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

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19

20 **Abstract**

21 1. Anthropogenic disturbance and climate change are the main drivers of biodiversity  
22 loss and ecological services around the globe. There is concern that climate change will  
23 exacerbate the impacts of disturbance and thereby promote biotic homogenization, but  
24 its consequences for ecological services are unknown.

25 2. We investigated the individual and interactive effects of increasing chronic  
26 anthropogenic disturbance (CAD) and aridity on seed dispersal services provided by  
27 ants in Caatinga vegetation of northeastern Brazil.

28 3. The study was conducted in Catimbau National Park, Pernambuco, Brazil. Within an  
29 area of 214 km<sup>2</sup>, we established nineteen 50 x 20 m plots that encompassed gradients of  
30 both CAD and aridity. We offered diaspores of six plant species, three myrmecochorous  
31 diaspores and three fleshy fruits that are secondarily dispersed by ants. We then  
32 quantified the number of interactions, seed removal rate and dispersal distances, and  
33 noted the identities of interacting ant species. Finally, we used pitfall trap data to  
34 quantify the abundances of ant disperser species in each plot.

35 4. Our results show that overall composition of ant disperser species varied along the  
36 gradients of CAD and aridity, but the composition of high-quality dispersers varied only  
37 with aridity. The total number of interactions, rates of removal and mean distance of  
38 removal all declined with increasing aridity, but they were not related to CAD. These  
39 same patterns were found when considering only high-quality disperser species, driven  
40 by the responses of the dominant disperser *Dinoponera quadriceps*. We found little  
41 evidence of interactive effects of CAD and aridity on seed dispersal services by ants.

42 5. Our study indicates that CAD and aridity act independently on ant-mediated seed  
43 dispersal services in Caatinga, such that the impacts of anthropogenic disturbance are  
44 unlikely to change under the forecast climate of increased aridity. However, our

45 findings highlight the vulnerability of seed dispersal services provided by ants in  
46 Caatinga under an increasingly arid climate due to low functional redundancy in high-  
47 quality disperser species. Given the large number of plant species dependent on ants for  
48 seed dispersal, this has important implications for future plant recruitment and,  
49 consequently, for the composition of Caatinga plant communities.

50

51 **Key-words:** human disturbance, climate change, biotic interactions, ant-plant  
52 mutualism, seasonally dry tropical forest.

53

54 **Introduction**

55 Both anthropogenic disturbance and climate change are primary conservation threats in  
56 virtually all ecosystems (Sala *et al.*, 2000), having the potential to rearrange species  
57 assemblages, with cascading effects on biotic interactions such as the disruption of  
58 mutualisms and the reduction of the provision of ecological services provided by these  
59 interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008; Kiers, Palmer, Ives,  
60 Bruno, & Bronstein, 2010). It has been suggested that anthropogenic disturbance and  
61 climate change may favour the same set of species, triggering a process of biotic  
62 homogenization (i.e. the reduction of multiple species assemblages into one overall  
63 simpler assemblage) that could make drier ecosystems similar to highly disturbed ones  
64 (Frishkoff *et al.*, 2016). Such homogenization is likely to reduce ecosystem resilience  
65 (Hirota, Holmgren, H Van Nes, & Scheffer, 2011) following the loss of key ecological  
66 services such as pollination and seed dispersal (Memmott, Craze, Wase, & Price, 2007;  
67 Tylianakis *et al.*, 2008; Hegland, Nielsen, Lázaro, Bjerknes, & Totland, 2009).  
68 Moreover, there is increasing concern that climate change might exacerbate the effects  
69 of anthropogenic disturbance by imposing an additional strong environmental filter in  
70 disturbed areas (Hirota *et al.*, 2011; Rito, Arroyo-Rodríguez, Querioz, Leal, &  
71 Tabarelli, 2017). However, the combined and interactive effects on biodiversity of  
72 anthropogenic disturbance and climate change remain poorly understood (Sirami *et al.*,  
73 2017; but see Brook, Sodhi, & Bradshaw, 2008; Gibb *et al.*, 2015; Frishkoff *et al.*,  
74 2016; Arnan, Arcoverde, Pie, Ribeiro-Neto, & Leal, 2018) and their consequences for  
75 ecological services are unknown.

76       Ants are providers of key ecological services in most terrestrial ecosystems (Del  
77 Toro, Ribbons, & Peline, 2012). The impacts of disturbance on ant communities acts  
78 primarily through habitat change (Andersen 2018), and an important determinant of

