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1 **Divergent responses of plant reproductive strategies to chronic anthropogenic disturbance and aridity in the Caatinga dry forest**

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23

#### 24 **Highlights**

- 25 • Disturbance and aridity affect Caatinga plant reproductive traits in different ways
- 26 • Aridity/disturbance reduced the richness of specialist pollination in the Caatinga
- 27 • Increases in aridity reduced the richness of animal-dispersed plants in the Caatinga
- 28 • Chronic anthropogenic disturbance affects the reproductive functional diversity
- 29 • Chronic anthropogenic disturbance and aridity threaten plant-animal interactions

30

#### 31 **Abstract**

32 Anthropogenic disturbance and climate change are major threats to biodiversity persistence and functioning of many tropical ecosystems.  
33 Although increases in the intensity of anthropogenic disturbance and climate change are associated with reduced taxonomic, phylogenetic and

34 functional diversities of several organisms, little is known about how such pressures interfere with the distribution of plant reproductive traits in  
35 seasonally dry tropical forests. Here we test the hypothesis that individual and combined effects of increasing chronic anthropogenic disturbance  
36 and water deficit negatively affect the richness, abundance and diversity of specialized reproductive strategies of native woody plants in the  
37 Caatinga dry forest. This study was carried out at the Catimbau National Park, northeastern Brazil (62,294ha). Chronic anthropogenic  
38 disturbance intensity was measured through different sources of disturbance (cattle/goat herbivory, wood extraction, and other people pressures).  
39 Water deficit data was obtained from hydrological maps and used as a proxy of aridity. We constructed generalized linear models and selected  
40 best-supported models for richness, abundance and functional diversity of reproductive traits. We documented that richness and abundance of  
41 plants with certain reproductive traits, regardless the specialization, can increase (in 18 out of the 49 trait categories analyzed; e.g. obligatory  
42 cross-pollination in response to increases in aridity and wood extraction), be impaired (in 20 categories; e.g. pollination by Sphingids/beetles  
43 with increase in aridity), or remain unchanged (in 21 categories; e.g. pollination by vertebrates with increases in chronic anthropogenic  
44 disturbance and aridity) with higher disturbance and aridity. There were combined effects of chronic anthropogenic disturbance and aridity on the  
45 richness of plants in nine traits (e.g. pollen flowers; dioecious and self-incompatible plants). Aridity affected 40% of the reproductive traits, while  
46 chronic anthropogenic disturbance affected 35.5%. The functional diversity of reproductive traits was affected only by disturbance. Changes in  
47 plant community structure promoted by chronic anthropogenic disturbance and aridity will likely threaten plant-animal interactions, thereby  
48 compromising the functioning of communities and the persistence of biodiversity in the Caatinga.

49

50 **Keywords:** floral traits, fruits type, functional diversity, pollination, reproductive biology, SDTF.

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## 51 **1. Introduction**

52 The accelerated expansion of human activities in tropical regions has converted extensive old-growth forest areas into much smaller remnants of  
53 old-growth and secondary forests, under different landscape contexts (Hansen et al., 2013; Keenan et al., 2015). As natural vegetation is  
54 converted into *human-modified tropical landscapes* (HMTLs), remaining forest areas are exposed to several sources of anthropogenic  
55 disturbance (e.g. Tabarelli et al., 2004; Leal et al., 2005; Pennington et al., 2006). Chronic anthropogenic disturbance, mainly represented by  
56 extensive livestock overgrazing and timber and non-timber extraction, is characterized by a long history of low-intensity but high-frequency  
57 biomass depletion (Singh, 1998; Martorell and Peters, 2005). The main consequences of augmented chronic anthropogenic disturbance in  
58 tropical forests is associated with the reduction of taxonomic, phylogenetic and functional diversity of several organisms (e.g. Martin and  
59 Possingham, 2005; Shahabuddin and Kumar, 2006; Ribeiro et al., 2015, 2016, 2019; Rito et al. 2017a; Arnan et al. 2018a), the disruption of  
60 ecological interactions, and compromised functioning and maintenance of communities (e.g. Leal et al., 2014, 2015; Xiao et al., 2016; Câmara et  
61 al., 2018). In addition, changes in land use are associated with increases in greenhouse gas emissions and biogeophysical and biogeochemical  
62 changes, which alter climatic conditions and water availability at local to regional scales (e.g. Levis, 2010; Mahmood et al., 2014). Climatic  
63 change inherent to the expansion of HMTLs, may also amplify the effects of anthropogenic disturbance (e.g. Hirota et al., 2011; Ponce-Reyes et  
64 al., 2013; Frishkoff et al., 2016; Maestre et al., 2016) and degrade biodiversity and forest dynamics in tropical regions.

65 Dry forests account for 40-43% of all tropical forests (Miles et al., 2006) and contain high levels of biodiversity (Silva et al., 2017) but  
66 harbor ~38% of the global human population, which often extract natural resources from these forests (Safriel and Adeel, 2005). Tropical dry

67 forests are also threatened by climate change (e.g. Silva et al., 2019). Specifically, increases in temperature associated with reductions in rainfall  
68 levels and more frequent extreme droughts, may result in a significant increase in late 21<sup>st</sup>-century aridity (IPCC, 2014; Goslin and Arnell, 2016).  
69 In fact, some tropical dry forest ecosystems are already responding to climate change (Allen et al., 2010). Aridity (or water deficit is defined as  
70 the difference between the amount of rainfall and temperature-driven evapotranspiration) in these forests acts by selecting plant species that use  
71 available soil water more efficiently, directly influencing species composition and plant community structure (Hulshof et al., 2013; Silva and  
72 Souza, 2018). Increases in aridity may alter the life cycle of plants from their establishment, through growth and reproduction, up to diaspore  
73 dispersal (Nunes et al., 2017). Aridity therefore favors species with (1) lower stature (Gross et al., 2013), (2) annual cycles, (3) ephemeral  
74 flowering and (4) wind dispersal (Nunes et al., 2017). In addition, plant responses to variations in soil water availability may negatively influence  
75 the attractiveness of pollinators through changes in floral traits, such as reduced flower numbers and size (e.g. Galen et al., 1999; Mal and Lovett-  
76 Doust, 2005; Caruso, 2006; Waser and Price, 2016). Wholesale changes in ecosystem functioning and dynamics may result from climate change  
77 intensification (Valencia et al., 2015; Nunes et al., 2017). The effects of chronic anthropogenic disturbance and aridity on plant communities may  
78 act synergistically, as the effects of one source of disturbance may positively or negatively augment the effects of aridity (Martorell et al., 2015;  
79 Rito et al., 2017a, b). Understanding how tropical dry forests simultaneously respond to these major drivers is extremely important especially in  
80 contexts where chronic anthropogenic disturbance combines with climate change to exert dramatic effects on species persistence.

81 The functional traits of organisms are intimately related to environmental conditions and generally associated with community assembly  
82 and ecosystem functioning (Díaz and Cabido, 2001; Petchey and Gaston, 2002; Bello et al., 2010). It has been well documented that plant species

83 with specialized reproductive life-history traits such as supra-annual flowering (i.e. one event every two years), pollination by vertebrates (e.g.  
84 bats and hummingbirds), self-incompatible reproductive system (i.e. obligatory cross-pollination), large seeds and dispersal by animals are  
85 negatively affected by depletion of biomass, fragmentation and habitat loss mediated by acute anthropogenic actions (Tabarelli et al., 2004; Girão  
86 et al., 2007; Lopes et al., 2009; Tabarelli et al., 2010; Sobrinho et al., 2016). Alternatively, increases in chronic anthropogenic disturbance and  
87 aridity resulted in reduced diversity of ant (e.g. Arnan et al., 2018b) and, vegetative plants traits (e.g. Arnan et al., 2018b; Ribeiro et al., 2016;  
88 Sfair et al., 2018) and changes in the structure of interaction networks of plants with extrafloral nectaries and ants (Câmara et al., 2019), as well  
89 as between diaspores and ants (Oliveira et al., 2019) in seasonally dry tropical forests. Chronic anthropogenic disturbance may also positively  
90 affect the abundance of *Croton sonderianus* and *Jatropha mollisiima* (Euphorbiaceae) (Rito et al., 2017b), which are both pollinated by  
91 generalist vectors, have self-compatible reproductive system and autochoric dispersed seeds (e.g. Machado and Lopes, 2004). Meanwhile,  
92 reductions in water availability decreased the abundance of rare plant species, such as *Libidibia ferrea* (Leguminosae) and *Handroanthus*  
93 *impetiginosus* (Bignoniaceae) (Rito et al., 2017a), both pollinated by specialist vectors (e.g. Machado and Lopes, 2004). However, the individual  
94 and combined effects of chronic anthropogenic disturbance and aridity on plant reproductive strategies in seasonally dry tropical forests (SDTFs)  
95 are yet to be well understood.

96 The Caatinga Phytogeographic Domain, one of the largest expanses of SDTF on Earth, is endemic to Brazil and occurs within an area of  
97 ~910,000 km<sup>2</sup> (Silva et al., 2017). The Caatinga flora is considered to be the most diversified among SDTFs, sheltering 31 endemic plant genera  
98 (Queiroz et al., 2017), and is represented by a mosaic of SDTF and shrub vegetation (Sampaio, 1995). In total, some 28 million people inhabit



99 the Caatinga (Silva et al., 2017), exerting intensive activities such as subsistence farming, raising domestic herbivore livestock, and chronic  
100 extraction of timber and non-timber forest products (e.g. Leal et al., 2005; Ramos et al., 2008; Ribeiro et al., 2015; Arnan et al., 2018a). In  
101 addition, climatic predictions for the Caatinga region indicate temperature increases of up to 6°C, decreases of 22% in rainfall (Chou et al., 2014;  
102 Magrin et al., 2014), and a 70% reduction in water discharge in the São Francisco River over the next 100 years (Chou et al., 2014), all of which  
103 will result in increased aridity.

