chi^2 = 0.15$, $p = 0.70$) nor with the interaction between precipitation and CAD ($\chi^2 = 3.14$, $p = 0.07$). The number of interactions involving low-quality dispersers (50.5% of all interactions) did not vary with precipitation (GLMM: $\chi^2 = 2.32$, $df = 678$, $p = 0.12$), CAD ($\chi^2 = 0.23$, $p = 0.63$) or their interaction ($\chi^2 = 0.01$, $p = 0.97$).

Removal rates varied markedly among diaspore species: *S. obtusifolium*, 26.4%; *J. ribifolia*, 25.3%; *C. nepetaefolius*, 24%; *J. mutabilis*, 18.7%; *M. bahiensis*, 4.6%; and *S. ferruginea*, 0.34%. The most common ant species removing diaspores were *D. quadriceps* (40.5% of total removals), *Pheidole radoskowskii* (11.8%), *E. muticum* (8.1%) and *Solenopsis tridens* (6.6%). The largest ant species by far was the high-quality disperser, *D. quadriceps* (Table 1), and it was a particularly dominant disperser of the largest diaspores, especially fleshy-fruited *S. ferruginea* (100% of removals) and *S. obtusifolium* (86.5%), and myrmecochorous *J. mutabilis* (86.5%). It removed very few smaller diaspores such as those of *C. nepetaefolius* (0.95%) and *J. ribifolia* (no removal). The overall removal rate ranged from 4.6% to 44% per plot; it was positively related to precipitation (Figure 2c), but did not vary with CAD nor with the interaction between CAD and precipitation (Supporting Information Table S4). These patterns were also shown by high-quality dispersers (Figure 2d), whereas removal rates by low-quality dispersers did not vary with precipitation, CAD or their interaction (Supporting Information Table S5).

Diaspores were removed up to 27.5 m, with a mean of 3.61 ± 4.87 m (\pm SD). *Dinoponera quadriceps* was responsible for the longest mean removal distance (7.58 ± 4.49 m), followed by *E. muticum* (2.05 ± 1.54 m) and *Atta sexdens* (1.55 ± 1.35 m). Mean removal distance per plot varied from 0.06 to 5.94 m; it was positively related to precipitation (Figure 2e) but did not vary with CAD or the interaction between CAD and precipitation (Supporting Information Table S4). As was the case for removal rates, these patterns were also shown by high-quality dispersers (Figure 2f), whereas dispersal distances obtained by low-quality dispersers did not vary with precipitation, CAD or their interaction (Supporting Information Table S5).

Relationships between removal rates and distances with precipitation and CAD varied markedly among diaspore species. Both removal rates and distances increased with increasing precipitation for *J. mutabilis* and *S. obtusifolium* (Supporting Information Table S4 and Figure S2), and there was an interactive effect of precipitation and CAD on removal rate and distance for *J. mutabilis* (Supporting Information Table S4 and Figure S3). Moreover, precipitation positively affected both removal rate and distance by *D. quadriceps*, the most common ant seed-disperser species (Figure 2g,h, Supporting Information Table S5).

4 | DISCUSSION

Our study addressed the individual and interactive effects of CAD and aridity on seed dispersal by ants in Brazilian Caatinga in the