79 species responses is body size (Gibb *et al.*, 2018). Given that climate variables such as  
80 temperature and rainfall play major roles in shaping ant communities (Kaspari,  
81 O'Donnell, & Kercher, 2000; Dunn *et al.*, 2009), climate change can be expected to  
82 interact with disturbance in complex ways, including mediation or intensification of  
83 disturbance effects on ant communities and the ecological service ants provide (Gibb *et*  
84 *al.*, 2015). One such service is myrmecochory, a globally important seed dispersal  
85 syndrome found among 11,000 angiosperm species from 77 plant families (Lengyel,  
86 Gove, Latimer, Majer, & Dunn, 2009), whose diaspores possess a lipid-rich appendage  
87 (elaiosome) for attracting and aiding transport by ants (Berg, 1975). Ants typically  
88 transfer the diaspores to their nests, remove the elaiosome and discard the intact seed in  
89 nest galleries or outside refuse piles (Beattie, 1985) where they can germinate and  
90 establish (Hughes & Westoby, 1992a; Manzaneda & Rey, 2012). The effects of  
91 anthropogenic disturbance on myrmecochory can be highly variable (Philpott *et al.*,  
92 2010). Although some studies have shown negative effects (i.e. decreasing removal rate  
93 and dispersal distance; Almeida *et al.*, 2013; Leal, Andersen, & Leal, 2014; Rocha-  
94 Ortega, Bartichami, Neves, Bruna, & Vasconcelos, 2017), others have shown effects to  
95 be positive (i.e. increasing removal rate and dispersal distance; Parr *et al.*, 2007;  
96 Dominguez-Haydar *et al.*, 2011, Beaumont, Mackay, & Whalen, 2013) or neutral (Ness,  
97 2004).

98         Changes in the quality of seed dispersal services provided by ants are usually  
99 related to changes in composition of ant disperser species. Highest quality seed-  
100 dispersal services are typically provided by large-bodied ant species because they  
101 readily collect seeds and transport them over large distances (Andersen & Morrison,  
102 1998; Leal, Lima Neto, Oliveira, Andersen, & Leal, 2014). Large ant species are  
103 especially sensitive to disturbance (Leal, Andersen, *et al.*, 2014; Gibb *et al.*, 2018), and

104 this can result in severe reductions in the quality of seed-dispersal services in disturbed  
105 habitats (Ness, Bronstein, Andersen, & Holland, 2004; Gove, Majer, & Dunn, 2007;  
106 Almeida *et al.*, 2013; Leal, Andersen, *et al.*, 2014). Although smaller insects are  
107 considered more sensitive to high temperatures through desiccation (Kühnel *et al.*, 2017,  
108 Baudier *et al.* 2015), recent studies have found that the most sensitive ants to climate  
109 change are in fact the largest (Gibb *et al.*, 2018, Andrew *et al.*, 2019). The sensitivity of  
110 large-bodied ants to disturbance might therefore be exacerbated under climate change,  
111 further reducing the loss of seed-dispersal services provided by ants.

112         Seed dispersal by ants is not restricted to myrmecochorous plants, as ants can  
113 opportunistically disperse a wide variety of fleshy fruits (or seeds from them) after  
114 being attracted by the pulp (Böhning-Gaese, Gaese, & Rabemanantsoa, 1999; Pizo &  
115 Oliveira, 2006; Passos & Oliveira, 2003). By secondarily dispersing fleshy fruits, ants  
116 can positively affect seed fate and germination of diaspores primarily adapted for  
117 vertebrate dispersal (Levey & Bryne, 1993; Passos & Oliveira, 2004, Christianini,  
118 Mayhé-Nunes, & Oliveira, 2007). Given that anthropogenic disturbance often has a  
119 particularly severe impact on vertebrate species (Dirzo *et al.*, 2014) and consequently on  
120 the seed dispersal services provided by them (Estes *et al.*, 2011), the dispersal of fleshy  
121 fruits by ants might be especially important at disturbed sites (Christianini, Oliveira,  
122 Bruna, & Vasconcelos, 2014). Both fleshy fruits and elaiosomes are attractive to  
123 omnivorous ants, and so it could be expected that ants providing high-quality services to  
124 myrmecochorous plants (i.e. large-bodied species with large foraging ranges) would do  
125 likewise to plants producing fleshy fruits. If so, then CAD and aridity would have the  
126 same effects on both dispersal types, and therefore have a broader impact on plant  
127 communities. However, all this remains to be investigated.



128           Our study aims to investigate how anthropogenic disturbance and increasing  
129   aridity interact to influence ant-mediated seed dispersal (both myrmecochory and non-  
130   myrmecochory) in Caatinga, the largest and most diverse of the world's seasonally dry  
131   tropical forest (Silva, Leal, & Tabarelli, 2017) that is recognized as a global hotspot for  
132   myrmecochory (Leal *et al.*, 2007; Leal, Lima Neto, *et al.*, 2014; Leal, Andersen, *et al.*,  
133   2014; Leal, *et al.*, 2017). Anthropogenic disturbance has been previously shown to  
134   reduce the quality of ant-mediated seed dispersal services for myrmecochorous  
135   diaspores at one Caatinga site (Leal, Andersen, *et al.*, 2014). However, it is unclear how  
136   representative this is of Caatinga, given the marked variation in soils, rainfall and  
137   vegetation within the biome (Moro *et al.*, 2015). We specifically tested three  
138   hypotheses. Our first hypothesis is that ant species providing high-quality dispersal  
139   services for myrmecochorous plants will also provide high-quality dispersal services for  
140   fleshy fruits. We predict that the same ant species that most rapidly remove  
141   myrmecochorous seeds and transport them the furthest distances will do likewise for  
142   fleshy fruits. Our second hypothesis is that increasing anthropogenic disturbance has  
143   similar effects as increasing aridity on seed dispersal by ants. We predict that both  
144   increasing anthropogenic disturbance and aridity will reduce the number of interactions  
145   between diaspores and ants as well as the quality of seed dispersal services (i.e. seed  
146   removal rate and seed dispersal distance). We also predict that these effects are due to  
147   changes in ant disperser species composition, particularly a reduction in the abundance  
148   of high-quality seed dispersers. Our third hypothesis is that there are also interactive  
149   effects of anthropogenic disturbance and aridity, such that the effects of disturbance are  
150   contingent on the level of aridity. We predict that disturbance has a greater impact in  
151   more arid sites, due to the lower primary productivity conferring lower resilience to ant  
152   communities and, consequently, to seed dispersal services by ants.