104 Here we seek to understand how individual and combined effects of increasing chronic anthropogenic disturbance and water  
105 deficit/aridity interfere with the composition and diversity of reproductive strategies of Caatinga woody flora. First, we describe the richness and  
106 abundance of reproductive traits and strategies of woody plants of the Caatinga. Based on these frequencies, we test the hypothesis that isolated  
107 and synergistic increases in chronic anthropogenic disturbance and aridity levels negatively interfere with the diversity of specialized  
108 reproductive strategies of woody species. We predict that (1) individual increases in chronic anthropogenic disturbance and aridity are associated  
109 with (i) reduction in the richness and abundance of plants with specialized reproductive strategies (e.g. self-incompatible reproductive system,  
110 mandatory cross-pollination system, vertebrate pollination systems and biotic dispersal), and (ii) lower diversity of these reproductive strategies;  
111 and (2) the combination of these drivers will intensify the negative effects on the richness, abundance and functional diversity of specialized  
112 reproductive strategies.

113

## 114 **2. Material and methods**

115 *2.1. Study area*

116 This study was carried out at the Catimbau National Park, state of Pernambuco, Brazil (8°24'00" to 8°36'35" S, 37°09'30" to 37°14'40" W),  
117 spanning an area of 62,294 ha (Freire, 2015). The climate is semiarid, hot and dry: BSh (Köppen, 1948), with a mean annual temperature of  
118 25°C, and annual rainfall ranging between 450 and 1,100 mm (Freire, 2015). Deep sandy soils are predominant in Catimbau National Park  
119 (quartzite sands, 70% of area), but planosols and lithosols are also present (Sociedade Nordestina de Ecologia, 2002). The vegetation is a mosaic  
120 of low stature dry forest and scrub vegetation due to geomorphological, topographic and climatic factors related to temperature and rainfall  
121 (Andrade-Lima, 1981; Rodal et al., 1998). The most representative plant families at Catimbau National Park in terms of species richness and  
122 abundance are Leguminosae and Euphorbiaceae (Rito et al., 2017a). The Park was officially designated as a strict protected area in 2002, as the  
123 core area of the UNESCO Caatinga Biosphere Reserve. However, Catimbau National Park is still home to many rural and indigenous  
124 inhabitants, who extract firewood and non-timber forest products, hunt wildlife, practice family agriculture and extensive livestock husbandry,  
125 and exert chronic disturbance at different intensities in several regions of the park (e.g. Arnan et al., 2018b). This growing human activity  
126 expanded land use throughout the study area by 704% between 2000 and 2014 (Freire, 2015).

127

128 *2.2. Experimental Design*

129 On the basis of 5-m RapidEye satellite images and soil maps, twenty 1,000 m<sup>2</sup> (50 m × 20 m) plots were selected to include gradients of  
130 chronic anthropogenic disturbance and water deficit, as a proxy of aridity, within the Catimbau National Park (Fig. 1). Plots were spaced apart by  
131 at least 2 km and covered a total area of 214.3 km<sup>2</sup> with similar sandy soil, altitude, and flat terrain (*sensu* Rito et al., 2017a).

132

### 133 2.3. Chronic anthropogenic disturbance index

134 The intensity of chronic anthropogenic disturbance at each plot was calculated based on three main chronic pressures in the park area  
135 (*sensu* Arnan et al., 2018b): (i) pressure induced by livestock grazing, specifically vegetation removal, trampling and other physical damage  
136 caused by cattle and goats (GPI); (ii) wood extraction pressure (WEI), including the removal of live or dead wood for fuel use, fence construction  
137 and handicrafts; and (iii) other pressures caused by people (PPI), including the collection of non-timber forest products, such as therapeutic  
138 plants, and hunting.

139 Each of these pressures integrated different sources of disturbance and were individually calculated using the following equation (*sensu*  
140 Arnan et al., 2018b):

141

$$I = \frac{\sum_{i=1}^n (y_i - y_{\min}) / (y_{\max} - y_{\min})}{n} \times 100$$

142

143 where  $I$  denote disturbance intensity,  $y_i$  is the observed value for a given metric of disturbance at plot  $i$ ;  $y_{\min}$  and  $y_{\max}$  respectively represent the  
144 minimum and the maximum observed values for this metric across all plots; and  $n$  is the number of each disturbance metric incorporated in the

145 index. This equation therefore standardizes metrics expressed in different units and results in a value between 0 and 1, allowing them to be  
146 combined into the same index. In the case of the indexes, values ranged from 0 to 100 (from no disturbance to maximum-intensity disturbance).  
147 Livestock grazing pressure (GPI) was calculated by measures of goat grazing and cattle dung frequency into the formula above; wood extraction  
148 pressure (WEI) was estimated the extraction of live wood and the collection of firewood according to the formula above; people pressure (PPI)  
149 was calculated by measures like plot proximity to the nearest house, plot proximity to the nearest road and the number of people living in the area  
150 that influence the plot. Detailed explanations for these three proxies of anthropogenic disturbance are given by Arnan et al. (2018b). The three  
151 sources of chronic anthropogenic disturbance varied independently among the plots examined here (Supplementary information Fig. S1).

152

#### 153 *2.4. Climatic water deficit*

154 We extracted water deficit/aridity (ARD) data obtained from hydrological maps of the CGIAR-CSI's Global Aridity and PET Database  
155 and Global High-Resolution Soil Water Database (Trabucco and Zomer, 2010). These maps have a 30-sec resolution, equivalent to 1 km. To plot  
156 these data onto maps, the annual average water deficit was calculated from the difference between the annual mean potential evapotranspiration  
157 (PET) and the actual evapotranspiration (AET) using the ArcGIS 10.1 software (ESRI, 2012). The range between 658 mm to 1,086 mm in water  
158 deficit values recorded among our plots (Supplementary information Fig. S1) represents a very wide gradient, making the study area an excellent  
159 opportunity to examine the effects of increased aridity on plant reproductive strategies. Aridity was not significantly correlated with the  
160 anthropogenic pressure indices (see Arnan et al., 2018a for details).

161

## 162 2.5. Sampling plant communities

163 All individuals of woody plants with a soil height diameter  $\geq 3$  cm and a total height  $\geq 1$  m were counted within each of the 20 plots and  
164 identified at the species level according to the APG IV system (APG 2016). In total, 5,081 individuals representing 98 species, 70 genera and 32  
165 families were recorded (see Rito et al., 2017a).

166

## 167 2.6. Plant reproductive traits

168 For the reproductive trait characterization each species was classified into 39 categories of six major classes of reproductive traits: 1)  
169 floral biology (including type, size and floral reward), 2) pollination systems, 3) sexual systems, 4) reproductive systems, 5) fruit type and 6)  
170 dispersal modes (see Table 1 for details). From this initial classification into 39 reproductive trait categories, we regrouped species according to  
171 their degree of specialization (i.e., generalist vs specialist) into five more general biologically meaningful reproductive strategies (following  
172 Girão et al., 2007), thus totaling 49 trait categories: 1) pollination system [generalist (e.g. small-sized bees, wasps, diverse small insects,  
173 butterflies, flies, moths, and wind) vs. specialized pollination systems (e.g. bats, medium-large bees, birds, beetles, SpHINGIDS)] (*sensu* Girão et  
174 al., 2007; Kang and Bawa, 2003); 2) reproductive system [(generalist (e.g. self-compatible) vs specialized reproductive system (e.g. self-  
175 incompatible + dioecious (obligatory cross-pollinated species))]; 3) dispersal mode [generalist or abiotic (e.g. wind-dispersed and ballistic  
176 species) vs specialized or biotic dispersal mode (e.g. animal dispersed species)]; 4) Floral type [(generalist (e.g. open/dish + inconspicuous; i.e.

177 flowers with easily accessible resource *sensu* Faegri and Pijl, 1979) vs specialized floral type (e.g. floral types other than open or inconspicuous;  
178 i.e. flowers with concealed resource *sensu* Faegri and Pijl, 1979)]; 5) Floral size [generalist (e.g. inconspicuous + small flowers *sensu* Machado  
179 and Lopes, 2004) vs specialized floral size (e.g. medium, large and very-large flowers *sensu* Machado and Lopes, 2004)]. Reproductive traits,  
180 such as floral size, resource and sexual systems, were used to support the classification of pollination and reproductive systems, respectively. All  
181 reproductive traits selected in this study are sensitive to anthropogenic disturbance (e.g. Girão et al., 2007; Lopes et al., 2009, Sobrinho et al.,  
182 2016; Silva et al., 2019).

183 Our hypotheses were based on this classification of generalization vs specialization since it brings together significant diagnostic traits of  
184 plant reproductive profile. The reproductive characterization of each species was based on: field observations (some of us have been working on  
185 the reproductive biology of Caatinga species for more than 20 years and have several papers published with both, case and community studies);  
186 published and referenced data (see Griz and Machado, 2001; Machado and Lopes, 2004; Machado et al., 2006; Soares et al., 2014; Leal et al.,  
187 2017; Silva et al., 2019 and references therein); and a survey of specimens from the UFP Herbarium. Although a few tree species were  
188 incompletely assigned to all life history trait categories (12.7%), this was unlikely to introduce biases to trait comparisons as the plots were  
189 compared in terms of number of species and individuals within reproductive categories and strategies.

190

191 *2.7. Data analysis*

192 The functional composition of reproductive strategies in woody plant communities at Catimbau National Park was calculated based on both the  
193 number of species and individuals of each reproductive trait category, which describes the prevailing characteristics and functional diversity of  
194 the community, and therefore its trait divergence across individuals or species (Arnan et al., 2014). The prevalence of all individual or grouped  
195 traits was quantified in terms of both the number of species (hereafter, trait richness) and individuals within each plot (hereafter, trait abundance).  
196 To estimate the functional diversity of community-wide reproductive traits, we used the Rao's coefficient of diversity (Botta-Dukát, 2005), which  
197 is based on the expected dissimilarity between any two individuals of different species randomly taken from each plot (Rao, 1982), as following:

$$\text{Rao} = \sum_{i=1}^n \sum_{j=1}^n d_{ij} P_i P_j$$

198  
199 where,  $d_{ij}$  is the functional distance between the species  $i$  and  $j$ , and  $P_i$  and  $P_j$  are their relative abundances (being 0 or 1 when applied to data on  
200 species richness). The functional distance between the species was measured as  $d_{ij}=1$  when  $i \neq j$ , and  $d_{ij}=0$  when  $i=j$ . This coefficient is  
201 independent from species richness, ranging from 0 to the maximum Simpson diversity value, where higher values indicate higher diversity.  
202 Moreover, the Rao coefficient also calculates not only the functional diversity for any given trait, but also for a combination of traits, and can be  
203 used for quantitative, categorical and binary data (Lepš et al., 2006). The Rao index was initially calculated based on the richness and abundance  
204 data for either generalist or specialized reproductive traits; and for the entire community by pooling together the richness and abundance of all  
205 trait categories considered here (e.g. floral type, floral size, pollination system, reproductive system, fruit type and dispersal mode). In total, we  
206 calculated the Rao index six times by estimating the functional diversity based on the richness and abundance for generalist and specialized traits,  
207

208 and for the entire sampled community. We used the *dbFD* function in the *FD* package in R (R Development Core Team, 2017) to estimate the  
209 functional diversity in the studied plant community.