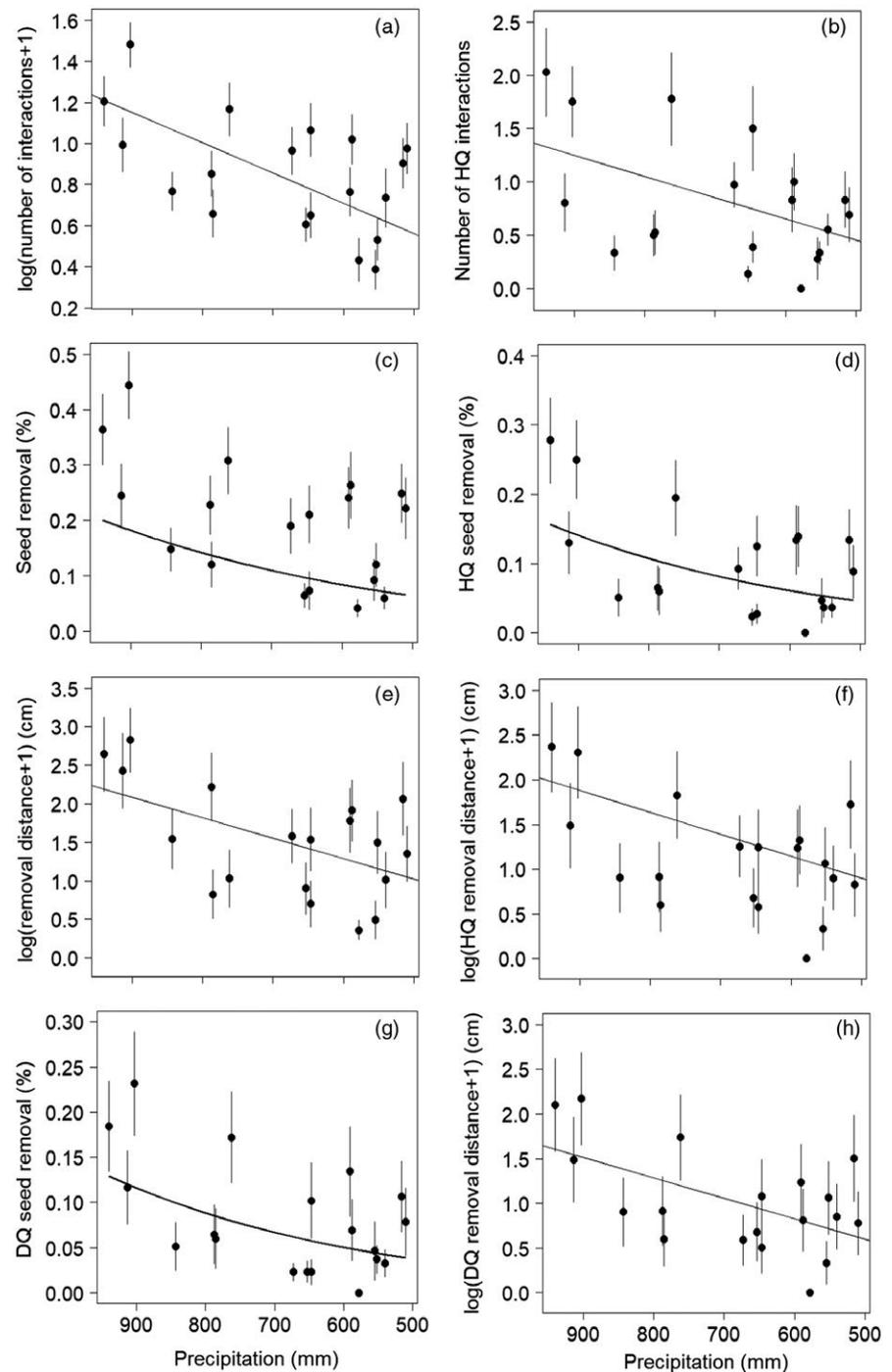


FIGURE 2 Number of interactions between diaspores and ants, removal rates and mean removal distances considering all ant species (a, c, e) and only high-quality ant dispersers (HQ) (b, d, f), and removal rate (g) and mean removal distance (h) considering only *Dinoponera quadriceps* (DQ) over the precipitation gradient at Catimbau National Park, Pernambuco, Brazil. Black dots represent means, and bars represent standard errors considering all stations per plot

context of predicting responses to disturbance under a future climate scenario. We first hypothesized that ant species providing high-quality dispersal services for myrmecochorous plants will also provide high-quality dispersal services for fleshy fruits. As predicted, the ant species that most rapidly removed myrmecochorous seeds and transport them the furthest distances did likewise for fleshy fruits. Previous studies have documented that large-bodied ants provide high-quality dispersal services exclusively for myrmecochorous seeds (Andersen & Morrison, 1998; Leal, Andersen, & Leal, 2014; Leal, Correia Neto Lima et al., (2014); Ness et al., 2004) or fleshy fruits (Christianini, Mayhé-Nunes, & Oliveira, 2012;

Passos & Oliveira, 2004). Our results indicate that the generalized nature of the relationship between disperser ants and myrmecochorous seeds can be extended further to fleshy fruits. For example, if benefits provided by ants to myrmecochorous plant species, like successful recruiting and seed/seedling post-dispersal protection (Beattie, 1985), can be spread to fleshy-fruit plant species (Christianini et al., 2007; Passos & Oliveira, 2004), so could also be spread the consequences of failures on seed dispersal services. Consequently, the proportion of Caatinga flora subjected to the pervasive effects of climate change and CAD on seed dispersal services must encompass also the non-myrmecochorous plant

species, especially species whose fruits and seeds show higher pulp or aril content (e.g. Leal et al., 2007).

Our second hypothesis was that increasing CAD and aridity would have similar effects on seed dispersal services, but we did not find evidence of this. The abundance of high-quality dispersers, number of interactions between ants and diaspores, rates of seed removal and mean removal distance all varied significantly with aridity, but not with CAD. We predicted that both increasing CAD and aridity would reduce the number of interactions between ants and diaspores, along with the quality of seed dispersal by ants by changing ant disperser species composition, and particularly by reducing the abundance of high-quality dispersers. This was not the case for CAD, but was true for aridity, because the abundance of the dominant high-quality disperser, *Dinoponera quadriceps*, decreased with increasing aridity. Of all disperser species, *D. quadriceps* had most interactions with diaspores, highest removal rates and by far the longest removal distances, and, as was the case for *D. quadriceps* abundance, all these variables were negatively affected by aridity. The importance of *D. quadriceps* as a high-quality disperser species is further illustrated by considering individual plant species. The two diaspore species with the highest removal rates, *Sideroxylon obtusifolium* and *Jatropha mutabilis*, both showed the same pattern of reduction in dispersal with increasing aridity as that of all species combined, and both were dispersed almost exclusively by *D. quadriceps*. Apparently, these diaspores are the most beneficial resources for *D. quadriceps* independently of diaspore type (myrmecochorous or fleshy-fruited). High-quality disperser ants show a strong preference for diaspore species with high elaiosome/seed size ratios (Hughes & Westoby, 1992b; Peters, Oberrath, & Böhning-Gaese, 2003; Reifenrath, Becker, & Poethke, 2012), and this is the case for *D. quadriceps* and *J. mutabilis*. However, *D. quadriceps* showed a similarly high preference for the fleshy-fruited diaspores of *S. obtusifolium*, probably because it possesses a large volume of pulp in relation to seed. The potential dispersal benefits provided by *D. quadriceps* are not only restricted to seed removal and transport, but also related to seed fate. Compared with control areas, post-dispersal seed predation is lower in areas near the nest entrances of *D. quadriceps* where dispersed seeds are deposited, and seedling abundance is more than twice as high (Leal et al., 2017). Therefore, the high-quality dispersal services provided by *D. quadriceps* extend to a positive influence on plant reproductive success following seed transport.