153

## 154 **Materials and Methods**

### 155 STUDY AREA

156 Caatinga is a mosaic of seasonally dry tropical forests and scrub vegetation (Pennington  
157 et al. 2009) that covers 826,411 km<sup>2</sup> of northeastern Brazil (MMA, 2011) (Fig. S1). It is  
158 considered one of the most endangered ecosystems in Brazil due to extensive  
159 conversion to agriculture (45% of its area has been deforested; MMA, 2011). In  
160 addition, remaining vegetation is exploited by high densities of people (26 inhabitants /  
161 km<sup>2</sup>) who are highly dependent on forest resources for their livelihoods, and therefore  
162 exert high levels of chronic anthropogenic disturbance (CAD; *sensu* Singh, 1998;  
163 Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal, 2015; Rito *et al.*, 2017). Under  
164 future climate change, the Caatinga region is projected to receive about 22% less  
165 rainfall than it currently does (Magrin *et al.*, 2014).

166         Our study was conducted in Catimbau National Park, Pernambuco State  
167 (8°24'00" and 8°36'35" S; 37°0'30" and 37°1'40" W, Fig. S1). Mean annual rainfall varies  
168 markedly in Catimbau, from 1100 mm in the southeast to 480 mm in the northwest, and  
169 the mean temperature is 23°C (Rito *et al.*, 2017). Approximately 70% of its 607 km<sup>2</sup> is  
170 covered by quartzite sandy soils supporting low stature caatinga vegetation (Rito *et al.*,  
171 2017). The Park was created in 2002, and low-income rural populations still live in the  
172 park, using it for grazing and browsing by livestock, collection of living and dead wood,  
173 harvesting of non-timber forest products, and hunting (Rito *et al.* 2017).

174         We selected nineteen 20 x 50 m plots to cover a wide range of disturbance and  
175 annual rainfall based on RapidEye satellite imagery and field observations (Fig. S1). All  
176 plots were on sandy soil, had similar slope, and supported old-growth vegetation that  
177 had not experienced slash-and-burn agriculture for at least 50 years. Plots were

178 separated by a minimum of 2 km, and occurred within an area of 214.3 km<sup>2</sup> (Rito *et al.*,  
179 2017).

180

## 181 MEASUREMENT OF CAD AND ARIDITY

182 To characterize the level of CAD in the 19 plots, we computed a global multi-metric  
183 index that integrates eight disturbance indicators related to the three main sources of  
184 CAD in Catimbau (see Appendix S1 and Arnan, Leal *et al.*, 2018 for more details of  
185 how to calculate the global multi-metric index): livestock pressure (herbivory by goats  
186 and cattle), wood extraction (live and dead wood) and extraction of non-timber forest  
187 products (medicinal plants, food items for humans, hunting and livestock fodder). These  
188 CAD indicators were measured using three approaches: (1) Geographic distances based  
189 on remote sensing: Two distances were measured, proximity to the nearest house and  
190 proximity to the nearest road, using satellite imagery and ArcGIS 10.1 software. Since  
191 distance is inversely related to level of disturbance, we used the inverse of distance as  
192 our metric; (2) Interviews with local inhabitants: we identified the nearest village to  
193 each plot using GIS and then conducted informal and semi structured interviews to  
194 assess the number of people in each village, which we weighted by distance from the  
195 plots; and, (3) Measures of disturbance in the field: we conducted field assessments of  
196 goat trail length, goat dung, cattle dung, alive wood extraction (stem cuts) and coarse  
197 woody debris extraction (litter) within each plots (see Arnan, Leal, *et al.*, 2018 for more  
198 details). The index ranges from 2 to 58 (from the lowest to the highest disturbance  
199 intensity) among the plots.