210 To characterize the distribution of reproductive traits in Caatinga plant communities, the richness and abundance of each reproductive  
211 trait were initially tested for normality using Shapiro-Wilk tests. Data with heteroscedastic distributions were sqrt-transformed. The number of  
212 species and individuals within the same reproductive trait were then compared through one-way ANOVAs followed by Tukey's post-hoc tests.  
213 We performed eight ANOVAs, one for each initial reproductive trait. Subsequently, we conducted six Student *t* tests to examine differences in  
214 trait richness and abundance between generalist and specialized strategies in relation to floral type, floral size, pollination and reproductive  
215 systems, fruit type and dispersal mode. Plots were maintained as replicates in all comparisons. For normality tests, ANOVAs and *t* tests, we used  
216 the functions *shapiro.test*, *aov* and *t.test* within the *car* package in R (R Development Core Team, 2017).

217 We used a model selection approach to identify the individual and combined effects of different sources of chronic anthropogenic  
218 disturbance and aridity on the trait richness and abundance and on the functional diversity of reproductive traits and reproductive strategies  
219 (generalists and specialized) of Catimbau woody plants. First, we constructed generalized linear models (GLMs) with Gaussian distribution error  
220 and "identity" link function (Sokal and Rohlf, 1995). We used separate models for each response variable (e.g. generalist and specialized  
221 strategies and categories within each reproductive trait) based on both the richness and abundance data. The explanatory variables were GPI, PPI,  
222 WEI, aridity, and the interactions between each single disturbance index and aridity. We, then, applied Akaike information criterion with a  
223 correction for finite sample sizes (AICc) to select the best-supported models. This approach reduces biases associated with multiple tests,



224 variable collinearity, and small sample sizes (Burnham and Anderson, 2002). We initially built full models, with the best-supported models  
225 selected based on their respective AICc weights, which inform the probability of a given model diverging from chance. We selected models with  
226 AICc differences lower than two ( $\Delta\text{AICc} < 2$ ). Predictors were considered to be most important if they were retained in the best-supported  
227 models that did not contain only the intercept. Model selection was performed using the *dredge* function in the *MuMIn* package (Burnham and  
228 Anderson, 2002) in R (R Development Core Team, 2017). All analyses were performed separately for the trait richness, abundance and  
229 functional diversity data within plots.

230

### 231 3. Results

#### 232 3.1. Plant reproductive trait prevalence at Catimbau National Park

233 Considering reproductive trait categories separately, plants species bearing open/dish flowers ( $F_{7,152} = 25.5, P < 0.0001$ ; Fig. 2A), small  
234 flowers ( $F_{4,95} = 24.1, P < 0.0001$ ; Fig. 2C) or those providing nectar as the main floral resource ( $F_{2,57} = 129.2, P < 0.0001$ ; Fig. 2B) were more  
235 numerous in relation to the other woody plants at the study area. In the case of pollination systems, plants species bearing bee-pollinated flowers  
236 were more representative ( $F_{8,11} = 65.1, P < 0.0001$ ; Fig. 2E). In addition, we observed a higher species richness of hermaphrodite ( $F_{2,57} = 62.9, P$   
237  $< 0.0001$ ; Fig. 2D) and self-incompatible plants ( $F_{2,57} = 28.5, P < 0.0001$ ; Fig. 2F) in relation to other categories within each trait. In terms of  
238 fruit type and dispersal mode, we observed also a higher richness of species bearing dry fruits ( $t = -6.7, P < 0.001$ ; Fig. 2H) and autochoric seeds  
239 ( $F_{2,17} = 31.4, P < 0.0001$ ; Fig. 2G) than other categories. In terms of strategies, the richness of species with specialized reproductive systems ( $t =$

240 5.5,  $P = 0.001$ ; Fig. 2E) and generalist fruit types ( $t = -6.7$ ,  $P < 0.0001$ ; Fig. 2G) were most common. We did not observe differences for the  
241 remaining analyzed strategies.

242 The abundance of reproductive trait categories varied similarly than the patterns previously reported for the richness of floral types, size  
243 and reward, pollination and sexual systems, except for reproductive systems and seed dispersal modes (Supplementary information Fig. S2). In  
244 particular, the abundance of self-incompatible and self-compatible plants was similar to each other, while autochoric dispersed individuals  
245 predominate (Supplementary information Fig. S2). Comparing generalist vs. specialized reproductive strategies, trait abundance was similar to  
246 the patterns reported for trait richness only for reproductive systems and fruit types (Supplementary information Fig. S2). However, in contrast to  
247 traits richness, we observed high abundance of plants with generalist pollination systems (see Supplementary information Fig. S2 for details).

248

### 249 *3.2. Plant reproductive traits responses to chronic disturbance and aridity*

250 Changes in the levels of chronic anthropogenic disturbance and aridity affected 41% of all trait categories and reproductive strategies,  
251 based on the best-supported models in relation to trait richness. Specifically, 35.5% and 40% of the reproductive traits were distinctly affected by  
252 individual changes in levels of chronic anthropogenic disturbance and aridity, respectively (Table 2; Supplementary information Table S1).

253 Analyzing our results in terms of reproductive strategies (generalist or specialist), increases in aridity were associated with reductions in  
254 the richness of plants with both generalist and specialist floral types, specialized pollination systems, fleshy fruit and biotic dispersal mode,  
255 corroborating our hypothesis for these specialized strategies (Tables 2-3; Supplementary information Table S1). On the other hand, individual

256 increases in any of the chronic anthropogenic pressures (PPI, GPI or WEI) were positively associated with the richness of plants with obligatory  
257 outcrossing reproductive systems and animal-dispersed seeds (Tables 2-3), both of them specialized strategies. Complex patterns were observed  
258 for the richness of generalist and specialist floral type, and specialized fruit types (e.g. fleshy fruits) (Tables 2-3; Supplementary information  
259 Table S1) with respect to the chronic anthropogenic pressures, partially corroborating our hypothesis about the effects of disturbance on these  
260 reproductive strategies. Specifically, the richness of specialized floral and fruits categories was positively related to wood extraction pressure but  
261 negatively related to livestock grazing (Tables 2-3; Supplementary information Table S1).

262         Considering each trait category separately, we observed, as for the strategies described above, positive, negative or complex effects.  
263 Specifically, examining the richness of specialized categories, individual increases in wood extraction and aridity were associated with increase  
264 in the richness of plants with self-incompatible reproductive system (Tables 2-3; Supplementary information Table S1). Pollination by Sphingids  
265 was negatively affected by livestock grazing, wood extraction and aridity, individually, while pollination by beetles was negatively affected by  
266 wood extraction and aridity, also individually (Tables 2-3). Curiously, the richness of plants with hermaphrodite sexual system (generalist  
267 category) was also negatively related to increases in at least one of the explanatory variables (Tables 2-3; Supplementary information Table S1).  
268 The richness of plants with traits such as bell/funnel, gullet and inconspicuous floral type, inconspicuous and very large floral sizes, pollen as  
269 floral reward, dioecious reproductive system, pollination by birds, bats and butterflies, and zoochory were affected in complex ways with  
270 increases in some of the sources of chronic anthropogenic disturbance and aridity (Table 2). All other reproductive traits analyzed were not  
271 affected by chronic anthropogenic disturbance or aridity (Tables 2-3; Supplementary information Table S1).

272           There were combined effects of chronic anthropogenic disturbance and aridity on the richness of plants in eight traits, but with respect to  
273 reproductive strategies, combined effects were documented only for generalist fruit type (dry fruits) (Fig. 3; Table 2; Supplementary information  
274 Table S1). For the combined effects, in areas of low aridity, the richness of plants with a) plants with gullet and bell/funnel flowers, pollen  
275 flowers and dioecious reproductive system were benefited with increases in livestock grazing (Fig. 3A, C, G, J; Table 3); b) plants with  
276 inconspicuous floral type, inconspicuous and very large sizes, dioecious, self-incompatible and with dry fruits were positively affected by  
277 increases in wood extraction (Fig. 3D, F, I, K-L; Table 3); c) plants with bell/funnel and pollen flowers were negatively affected by increases in  
278 people pressure (Fig. 3B, H; Table 3); d) plants with dry fruits were positively affected by decreases in livestock grazing (Fig. 3M; Table 3;  
279 Supplementary information Table S1).

280           Considering the abundance of individuals, we observed similar patterns to those observed for species richness with respect to their  
281 individual or combined responses of reproductive traits to the examined environmental gradients at both levels, strategies and traits (Table 4;  
282 Supplementary information Fig. S3 and Table S2 for details). Additionally, we observed that reductions in aridity and livestock grazing were  
283 associated with an increase in the number of individuals pollinated by Sphingids (Table 4; Supplementary information Fig. S3 and Table S2 for  
284 details). Only fruit types and dispersal modes were not affected by any of the explanatory variables (Table 4; Supplementary information Fig. S3  
285 and Table S2 for details).