Although CAD modified overall ant species composition, it did not affect the abundance of any of the high-quality dispersers, and this explains why it had no effects on seed dispersal services. Such results are contrary to those of Leal, Andersen, & Leal, (2014), who found at another Caatinga location that CAD had negative effects on the abundance of high-quality dispersers and consequently on seed dispersal services by ants. However, our study was conducted on sandy soils while the previous study included clay soils, and Caatinga ant communities on sandy soils have been previously shown to be particularly resilient to CAD (Oliveira, Ribeiro-Neto, Andersen, & Leal, 2017). In addition, mean annual rainfall in the previous study was only 550 mm, at the arid extreme of our study, and this might

also be a factor explaining the higher sensitivity of seed-disperser ants to disturbance.

If differences in rainfall were a factor explaining different results in the two Caatinga localities, then this would indicate an interaction between CAD and aridity. However, contrary to our third hypothesis we found little evidence of such an interaction at Catimbau. We found interactive effects for only one diaspore species – removal rates and distances for diaspores of *J. mutabilis* declined with increasing aridity in less-disturbed areas, but they increased slightly with increasing aridity in more disturbed areas. Most studies that have found interactive effects between climate variables and anthropogenic disturbance were conducted at larger spatial scales than our study (Brook et al., 2008; Frishkoff et al., 2016; Gibb et al., 2015). For example, Gibb et al. (2015) found interactive effects of disturbance and precipitation on ant communities, but over a precipitation range from 500 mm to 3000 mm (more than five times the range in our study), and covered a broad range of ecosystem types. However, Rito et al. (2017) found interactive effects of CAD and aridity on plant communities at our study sites. They showed that CAD reduces plant diversity only in drier areas, suggesting high resilience in the wetter and more-productive end of the rainfall gradient. The higher sensitivity of plants compared with ants to disturbance at low-rainfall sites can be explained by the fact that resource extraction directly affects plants but not ants making ant community less prone to be affected by CAD (Ribeiro-Neto, Arnan, Tabarelli, & Leal, 2016).

We found little evidence of interactive effects of CAD and aridity on seed dispersal services provided by ants in our Caatinga study system. However, our findings of negative effects of aridity have important implications for the vulnerability of these seed dispersal services to climate change. To a large extent, high-quality seed dispersal services across our full rainfall gradient in Caatinga are provided by a single species, *Dinoponera quadriceps*, and its abundance and consequently the overall provision of dispersal services by ants declined markedly with increased aridity. The high sensitivity of ant dispersal services to increasing aridity can therefore be attributed to the functional rarity (sensu Violle et al., 2017) of *D. quadriceps* among seed-disperser ants, and it highlights the threat of low functional diversity to the maintenance of ecological services (Violle et al., 2017). *Dinoponera quadriceps* is the highest quality seed disperser elsewhere in Caatinga (Leal et al., 2007; Leal, Andersen, & Leal, 2014; Leal, Correia Neto Lima et al., 2014); Leal et al., 2017, and so low functional redundancy in high-quality disperser ants appears to be typical of the biome. Given that such a large proportion of species of the Caatinga flora are dispersed by ants (e.g. one quarter of local woody flora in Leal et al., 2007), such low functional redundancy has important implications for plant recruitment and, consequently, for the composition of plant communities under a future climate of lower rainfall. Other biomes with high concentrations of myrmecochores can also have low functional redundancy in high-quality disperser ants (Gove et al., 2007; Manzaneda & Rey, 2009; Ness, Morin, & Giladi, 2009), which makes them likewise vulnerable to the impacts of global change.

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AUTHORS' CONTRIBUTIONS

F.M.P.O., A.N.A. and I.R.L. conceived the ideas and designed the experiments. F.M.P.O. and G.B.A. collected the data. X.A. and J.D.R.-N. contributed to the statistical analysis. F.M.P.O. 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/doi:10.5061/dryad.n3t3f8h> (Oliveira et al., 2018).

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