200 To characterize the aridity gradient, data on mean annual precipitation were  
201 acquired from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis,  
202 2005). We downloaded the dataset at 30 arc seconds resolution

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

215

#### 216 SEED DISPERSAL BY ANTS

217 To quantify ant-mediated seed dispersal services, we used diaspores from six locally  
218 abundant plant species that represent the morphological range of diaspores dispersed by  
219 ants in the region: three myrmecochores (*Jatropha mutabilis*, *Jatropha ribifolia* and  
220 *Croton nepetaefolius*) and three fleshy-fruited (*Simaba ferruginea*, *Sideroxylon*  
221 *obtusifolium* and *Melocactus bahiensis*) (Table S1). Diaspores were collected earlier in  
222 the rainy season when our experiments were conducted, and were stored in paper bags  
223 at  $-20^{\circ}$  C prior to use. We observed ant-diaspore interactions at six stations separated by  
224 10 m along each of two parallel 50 m transects (separated by 20 m) established in each  
225 plot. At each station, five conspecific diaspores were placed on a white filter paper card  
226 (6 cm x 6 cm) as described in Leal, Andersen, *et al.* (2014). During each observation  
227 period, all diaspores on a transect were from the same species, and the two transects

228 within a plot had different species, one a myrmecochore and the other not. There were  
229 three observation periods (between March and May 2015 and in April 2016), such that  
230 all six diaspore species were observed once in each plot. Stations were monitored at 15-  
231 min intervals from 06:00 h to 18:00 h over one day for each monitoring period, and  
232 removed diaspores were not replaced. Any ant contact with a diaspore for the apparent  
233 purpose of feeding (i.e. ants manipulating the diaspores trying collect part of them) was  
234 considered as an interaction (Leal *et al.*, 2007), and different ant species could interact  
235 more than once with a diaspore (i.e. more than one interaction event for each diaspore).  
236 For each observed interaction, we recorded the identity of the ant species, whether or  
237 not the diaspore was removed (we considered a removal event when a diaspore was  
238 moved  $\geq 5$  cm), and the distance of any removal (defined as the displacement from the  
239 station to where the diaspore was either dropped or taken into an ant nest).

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

251

252 ABUNDANCE OF SEED-DISPERSER ANTS

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

260

## 261 DATA ANALYSES

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

268 To evaluate the effects of CAD, precipitation and their interaction on the  
269 composition of ant seed disperser species at the plot level (based on pitfall data), we  
270 conducted a Canonical Correspondence Analysis (CCA) using the frequency of  
271 occurrence of species as a measure of species abundance. We performed a  
272 randomization test (1000 aleatorizations) to obtain the statistical significance of  
273 explanatory variables. Further, we performed Spearman's correlations between the  
274 abundance of each ant disperser species and the CCA axes significantly associated with  
275 the CAD and aridity gradients considering the first two axes.

276 We used GLMMs with Poisson error distribution to analyse the effects of CAD,  
277 precipitation and their interaction on the total number of interactions between ants and

278 diaspores, and on the number of interactions performed by low- and high-quality  
279 dispersers separately. We also used GLMMs to evaluate the effects of CAD,  
280 precipitation and their interaction on removal rates and mean removal distances,  
281 considering all ant disperser species and high- and low-quality dispersers separately.  
282 For all these models, we used plot and diaspore species as random factors. Additionally,  
283 we built GLMMs to evaluate the effects of CAD, precipitation and their interaction on  
284 removal rates and mean removal distances for each diaspore species individually (using  
285 plot as a random factor), as well as for the four most common ant species removing the  
286 diaspores (using plot and diaspore species as random factors).

287         For all the removal rate-models we used a binomial error distribution, and for  
288 the removal distance models we used a Gaussian error distribution. Analyses were  
289 performed in R. We checked residuals for normality and homoscedasticity in all  
290 models. Data that did not meet homoscedastic criteria were  $\log(x) + 1$  transformed. We  
291 also checked for overdispersion in all models. When detected, we fitted a Poisson-  
292 lognormal model (Harrison, 2014). We used the packages *vegan* version 2.3 (Oksanen  
293 *et al.*, 2015) for CCA analysis and *lme4* version 1.1-7 (Bates *et al.*, 2004) to build the  
294 GLMM models.

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

299

## 300 **Results**

### 301 SEED-DISPERSER ANTS

302 We observed 1449 ant-diaspore interactions involving 33 ant species, with 66.1% of  
303 these interactions involving myrmecochorous seeds. Diaspores were removed in 60.6%  
304 of the interactions (68.5% for myrmecochorous seeds), involving 20 ant species (Table  
305 1). Two ant species were classified as high-quality dispersers: *Dinoponera quadriceps*  
306 and *Ectatomma muticum*, and they were responsible for 49% of all removals (48.6% for  
307 myrmecochorous seeds, 51.4% for fleshy fruits). Low-quality dispersers were species of  
308 *Dorymyrmex*, *Pheidole*, *Solenopsis* and *Tetramorium* (Table 1). The abundance of high-  
309 quality dispersers (*D. quadriceps* and *E. muticum*) based on pitfall catches was  
310 positively correlated with the removal rates from observation stations for  
311 myrmecochorous seeds (Spearman's  $r = 0.35$ ,  $p = 0.05$ ), fleshy fruits ( $r = 0.45$ ,  $p =$   
312  $0.04$ ) and all diaspores ( $r = 0.53$ ,  $p = 0.02$ ). It was also positively correlated with mean  
313 dispersal distance for myrmecochorous seeds (Spearman's  $r = 0.61$ ,  $p < 0.01$ ), fleshy  
314 fruits ( $r = 0.34$ ,  $p = 0.05$ ) and all diaspores ( $r = 0.52$ ,  $p = 0.02$ ). Removal rates by high-  
315 quality dispersers did not vary with diaspore type (GLMM:  $F = 3.67$ ,  $p = 0.19$ ) and this  
316 same pattern was found for mean removal distance (GLMM:  $F = 4.03$ ,  $p = 0.18$ ).