286

287 *3.3. Changes in reproductive functional diversity at Catimbau National Park*

288 Based on the reproductive strategies, we did not observe neither individual nor combined effects of chronic anthropogenic disturbance  
289 and aridity on the functional diversity of generalist and specialized reproductive strategies richness of woody plants at Catimbau National Park,  
290 whether analyzed with richness or abundance data (Supplementary information Table S3-S5). However, when considering the richness of all  
291 reproductive traits (without grouping them in strategies), functional trait diversity varied negatively with individual increases of livestock grazing  
292 pressure (corroborating our second hypothesis) (Fig. 4A; Table 3) and positively with wood extraction (Fig. 4B; Table 3; Supplementary  
293 information Table S3) (contrary to our second hypothesis).

294 In terms of trait abundance, increases in livestock grazing were related to reduced diversity of reproductive traits (Fig. 4C; Table 4;  
295 Supplementary information Table S3), (corroborating our second hypothesis), whereas increases in people pressure were related to increased  
296 diversity of reproductive traits (Fig. 4D; Table 4; Supplementary information Table S3) (contrary to our second hypothesis).

297

#### 298 **4. Discussion**

299 Elevated levels of chronic anthropogenic disturbance and aridity affect the richness and abundance and diversity of plant reproductive strategies  
300 in Caatinga dry forest in different ways, partially corroborating our hypotheses. High richness and abundance of generalist reproductive traits,  
301 such as open/dish and small flowers, dry fruits and hermaphrodite sexual system, associated with specialized traits related to self-incompatible  
302 breeding systems, characterized plant communities along anthropogenic disturbance and aridity gradients at Catimbau National Park.  
303 Remarkably, although these gradients were often complex, they generally exerted detrimental effects on the richness and abundance of

304 specialized reproductive strategies. Indeed, individual increases in chronic anthropogenic disturbance and aridity negatively affected the richness  
305 of plants with traits such as very large flowers, self-incompatible reproductive system, pollinated by Sphingids and beetles, and the abundance of  
306 plants with traits as bell/funnel flowers, pollinated by Sphingids or vertebrates. Concerning the combined effects of environmental drivers, aridity  
307 mediated the effects of chronic anthropogenic disturbance in determining the richness and abundance of plants with specialized reproductive  
308 traits such as bell/funnel and gullet flowers, flowers that provide pollen as resource and dioecious sexual system. Contrary to our hypotheses,  
309 however, despite the divergent effects on specialized plant reproductive strategies, individual and combined effects of chronic anthropogenic  
310 disturbance and aridity did not affect the reproductive functional diversity in terms of strategies (generalist and specialized), only in terms of trait  
311 categories (without grouping traits in strategies).

312 We emphasize that Caatinga plant communities, such as those at Catimbau, show a high degree of generalist reproductive traits, a pattern  
313 that has been previously observed in other seasonally dry tropical forests regions (see Quesada et al., 2011; Leal et al., 2017). The high number  
314 of species and individuals with generalist reproductive traits, including flower size, pollination, sexual and reproductive systems, fruit type and  
315 seed dispersal mode, were similar to other areas in Caatinga (e.g. Griz and Machado, 2001; Machado and Lopes, 2004; Machado et al., 2006) and  
316 in the Brazilian Cerrado (Oliveira, 1996; Oliveira and Gibbs, 2000). This dominance of generalist reproductive traits is expected for open-canopy  
317 forests under severe climatic conditions, such as the Caatinga (Machado and Lopes, 2004), as this provides insurance against strong spatial  
318 and/or temporal turnover in species composition.

319 Our results suggest that chronic anthropogenic disturbance and aridity interact in a complex way considering the richness and abundance  
320 of the reproductive traits examined individually, especially richness of specialized traits. The interaction between these drivers also affected the  
321 functional diversity of reproductive traits, but only in terms of each trait category, but not in terms of reproductive strategies (generalist vs.  
322 specialist). Aridity affected more reproductive traits than chronic anthropogenic disturbance, regardless of source. Several studies have shown  
323 that water availability in tropical dry forests is associated with changes in plant species composition (Segura et al., 2002; Esquivel-Muelbert et  
324 al., 2016; Hiltner et al., 2016) and the distribution of life-history traits (Gentry, 1982, Bullock, 1995; Medina, 1995). Different responses in terms  
325 of species richness and abundance of specialized traits to elevated water stress can be explained by the physiological strategies of each species,  
326 which ensures the establishment of individuals along a drought stress gradient (Souza et al., 2010; Frosi et al., 2017). Indeed, some species of the  
327 Leguminosae, such as *Trischidium mole* (Leguminosae), are highly tolerant to water stress indicating that they may occur in highly desiccated  
328 soil patches (Souza et al., 2010). Other Caatinga species had different responses following rehydration. For instance, *Handroanthus*  
329 *impetiginosus* (Bignoniaceae) fully recovers gas exchange and biochemical metabolism after rehydration (Dombroski et al., 2014) compared to  
330 *Pachira aquatica* (Malvaceae) (Frosi et al., 2017). Rapid rehydration may confer advantages related to faster regrowth after the dry season. The  
331 irregular distribution of soil patches and precipitation (e.g. Silva et al., 2018) are strongly associated with the distribution and abundance of plant  
332 species in the entire Caatinga phytogeographic domain (e.g. Moro et al., 2015). In this sense, drier areas tend to have impoverished plant  
333 assemblages in terms of taxonomic diversity (Rito et al., 2017a).

334 Although the richness and/or abundance of woody plants pollinated by bats, Sphingid moths, vertebrates and bearing bell/funnel flowers  
335 were negatively affected by increases in chronic anthropogenic disturbance and aridity, plants with other specialized reproductive traits, such as  
336 flag flowers, medium, large and very large flowers and fleshy fruits, may be positively affected or had complex responses in relation to the  
337 severity of these pressures. The complex effects of chronic anthropogenic disturbance on plants is closely associated with economic imperatives,  
338 such as livestock production and wood harvesting (Ribeiro et al., 2015; Rito et al., 2017b). Indeed, species with specialized reproductive traits  
339 such as *Cenostigma microphyllum* (Leguminosae) is widely exploited as medicinal plants and in the construction and furniture industry (Almeida  
340 and Bandeira, 2010). Other species, however, such as *Jatropha molissima* (Euphorbiaceae), are not attractive in terms of wood and forage  
341 production, despite its specialized reproductive traits. *Jatropha molissima* has reduced palatability and low wood density (Ribeiro et al., 2015),  
342 which may be related to low rates of herbivory and human exploitation, combined with a higher colonization ability, resulting in the hyper-  
343 abundance of this species in disturbed areas (Rito et al., 2017b). Therefore, chronic anthropic disturbance first affects the vegetative  
344 characteristics of plants.

345 The observed changes in the distribution of reproductive traits in response to the environmental gradients we analyzed, considering either  
346 trait richness or abundance, were also followed by changes in the functional diversity of reproductive traits of plant communities in the Catimbau  
347 National Park. Changes in the richness and abundance of species with specialized reproductive traits may, in the long term, contribute to the  
348 differential establishment of species and interfere in landscape scale coevolutionary processes. For example, losing or replacing less abundant  
349 species that play key ecological roles typically has an impact on ecosystem functioning, including the provision of ecosystems goods and



350 services (Clavel et al., 2010). In this case, it is expected that generalist species, which possess traits favorable to the occupation of various types  
351 of habitat, are benefited or less affected by anthropic disturbance than species with specialized traits (Devictor et al., 2008; Clavel et al., 2010;  
352 Abadie et al., 2011). Thus, populations of pollinators and frugivores that rely on specialized plant resources will therefore tend towards a decline,  
353 with the weakening and even the disruption of plant-animal interactions. We expected that this functional homogenization (systematic  
354 substitution of species with specialized strategies by more species with generalist strategies) (e.g. McKinney and Lockwood, 1999; Smart et al.,  
355 2006; Abadie et al., 2011) of plant communities also occurs at the landscape level, expanding to the entire Caatinga.

356

## 357 **5. Conclusions**

358 In sum, changes in plant species composition in Caatinga communities driven by chronic anthropogenic disturbance and aridity (as a  
359 proxy of climate change), whether independently or synergistically, lead to changes in the representativeness of reproductive traits, especially  
360 those related to specialized reproductive strategies. Contrary to what we expected, generalist traits were also affected, and specialized traits were  
361 sometimes favored by disturbance and/or aridity. These parallels other key contemporary drivers of global scale biodiversity loss involving the  
362 interaction of anthropogenic disturbance and climate change (Segan et al. 2016), which are particularly severe in SDTFs (Mancheogo et al. 2018),  
363 such as the Caatinga. In relation to pollination, ca. 90% of the flowering plants depend on biotic vectors, particularly in tropical regions (Ollerton  
364 et al., 2011), and this also occurs in the Caatinga (Machado and Lopes, 2004). Climate change also threatens pollinator diversity, especially bees  
365 (e.g. Giannini et al., 2012), and is expected to reduce suitable Caatinga dry forest habitat for endemic plants with disproportionate impacts on

366 specialized reproductive strategies (Silva et al., 2019). Our study reinforces the importance of using specialization (e.g. trait types, specialized  
367 groups, level of specialization) in functional approaches to investigate ecological mechanisms responsible for driving biodiversity. Future studies  
368 should focus on diverse aspects of plant-pollinator interactions per se, which combined with our findings on the distribution of plant reproductive  
369 traits, can provide a better understanding of the mutual responses to chronic anthropogenic pressures and aridity. In order to reduce the  
370 detrimental impacts of these drivers on plant communities and mutualistic interactions in the Caatinga, there is a need to develop management  
371 techniques and policies that maintain the flow of ecosystem services. More specifically, these practices should consider the different relationships  
372 among anthropogenic disturbance, climate change and the frequency of plant reproductive traits.

373

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380

#### 381 **Declaration of Competing Interest**

382 The authors declare that they have no conflict of interest.

383

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575 868.
- 576 **Appendix A. Supplementary data**
- 577 Supplementary data to this article can be found online.

578 **Figure legends**

579 **Figure 1.** Description and location of the study area. Map of South America highlighting the region of northeastern Brazil and the distribution of  
580 the Caatinga vegetation (A); Location of Catimbau National Park (CNP) in the State of Pernambuco (B); boundaries of CNP highlighting the  
581 location (solid dots) and identification (numbers) of each plot surveyed (C). Plot codes refer to those listed in Supplementary information Fig. S1.