317         According to our CCA, the composition of ant disperser species varied  
318 significantly with precipitation ( $F_{1,15} = 1.96$ ,  $p = 0.03$ , Fig. 1) and CAD ( $F_{1,15} = 1.91$ ,  $p =$   
319  $0.04$ , Fig. 1), but not with their interaction ( $F_{1,15} = 1.44$ ,  $p = 0.19$ , see Table S2 for more  
320 details on CCA results). Precipitation was associated with axis 1 while CAD was  
321 associated with axis 2. The abundance of *D. quadriceps* increased with increasing  
322 precipitation (Spearman's  $r = 0.74$ ,  $p < 0.01$ ), but that of *E. muticum* decreased  
323 (Spearman's  $r = -0.48$ ,  $p = 0.04$ ). However, CAD had no effect on the abundance of  
324 either ant species (Spearman's  $r = -0.05$ ,  $p = 0.82$ ; and Spearman's  $r = 0.14$ ,  $p = 0.56$  for  
325 *D. quadriceps* and *E. muticum* respectively). The responses of the abundance of low-  
326 quality dispersers were highly variable among species. For example, CAD was



327 negatively related to the abundance of *Solenopsis* sp. 1 (Spearman's  $r = -0.47$ ,  $p = 0.04$ ),  
328 but positively to that of *Acromyrmex rugosus* (Spearman's  $r = 0.50$ ,  $p = 0.03$ ).  
329 Similarly, increasing precipitation was negatively related to the abundance of *Solenopsis*  
330 *virullens* (Spearman's  $r = -0.51$ ,  $p = 0.02$ ), but positively for *Dorymyrmex thoracicus*  
331 (Spearman's  $r = 0.54$ ,  $p = 0.01$ ) and *Pheidole* sp. C (Spearman's  $r = 0.59$ ,  $p < 0.01$ ,  
332 Table S3).

333

### 334 *Seed dispersal*

335 The number of interactions per plot ranged from 27 to 144. It increased with increasing  
336 precipitation (GLMM:  $\chi^2 = 5.94$ ,  $DF = 678$ ,  $p = 0.01$ ; Fig. 2a), but did not vary with  
337 CAD ( $\chi^2 = 0.16$ ,  $p = 0.69$ ) nor with the interaction between precipitation and CAD ( $\chi^2 =$   
338  $1.13$ ,  $p = 0.28$ ). The number of interactions by high-quality dispersers likewise  
339 increased with increasing precipitation (GLMM:  $\chi^2 = 4.17$ ,  $DF = 678$ ,  $p = 0.04$ , Fig. 2b),  
340 and did not vary with CAD ( $\chi^2 = 0.15$ ,  $p = 0.70$ ) nor with the interaction between  
341 precipitation and CAD ( $\chi^2 = 3.14$ ,  $p = 0.07$ ). The number of interactions involving low-  
342 quality dispersers (52% of all interactions) did not vary with precipitation (GLMM:  $\chi^2 =$   
343  $2.32$ ,  $DF = 678$ ,  $p = 0.12$ ), CAD ( $\chi^2 = 0.23$ ,  $p = 0.63$ ), or their interaction ( $\chi^2 = 0.01$ ,  $p =$   
344  $0.97$ ).

345 Removal rates varied markedly among diaspore species: *S. obtusifolium*, 40.2%;  
346 *J. ribifolia*, 38.6%; *C. nepetaefolius*, 33.7%; *J. mutabilis*, 28.6%; *M. bahiensis*, 7%; and  
347 *S. ferruginea*, 0.53%. The most common ant species removing diaspores were *D.*  
348 *quadriceps* (41.2% of total removals), *Pheidole radoskowskii* (12.2%), *E. muticum*  
349 (8.1%) and *Solenopsis tridens* (6.3%). The largest ant species by far was the high-  
350 quality disperser *D. quadriceps* (Table 1), and it was a particularly dominant disperser  
351 of the largest diaspores, especially fleshy-fruited *S. ferruginea* (100% of removals) and

352 *S. obtusifolium* (94.3%), and myrmecochorous *J. mutabilis* (92.2%). It removed very  
353 few smaller diaspores such as those of *C. nepetaefolius* (1.1%) and *J. ribifolia* (no  
354 removal). The overall removal rate ranged from 4.6% to 44% per plot; it was positively  
355 related to precipitation (Fig. 2c), but did not vary with CAD nor with the interaction  
356 between CAD and precipitation (Table S4). These patterns were also shown by high-  
357 quality dispersers (Fig. 2d), whereas removal rates by low-quality dispersers did not  
358 vary with precipitation, CAD or their interaction (Table S5).