582 **Figure 2.** Number of species (mean  $\pm$  SD) within categories of plant reproductive traits and reproductive strategies at Catimbau National Park,  
583 northeastern Brazil. Floral types (A), flower size (B), floral resources (C), pollination system (D), sexual system (E), reproductive system (F),  
584 dispersal mode (G) and fruit type (H) occurring within the 20 sampled plots. Bars within the same plot showing different lowercase letters are  
585 statistically different at  $P < 0.05$  according to Tukey post-hoc comparisons. Bars within the plot showing different uppercase letters are  
586 significantly different at  $P < 0.05$  according one-tailed  $t$ -student test.

587 **Figure 3.** Combined effects of chronic anthropogenic disturbance, i.e. people pressure (PPI), livestock grazing (GPI) and wood extraction (WEI),  
588 and aridity (ARD) on the richness of plant reproductive traits and strategies in the Catimbau National Park. Colors closer to red indicates high  
589 richness (mean  $\pm$  SD) of the reproductive trait.

590 **Figure 4.** Effects of chronic anthropogenic disturbance on the overall functional diversity of richness (A and B) and abundance (C and D) of  
591 reproductive traits (FD) at Catimbau National Park, northeastern Brazil. Grey shading indicates 95% confidence intervals.

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#### CONFLIC OF INTEREST STATEMENT

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**Manuscript Title:** “Divergent responses of plant reproductive strategies to chronic anthropogenic disturbance and aridity in the Caatinga dry forest”, by Jéssica L. S. Silva, Oswaldo Cruz-Neto, Kátia F. Rito, Xavier Arnan, Inara R. Leal, Carlos A. Peres, Marcelo Tabarelli, and Ariadna Valentina Lopes

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**Declaration of Competing Interest:** The authors declare that they have no conflict of interest.

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The corresponding author (Ariadna Valentina Lopes) is signing on behalf of all co-authors,

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*Ariadna Valentina Lopes*

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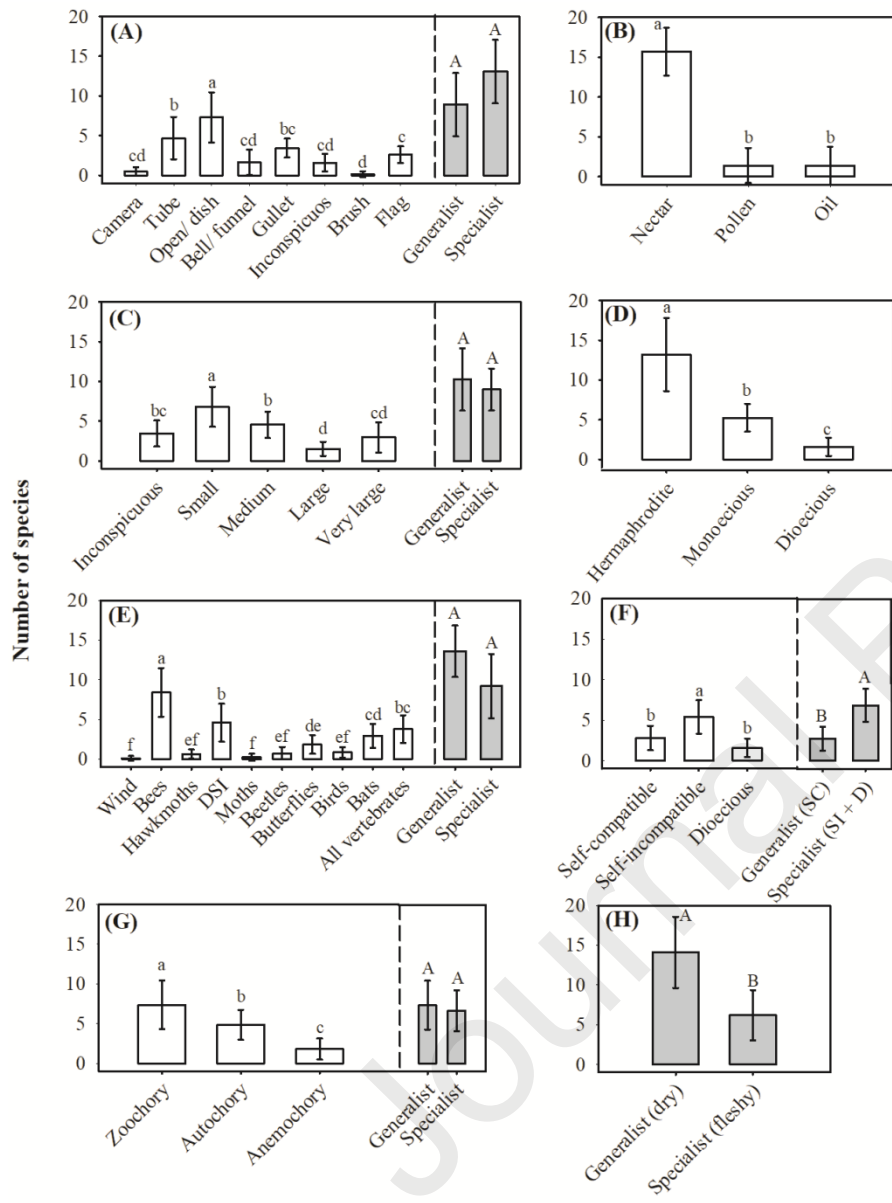
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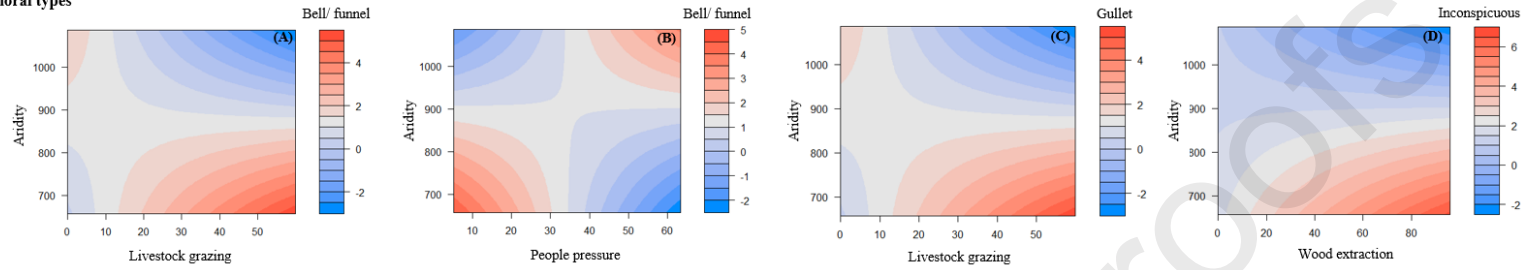
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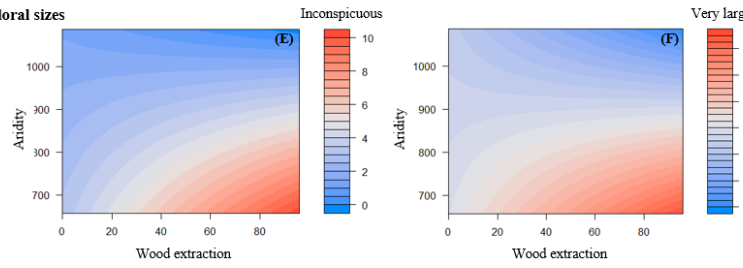
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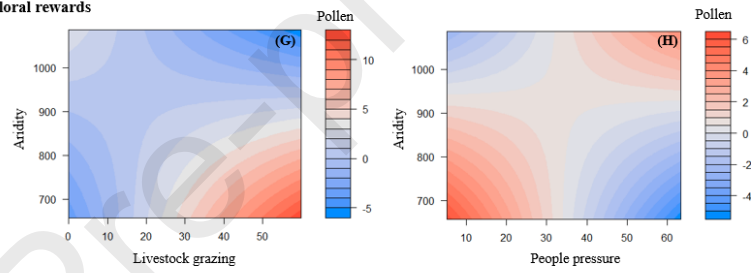
**Floral types**



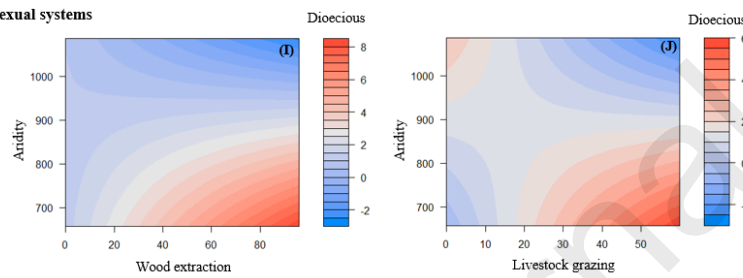
**Floral sizes**



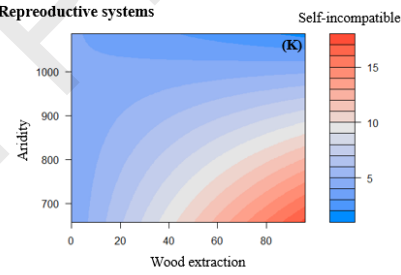
**Floral rewards**



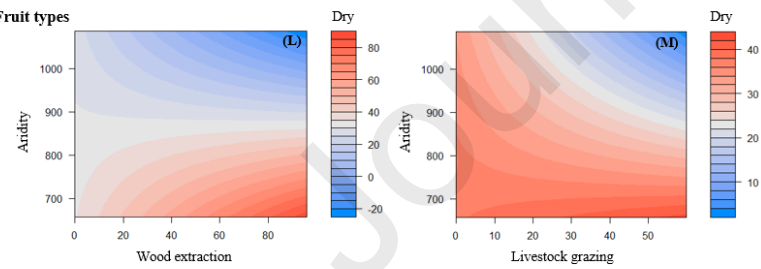
**Sexual systems**

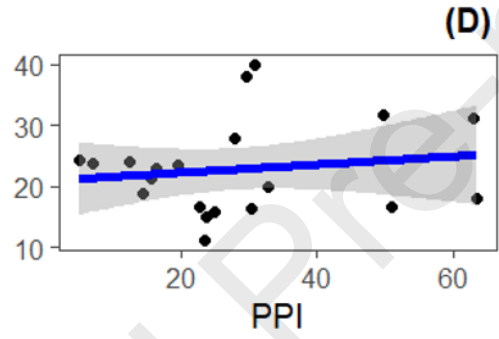
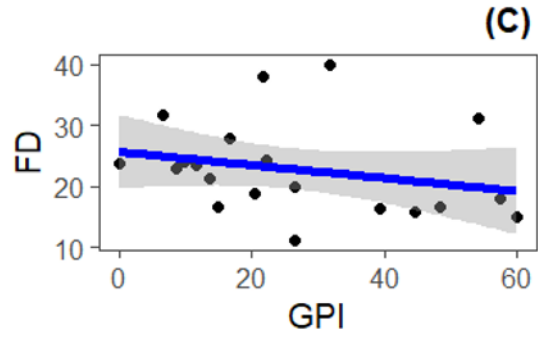
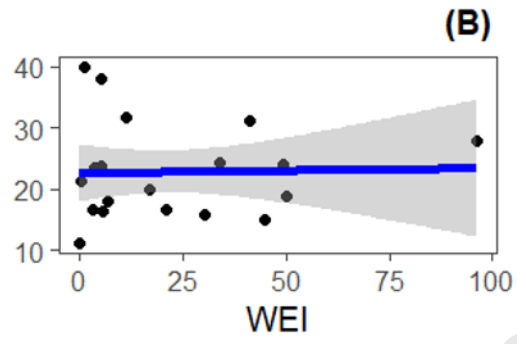
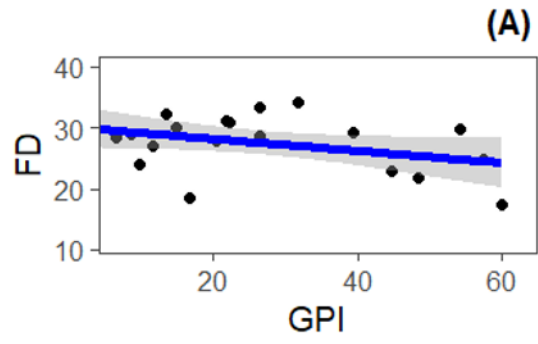


**Reproductive systems**



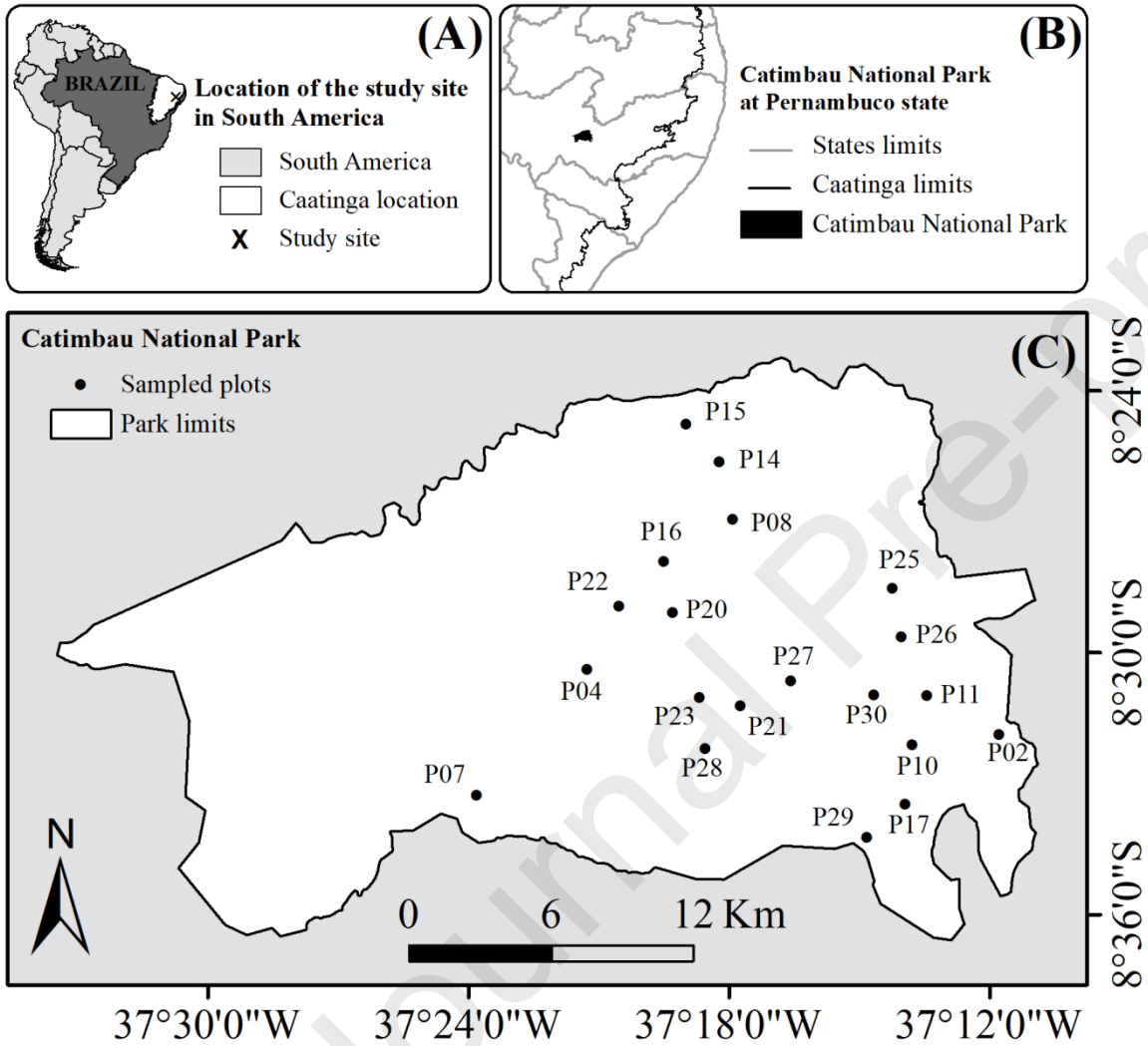
**Fruit types**

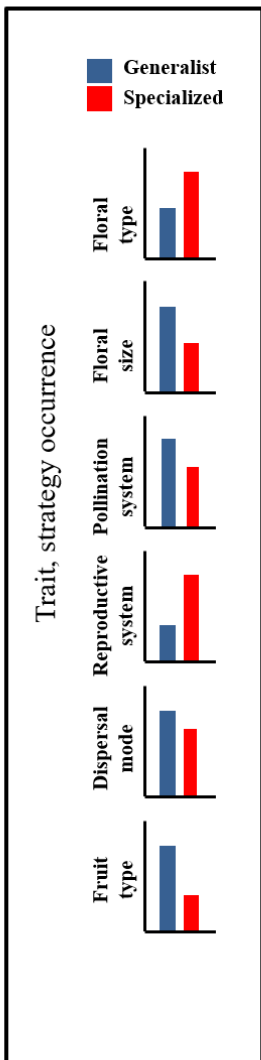




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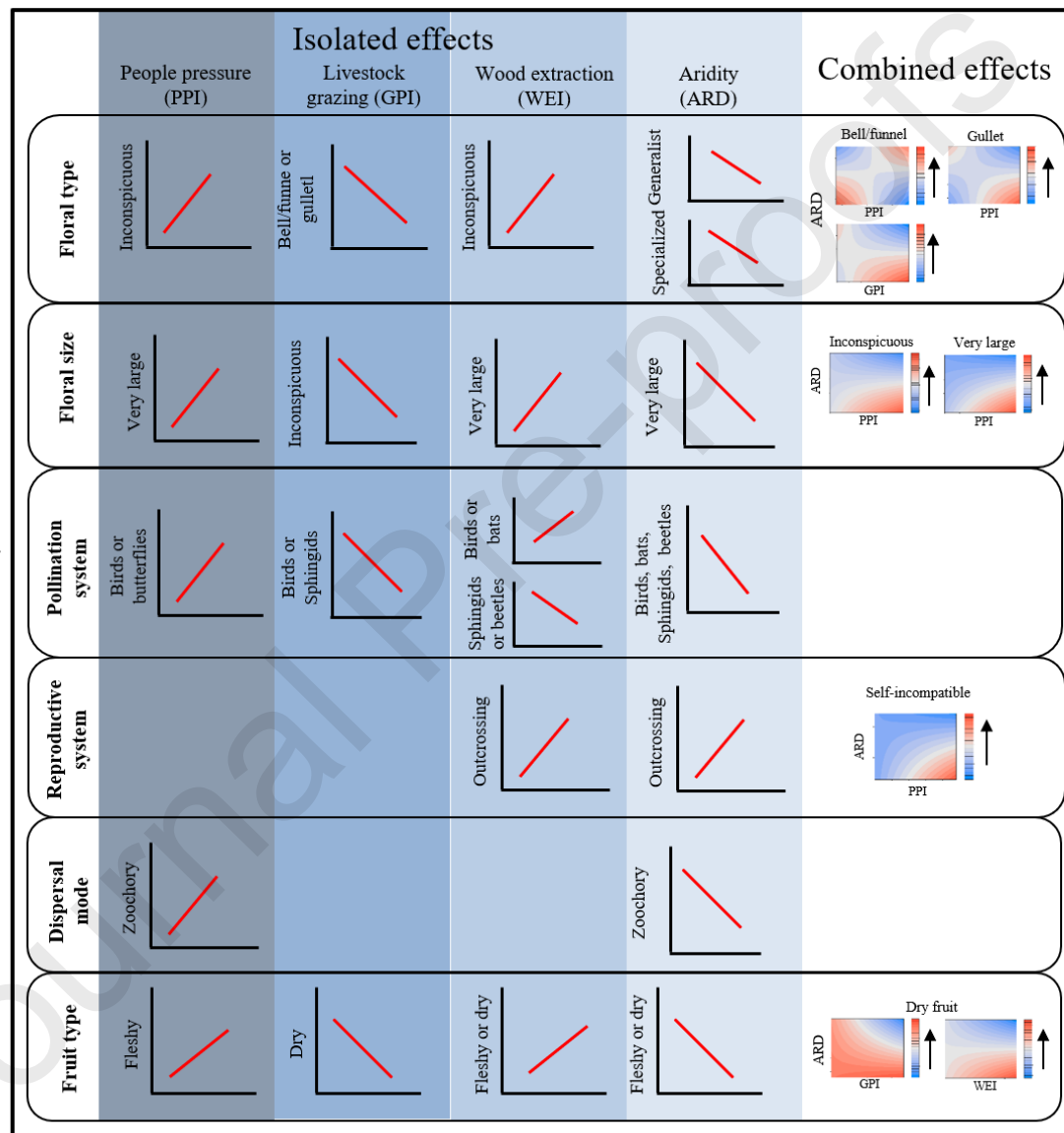


Anthropogenic disturbances

PPI  
GPI  
WEI



Aridity



Complex effects mainly reducing the occurrence of specialized traits and strategies

Journal Pre-proofs



638 **Table 1.** Classes of reproductive life history traits with their respective categories used in this study.