359         Diaspores were removed up to 27.5 m, with a mean of  $3.72 \pm 2.05$  m ( $\pm$  SD).  
360 *Dinoponera quadriceps* was responsible for the longest mean removal distance ( $7.67 \pm$   
361  $4.49$  m), followed by *Atta sexdens* ( $1.55 \pm 1.35$  m) and *E. muticum* ( $0.90 \pm 1.54$  m)  
362 (Table 1). Mean removal distance per plot varied from 0.06 to 5.94 m; it was positively  
363 related to precipitation (Fig. 2e) but did not vary with CAD or the interaction between  
364 CAD and precipitation (Table S4). As was the case for removal rates, these patterns  
365 were also shown by high-quality dispersers (Fig. 2f), whereas dispersal distances  
366 obtained by low-quality dispersers did not vary with precipitation, CAD or their  
367 interaction (Table S5).

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

375

376 **Discussion**

377 Our study addressed the individual and interactive effects of CAD and aridity on seed  
378 dispersal by ants in Brazilian Caatinga in the context of predicting responses to  
379 disturbance under a future climate scenario. We first hypothesized that ant species  
380 providing high-quality dispersal services for myrmecochorous plants will also provide  
381 high-quality dispersal services for fleshy fruits. As predicted, the ant species that most  
382 rapidly removed myrmecochorous seeds and transport them the furthest distances did  
383 likewise for fleshy fruits. Previous studies have documented that large-bodied ants  
384 provide high-quality dispersal services exclusively for myrmecochorous seeds  
385 (Andersen & Morrison, 1998; Ness *et al.*, 2004; Leal, Lima Neto, *et al.*, 2014; Leal,  
386 Andersen, *et al.*, 2014) or fleshy fruits (Passos & Oliveira, 2004; Christianini &  
387 Oliveira, 2009; Christianini, Mayhé-Nunes, & Oliveira, 2012). Our results indicate that  
388 the generalised nature of the relationship between disperser ants and myrmecochorous  
389 seeds can be extended further to fleshy fruits. For example, if benefits provided by ants  
390 to myrmecochorous plant species, like successful recruiting and seed/seedling post-  
391 dispersal protection (Beattie, 1985; Giladi, 2006) can be spread to fleshy-fruit plant  
392 species (Passos & Oliveira, 2004; Christianini *et al.*, 2007), so could also be spread the  
393 consequences of failures on seed dispersal services. Consequently, the proportion of  
394 Caatinga flora subjected to the pervasive effects of climate change and CAD on seed  
395 dispersal services must encompass also the non-myrmecochorous plant species,  
396 especially species whose fruits and seeds show higher pulp or aril content (e.g. Leal *et*  
397 *al.*, 2007).

398 Our second hypothesis was that increasing CAD and aridity would have similar  
399 effects on seed dispersal services, but we did not find evidence of this. The abundance  
400 of high-quality dispersers, number of interactions between ants and diaspores, rates of  
401 seed removal, and mean removal distance all varied significantly with aridity, but not

402 with CAD. We predicted that both increasing CAD and aridity would reduce the  
403 number of interactions between ants and diaspores, along with the quality of seed  
404 dispersal by ants by changing ant disperser species composition, and particularly by  
405 reducing the abundance of high-quality dispersers. This was not the case for CAD, but  
406 was true for aridity, because the abundance of the dominant high-quality disperser,  
407 *Dinoponera quadriceps*, decreased with increasing aridity. Of all disperser species, *D.*  
408 *quadriceps* had most interactions with diaspores, highest removal rates and by far the  
409 longest removal distances, and, as was the case for *D. quadriceps* abundance, all these  
410 variables were negatively affected by aridity. The importance of *D. quadriceps* as a  
411 high-quality disperser species is further illustrated by considering individual plant  
412 species. The two diaspore species with the highest removal rates, *Sideroxylon*  
413 *obtusifolium* and *Jatropha mutabilis*, both showed the same pattern of reduction in  
414 dispersal with increasing aridity as that of all species combined, and both were  
415 dispersed almost exclusively by *D. quadriceps*. Apparently, these diaspores are the most  
416 beneficial resources for *D. quadriceps* independently of diaspore type (myrmecochorous  
417 or fleshy-fruited). High-quality disperser ants show a strong preference for diaspore  
418 species with high elaiosome/seed-size ratios (Hughes & Westoby, 1992b; Peters *et al.*,  
419 2003; Reinferath, Becker, & Poethke, 2012), and this is the case for *D. quadriceps* and  
420 *J. mutabilis*. However, *D. quadriceps* showed a similarly high preference for the fleshy-  
421 fruited diaspores of *S. obtusifolium*, probably because it possesses a large volume of  
422 pulp in relation to seed. The potential dispersal benefits provided by *D. quadriceps* are  
423 not restricted to seed removal and transport, but also relate to seed fate. Compared with  
424 control areas, post-dispersal seed predation is lower in areas near the nest entrances of  
425 *D. quadriceps* where dispersed seeds are deposited, and seedling abundance is more  
426 than twice as high (Leal *et al.*, 2017). Therefore, the high-quality dispersal services

427 provided by *D. quadriceps* extend to a positive influence on plant reproductive success  
428 following seed transport.

429         Although CAD modified overall ant species composition, it did not affect the  
430 abundance of any of the high-quality dispersers, and this explains why it had no effects  
431 on seed dispersal services. Such results are contrary to those of Leal, Andersen, *et al.*  
432 (2014), who found at another Caatinga location that CAD had negative effects on the  
433 abundance of high-quality dispersers and consequently on seed dispersal services by  
434 ants. However, our study was conducted on sandy soils while the previous study  
435 included clay soils, and Caatinga ant communities on sandy soils have been previously  
436 shown to be particularly resilient to CAD (Oliveira, Ribeiro-Neto, Andersen, & Leal,  
437 2017). In addition, mean annual rainfall in the previous study was only 550 mm, at the  
438 arid extreme of our study, and this might also be a factor explaining the higher  
439 sensitivity of seed-disperser ants to disturbance.

440         If differences in rainfall were a factor explaining different results in the two  
441 Caatinga localities then this would indicate an interaction between CAD and aridity.  
442 However, contrary to our third hypothesis we found little evidence of such an  
443 interaction at Catimbau. We found interactive effects for only one diaspore species -  
444 removal rates and distances for diaspores of *J. mutabilis* declined with increasing aridity  
445 in less-disturbed areas, but they increased slightly with increasing aridity in more  
446 disturbed areas. Most studies that have found interactive effects between climate  
447 variables and anthropogenic disturbance were conducted at larger spatial scales than our  
448 study (Brook *et al.*, 2008; Gibb *et al.*, 2015; Frishkoff *et al.*, 2016). For example, Gibb  
449 *et al.* (2015) found interactive effects of disturbance and precipitation on ant  
450 communities, but over a precipitation range from 500 mm to 3000 mm (more than five  
451 times the range in our study), and covered a broad range of ecosystem types. However,

452 Rito *et al.* (2017) found interactive effects of CAD and aridity on plant communities at  
453 our study sites. They showed that CAD reduces plant diversity only in drier areas,  
454 suggesting high resilience in the wetter and more-productive end of the rainfall gradient.  
455 The higher sensitivity of plants compared with ants to disturbance at low-rainfall sites  
456 can be explained by the fact that resource extraction directly affects plants but not ants  
457 making ant community less prone to be affected by CAD (Ribeiro-Neto, Arnan,  
458 Tabarelli, & Leal, 2016).

459 We found little evidence of interactive effects of CAD and aridity on seed-  
460 dispersal services provided by ants in our Caatinga study system. However, our findings  
461 of negative effects of aridity have important implications for the vulnerability of these  
462 seed dispersal services to climate change. To a large extent, high-quality seed-dispersal  
463 services across our full rainfall gradient in Caatinga are provided by a single species,  
464 *Dinoponera quadriceps*, and its abundance and consequently the overall provision of  
465 dispersal services by ants declined markedly with increased aridity. The high sensitivity  
466 of ant dispersal services to increasing aridity can therefore be attributed to the functional  
467 rarity (*sensu* Violle *et al.*, 2017) of *D. quadriceps* among seed disperser ants, and it  
468 highlights the threat of low functional diversity to the maintenance of ecological  
469 services (Violle *et al.*, 2017). *Dinoponera quadriceps* is the highest-quality seed  
470 disperser elsewhere in Caatinga (Leal *et al.*, 2007, 2017; Leal, Lima Neto, *et al.*, 2014;  
471 Leal, Andersen, *et al.*, 2014), and so low functional redundancy in high-quality  
472 disperser ants appears to be typical of the biome. Given that such a large proportion of  
473 species of the Caatinga flora are dispersed by ants (e.g. one quarter of local woody flora  
474 in Leal *et al.*, 2007), such low functional redundancy has important implications for  
475 plant recruitment and, consequently, for the composition of plant communities under a  
476 future climate of lower rainfall. Other biomes with high concentrations of

477 myrmecochores can also have low functional redundancy in high-quality disperser ants  
478 (Gove *et al.*, 2007; Manzaneda & Rey, 2009; Ness *et al.*, 2009), which makes them  
479 likewise vulnerable to the impacts of global change.

480

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498

#### 499 **Authors’ contributions**

500 FMPO, ANA and IRL conceived the ideas and designed the experiments. FMPO and  
501 GBA collected the data. XA and JDR contributed to the statistical analysis. FMPO

502 conducted the analyses and coordinated the writing of the manuscript. All the authors  
503 significantly contributed to the manuscript drafts and gave their final approval for  
504 submission.

505

#### 506 **Data accessibility**

507 The data are available from the Dryad Digital Repository: (XXXXXX)

508

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**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, Arcoverde, et al., 2018).