639

Traits	Trait categories
Floral biology	
Type <sup>1</sup>	camera, tube, disc, bell/funnel, gullet, inconspicuous, brush, flag
Size <sup>2</sup>	inconspicuous ( $\leq 4$ mm), small ( $>4 \leq 10$ mm), medium ( $>10 \leq 20$ mm), large ( $>20 \leq 30$ mm), very large ( $>30$ mm)
Reward <sup>3</sup>	nectar, pollen, oil
Pollination systems <sup>3</sup>	birds, bats, wind, small bees ( $<12$ mm), medium-large bees ( $\geq 12$ mm), diverse small insects (DSI), moths, Sphingids (hawkmoths), flies, beetles, butterflies and vertebrates
Sexual systems <sup>4</sup>	hermaphrodite, monoecious, dioecious
Reproductive systems <sup>4,5</sup>	self-compatible, self-incompatible, obligatory cross-pollination (self-incompatible species + dioecious)
Fruit type <sup>6</sup>	dry, fleshy
Dispersal mode <sup>7</sup>	zoochory, autochory, anemochory

640 <sup>1</sup>According to Girão et al. (2007), Lopes et al. (2009), Faegri and Pijl (1979); <sup>2</sup>According to Machado and Lopes (2004); <sup>3</sup>According to Faegri and Pijl (1979), Endress (1994), Proctor  
641 et al. (1996) and to Frankie et al. 1983 for bee body size; <sup>4</sup>According to Endress (1994), Proctor et al. (1996), Bawa (1980); <sup>5</sup>Outcrossing (i.e. obligatory cross-pollination) according to  
642 Richards (1997); <sup>6</sup>According to Spjut (1994); <sup>7</sup>According to Pijl (1982).

643 **Table 2.** Individual and combined effects of chronic anthropogenic disturbances (PPI: pressures caused by people, GPI: pressure induced by

644 livestock grazing and WEI: wood extraction pressure) and aridity (ARD) on plant reproductive traits based on the richness and abundance of

645 plants at Catimbau National Park, northeastern Brazil. The positive and negative signs indicate the direction of each relationship; an “X” signals  
 646 that an interaction was present. The absence of any sign indicates no relationship between the response and explanatory variables.

647

Response variable	RICHNESS						ABUNDANCE							
	PPI	GPI	WEI	ARD	ARD:PPI	ARD:GPI	ARD:WEI	PPI	GPI	WEI	ARD	ARD:PPI	ARD:GPI	ARD:WEI
<b>Floral types</b>														
Camera														
Tube														
Open/ dish														
Bell/ funnel	+	-		-	X	X		-	-	+	+			X
Gullet	+	-		+	X			+		-	-			
Inconspicuous	+		+	-			X	-	+	-	-	X	X	
Brush														
Flag								+	-		+		X	
-----														
Generalist (Flowers with easily accessible resources)	+		-	-							-			
Specialist (Flowers with concealed resources)			-	+	-									
<b>Floral sizes</b>														
Inconspicuous		-	+	-			X							
Small														
Medium														

Large														
Very large	+		+	-			X		+		-			
Generalist (Inconspicuous + Small)														
Specialist (Medium + Large + Very large)														
<b>Floral rewards</b>														
Nectar														
Pollen	+	-	+	+	X	X	X	-	+		-	X	X	
Oil														
<b>Sexual systems</b>														
Hermaphrodites (H)			-		-									
Monoecious (M)														
Dioecious (D)	-	+	+	-		X	X	-	+	+	-	X	X	X
<b>Reproductive system</b>														
Self-compatible (SC)														
Self-incompatible (SI)				+	+		X				-	+		
Generalist (Self-compatible = SC)														
Specialist (Outcrossing = SI + D)				+	+									
<b>Pollination systems</b>														
Birds	+	-	+	-										
Bats			+	-						+	-			X
Wind														
Bees (small and medium-large)					-									
DSI														
Sphingids			-	-	-					-	-	-		X
Moths														
Beetles				-	-					-	-			

Butterflies	+	-	+			
All vertebrates						
<hr/>						
Generalist *						
Specialist*		-		-		
<hr/>						
<b>Fruit types</b>						
Generalist (Dry)		-	+	-	X	X
Specialist (Fleshy)	+		+	-		
<hr/>						
<b>Dispersal modes</b>						
Zoochory	+			-		
Autochory						
Anemochory						
<hr/>						
Generalist (Abiotic)						
Specialist (Biotic)	+			-		
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648 \*Pollination system generalist: small-sized bees, wasps, diverse small insects, butterflies, flies, moths, and wind. Specialized pollination  
649 systems: bats, medium-large bees, birds, beetles, Sphingids.  
650 **Table 3.** Best-supported models ( $\Delta AICc < 2$ ) analyzing the isolated and combined effects of chronic anthropogenic disturbances (people  
651 pressure - PPI, livestock grazing - GPI and wood extraction - WEI) and aridity (ARD) on the richness and diversity of reproductive traits (RaoQ  
652 index) at Catimbau National Park, Pernambuco, Brazil. Models with (-) on the column “Variable selected” means that only the intercept has  
653 been included in that model.  
654

Response variable	Variables selected	df	AICc	$\Delta AICc$	Weight	R <sup>2</sup>
<b>Floral types</b>						
Camera	-	2	101.2	0.00	0.343	0.00

	ARD + PPI + ARD:PPI	5	102.6	1.36	0.174	0.33
	WEI	3	102.7	1.48	0.164	0.06
Tube	-	2	208.3	0.00	0.433	0.00
Open/ dish	-	3	221.3	0.00	0.346	0.00
	ARD	2	222.0	0.68	0.247	0.15
Bell/ funnel	ARD + WEI + ARD:WEI	5	187.3	0.00	0.378	0.70
	ARD + GPI + WEI + ARD:WEI	6	187.4	0.10	0.360	0.75
	ARD + PPI + WEI + ARD: WEI	6	188.9	1.62	0.168	0.73
Gullet	ARD	3	210.9	0.39	0.255	0.14
	ARD + PPI	2	211.3	1.01	0.210	0.23
	PPI	4	211.9	1.06	0.154	0.10
	ARD + WEI	3	212.0	1.11	0.150	0.23
Inconspicuos	ARD + GPI + PPI + ARD:GPI + ARD:PPI	7	150.8	0.00	0.246	0.61
	ARD + GPI + PPI + WEI + ARD:GPI + ARD:PPI + ARD:WEI	9	150.9	0.08	0.236	0.79
	ARD	2	151.1	0.36	0.205	0.12
	PPI	3	151.3	0.54	0.187	0.02
Brush	-	5	33.6	0.00	0.345	0.00
	ARD + GPI + ARD:GPI	2	34.5	0.89	0.221	0.52
	GPI	3	35.1	1.45	0.167	0.13
Flag	GPI + PPI	4	178.6	0.00	0.283	0.34
	ARD + GPI + PPI	5	179.2	0.54	0.216	0.43
	ARD + GPI + ARD:GPI	5	179.7	1.08	0.165	0.42
	GPI	3	180.1	1.43	0.139	0.17
	ARD + GPI	4	180.6	1.95	0.107	0.27
Generalist (flowers with easily accessible resources)	-	3	231.5	0.00	0.362	0.19
	WEI + ARD	4	232.4	0.84	0.237	0.28

Specialist (flowers with concealed resources)	-	2	201.4	0.00	0.372	0.00
	ARD	3	202.3	0.94	0.232	0.08
	GPI	3	203.4	1.99	0.137	0.03
<b>Floral sizes</b>						
Inconspicuous	-	3	225.2	0.00	0.207	0.00
	GPI	2	225.4	0.17	0.190	0.13
	GPI + PPI	4	225.5	0.24	0.184	0.25
	WEI	3	225.6	0.36	0.174	0.12
	GPI + WEI	4	225.7	0.49	0.162	0.24
	ARD + GPI	4	227.1	1.84	0.083	0.19
	-	3	226.1	0.00	0.358	0.26
Small	ARD	4	227.0	0.91	0.227	0.34
	ARD + PPI	4	227.3	1.24	0.193	0.33
	ARD + WEI	5	229.0	2.93	0.082	0.39
	-	2	192.0	0.00	0.406	0.00
Medium	PPI	3	193.6	1.65	0.178	0.05
	WEI	3	193.9	1.91	0.156	0.04
	-	2	236.5	0.00	0.351	0.00
Large	ARD	3	238.0	1.44	0.171	0.06
	WEI	3	238.1	1.58	0.159	0.05
	-	2	233.1	1.59	0.164	0.00
Very large	GPI	3	193.1	0.00	0.407	0.25
	ARD + GPI	4	194.8	1.62	0.181	0.31
	-	2	201.4	0.00	0.372	0.00
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Generalist (Inconspicuous + Small)	WEI	3	231.5	0.00	0.362	0.19
	ARD + WEI	4	232.4	0.84	0.237	0.28
	-	2	233.1	1.59	0.164	0.00
Specialist (Medium + Large + Very large)	-	2	201.4	0.00	0.372	0.00