Ant species	Mean ( $\pm$ SD) Weber's length (mm)	Number of removed seeds		Mean removal distance (cm)	
		M	F	M	F
<b>High-Quality dispersers</b>					
<i>Dinoponera quadriceps</i>	8.8 $\pm$ 0.28	143	206	663.8 $\pm$ 483.6	816.5 $\pm$ 426.7
<i>Ectatomma muticum</i>	3.6 $\pm$ 0.30	61	10	212.4 $\pm$ 121.7	200.1 $\pm$ 138.5
<b>Low-Quality dispersers</b>					
<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 ± 0.09	1	0	5.0 ± 0.0	-
<i>Pheidole radoskowskii</i>	0.8 ± 0.04	99	3	15.1 ± 23.7	4.7 ± 0.7
<i>Pheidole sp.A</i>	0.8 ± 0.12	1	0	8.0 ± 0.0	-
<i>Pheidole sp.B</i>	0.6 ± 0.09	14	0	9.1 ± 4.6	-
<i>Pheidole sp.C</i>	0.6 ± 0.03	19	1	17.1 ± 35.0	5.0 ± 0.0
<i>Pheidole sp.D</i>	0.8 ± 0.06	13	3	7.6 ± 6.0	6.3 ± 3.7
<i>Pheidole sp.E</i>	0.6 ± 0.06	27	1	12.0 ± 11.9	5.0 ± 0.0
<i>Pheidole sp.P</i>	0.7 ± 0.03	4	0	9.1 ± 7.3	-
<i>Pheidole triconstricta</i>	0.9 ± 0.03	2	0	6.0 ± 1.0	-
<i>Solenopsis sp.B</i>	0.8 ± 0.05	2	0	10.0 ± 5.6	-
<i>Solenopsis sp.C</i>	0.7 ± 0.07	3	0	5.3 ± 2.8	-
<i>Solenopsis tridens</i>	0.4 ± 0.04	55	0	10.8 ± 12.9	-
<i>Solenopsis virullens</i>	0.4 ± 0.07	22	0	16.4 ± 20.7	-
<i>Tetramorium sp.A</i>	0.4 ± 0.05	1	0	40.0 ± 0.0	-

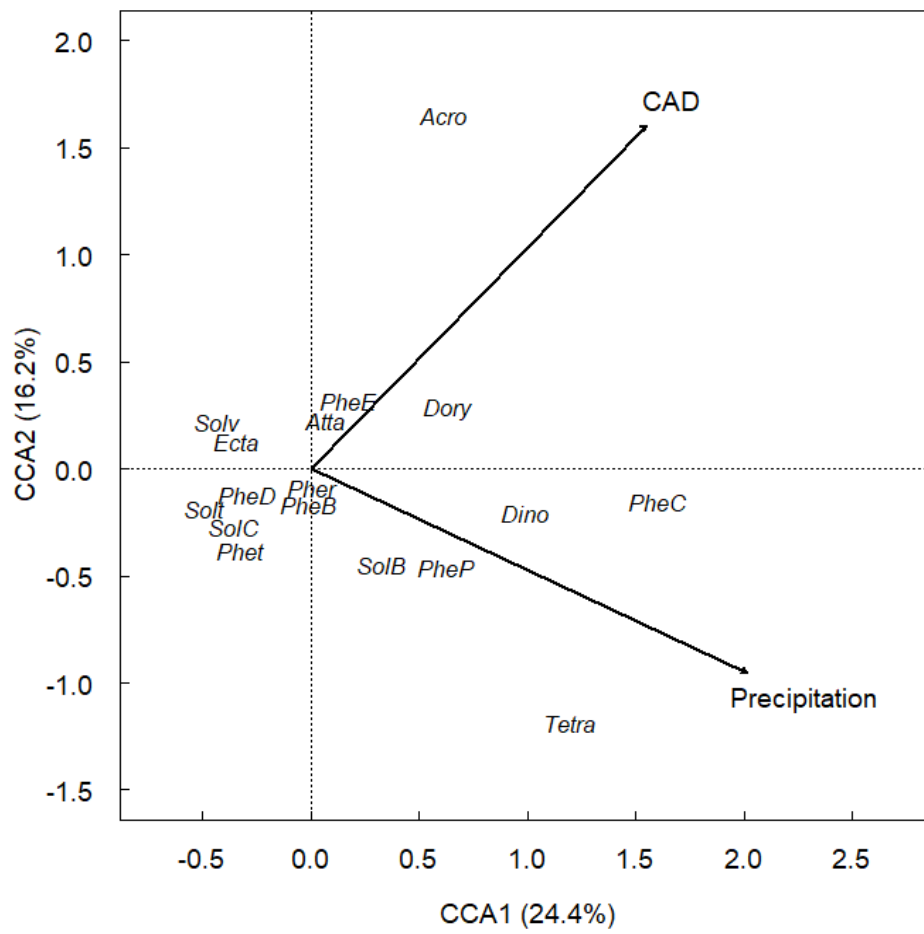
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## Figure legends

**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 quadriciceps*; *Dory*, *Dorymyrmex thoracicus*; *Ecta*, *Ectatomma muticum*; *Pheir*, *Pheidole radoskowskii*; *Pheit*, *Pheidole triconstricta*; *PheB*, *Pheidole* sp. B; *PheC*, *Pheidole* sp. C; *PheD*, *Pheidole* sp. D; *PheiE*, *Pheidole* sp. E; *PheiP*, *Pheidole* sp. P; *Solt*, *Solenopsis tridens*; *Solv*, *Solenopsis virulens*; *SolB*, *Solenopsis* sp. B; *SolC*, *Solenopsis* sp. C; *Tetra*, *Tetramorium* sp. 1.

**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 quadriciceps* (*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.

**Figure 1**



**Figure 2**