	ARD	3	202.3	0.94	0.232	0.08
	GPI	3	203.4	1.99	0.137	0.03
<b>Floral rewards</b>						
Nectar	-	3	235.8	0.00	0.341	0.00
	ARD	2	236.6	0.75	0.234	0.16
	ARD + PPI	4	237.2	1.40	0.169	0.23
Pollen	ARD + GPI + PPI + ARD:GPI + ARD:PPI	7	154.4	0.00	0.438	0.73
	ARD	3	155.8	1.42	0.216	0.36
Oil	-	2	172.6	0.00	0.00	0.25
	GPI	3	172.8	0.17	0.17	0.23
	WEI	3	173.3	0.68	0.68	0.18
	GPI + WEI	4	173.8	1.20	1.20	0.14
	ARD	3	174.4	1.72	0.108	0.05
<b>Sexual systems</b>						
Hermaphrodites (H)	-	2	222.4	0.00	0.252	0.00
	GPI + PPI	4	223.0	0.61	0.186	0.23
	ARD + GPI + PPI	5	223.3	0.92	0.159	0.35
	ARD	3	223.3	0.95	0.157	0.08
	WEI	3	223.6	1.29	0.132	0.07
	PPI	3	223.9	1.59	0.114	0.05
Monoecious (M)	-	3	224.9	0.00	0.307	0.00
	ARD	2	225.3	0.38	0.254	0.14
	ARD + WEI	4	225.8	0.89	0.197	0.23
Dioecious (D)	ARD + GPI + PPI + WEI + ARD:GPI + ARD:PPI + ARD:WEI	9	150.4	0.00	0.434	0.82
	ARD + GPI + PPI + ARD:GPI + ARD:PPI	7	150.4	0.08	0.417	0.67
<b>Reproductive systems</b>						
Self-compatible (SC)	-	3	192.3	0.00	0.351	0.00

	PPI	2	192.8	0.51	0.273	0.15
Self-incompatible (SI)	ARD + WEI	5	183.2	0.00	0.354	0.55
	ARD	4	183.3	0.15	0.329	0.45
Outcrossing (SI+ D)	-	2	197.0	0.00	0.317	0.00
	GPI	3	197.5	0.49	0.248	0.15
	PPI	3	198.5	1.51	0.149	0.08
<b>Pollination systems</b>						
Birds	-	2	190.5	0.00	0.388	0.00
	ARD + WEI	3	192.3	1.74	0.163	0.05
	ARD	3	192.5	1.94	0.147	0.04
Bats	ARD	3	169.8	0.00	0.400	0.24
	ARD + WEI + ARD:WEI	5	170.9	1.06	0.235	0.43
Wind	-	2	132.1	0.00	0.409	0.00
	ARD	3	133.7	1.65	0.179	0.05
	WEI	3	134.0	1.92	0.157	0.04
Bees	-	3	222.2	0.00	0.442	0.00
	WEI	2	223.9	1.75	0.185	0.20
Sphingids	ARD + GPI + WEI	5	128.4	0.00	0.430	0.61
	ARD + GPI + WEI + ARD:GPI	6	130.2	1.77	0.177	0.65
DSI	-	2	224.9	0.00	0.292	0.00
	WEI	3	225.0	0.10	0.279	0.12
	ARD + WEI	4	226.2	1.34	0.150	0.20
Moths	-	4	56.6	0.00	0.357	0.00
	GPI + PPI	3	57.6	1.01	0.216	0.33
	GPI	2	58.2	1.57	0.163	0.16
Beetles	ARD	3	105.0	0.00	0.391	0.30
	ARD + WEI	4	106.3	1.30	0.204	0.36
Butterflies	-	2	163.7	0.00	0.289	0.00



	ARD	3	164.4	0.73	0.200	0.09
	GPI	4	165.0	1.32	0.149	0.20
	PPI	3	165.1	1.43	0.141	0.06
	ARD + PPI	5	165.3	1.55	0.133	0.33
All vertebrates	-	2	193.0	0.00	0.346	0.00
	WEI	3	193.6	0.57	0.260	0.10
Generalist	-	2	226.6	0.00	0.337	0.00
	WEI	3	227.8	1.15	0.190	0.07
Specialist	ARD	3	228.1	1.46	0.163	0.06
	-	2	291.8	0.00	0.347	0.00
	ARD	3	292.7	0.87	0.225	0.09
	WEI	3	293.2	1.36	0.176	0.06
<b>Fruit types</b>						
Dry	-	2	235.4	0.00	0.402	0.00
Fleshy	-	2	191.9	0.00	0.434	0.00
	WEI	3	193.2	1.32	0.224	0.18
<b>Dispersal modes</b>						
Zoochory	-	2	193.7	0.00	0.405	0.00
	WEI	3	195.2	1.52	0.190	0.00
Autochory	-	2	231.5	0.00	0.419	0.00
	PPI	3	233.4	1.84	0.167	0.04
Anemochory	-	2	195.8	0.00	0.396	0.00
	GPI	3	197.5	1.75	0.165	0.05
Generalist (abiotic)	-	2	232.5	0.00	0.435	0.00
	PPI	3	234.7	2.25	0.142	0.02
Specialist (biotic)	-	2	193.7	0.00	0.405	0.00
	WEI	3	195.2	1.52	0.190	0.06
<b>Rao Q</b>	GPI + WEI	4	104.5	0.00	0.436	0.38

655  $\Delta AICc$  represents the difference between the current and the best-supported models. Weight represents the relative probability of each model.

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658 **Table 4.** Best-supported models ( $\Delta AICc < 2$ ) analyzing the isolated and combined effects of chronic anthropogenic disturbances (people  
 659 pressure - PPI, livestock grazing - GPI and wood extraction - WEI) and aridity (ARD) on the abundance and diversity of reproductive traits  
 660 (RaoQ index) at Catimbau National Park, Pernambuco, Brazil. Models with (-) on the column “Variable selected” means that only the intercept  
 661 has been included in that model.

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Response variable	Variables selected	df	AICc	$\Delta AICc$	Weight	R <sup>2</sup>
<b>Floral types</b>						
Camera	WEI	3	33.6	0.00	0.304	0.18
	-	2	33.7	0.18	0.277	0.00
	ARD + WEI	4	34.9	1.31	0.158	0.28
Tube	ARD	3	99.5	0.00	0.320	0.13
	-	2	99.5	0.01	0.318	0.00
Open/ dish	-	2	105.2	0.00	0.199	0.00
	ARD	3	106.5	1.30	0.381	0.18
	ARD + WEI	4	107.1	1.89	0.148	0.23
Bell/ funnel	ARD + GPI + WEI	5	62.1	0.00	0.411	0.75
	ARD + GPI + PPI + WEI + ARD:GPI + ARD:PPI	8	62.8	0.76	0.281	0.89
Gullet	ARD + GPI + PPI + ARD:PPI	6	62.8	0.00	0.347	0.62
	GPI	3	63.2	0.40	0.284	0.30
	ARD + GPI + ARD:GPI	5	64.7	1.85	0.138	0.48

Inconspicuous	ARD + WEI + ARD:WEI	5	56.3	0.14	0.299	0.61
	ARD + PPI	4	56.7	0.38	0.247	0.51
	ARD	3	57.0	0.69	0.212	0.41
	ARD + PPI + WEI + ARD:WEI	6	58.1	1.78	0.123	0.66
Brush	-	2	20.3	0.00	0.379	0.00
	GPI	3	21.7	1.48	0.181	0.11
Flag	-	2	62.2	0.00	0.409	0.00
	PPI	3	63.9	1.66	0.179	0.05
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Generalist (flowers with easily accessible resources)	ARD	3	112.4	0.00	0.376	0.26
	ARD + WEI + ARD:WEI	5	114.0	1.58	0.171	0.43
	ARD + PPI	4	114.2	1.81	0.152	0.31
	ARD + WEI	4	114.3	1.85	0.149	0.31
Specialist (flowers with concealed resources)	ARD	3	112.3	0.00	0.406	0.27
	ARD + GPI	4	113.7	1.32	0.210	0.33
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<b>Floral sizes</b>						
Inconspicuous	ARD	3	73.9	0.00	0.357	0.37
	ARD + WEI + ARD:WEI	5	75.6	1.69	0.153	0.51
	ARD + GPI	4	75.6	1.71	0.152	0.41
Small	-	2	97.5	0.00	0.266	0.00
	WEI	3	98.0	0.55	0.202	0.10
	ARD	4	98.6	1.09	0.154	0.21
	ARD + WEI	3	98.8	1.29	0.140	0.07
	PPI	3	98.9	1.38	0.133	0.06
	GPI + PPI	4	99.4	1.89	0.104	0.18
Medium	-	2	80.9	0.00	0.337	0.00
	GPI	3	81.1	0.15	0.312	0.12

Large	ARD + GPI + ARD:GPI	5	55.1	0.00	0.293	0.43
	GPI	3	55.7	0.57	0.220	0.14
	-	2	55.7	0.58	0.219	0.00
Very large	ARD + GPI	4	78.9	0.00	0.253	0.49
	ARD	3	78.9	0.08	0.243	0.40
	ARD + WEI	4	79.9	1.07	0.148	0.46
	ARD + WEI + ARD:WEI	5	79.9	1.08	0.148	0.55
	ARD + GPI + WEI	5	80.1	1.22	0.138	0.55
Generalist (Inconspicuous + Small)	-	3	113.9	0.00	0.296	0.18
	ARD + WEI + ARD:WEI	5	114.9	1.07	0.174	0.38
	ARD + WEI	4	115.0	1.15	0.167	0.26
Specialist (Medium + Large + Very large)	ARD	3	97.6	0.00	0.296	0.19
	ARD + WEI	4	97.9	0.33	0.251	0.30
	-	3	98.5	0.95	0.184	0.16
<b>Floral rewards</b>						
Nectar	-	2	121.5	0.00	0.363	0.00
	WEI	3	123.3	1.81	0.147	0.04
	PPI	3	123.3	1.84	0.145	0.04
Pollen	ARD + GPI + PPI + WEI + ARD:PPI + ARD:GPI + ARD:WEI	9	77.6	0.00	0.617	0.91
Oil	PPI	3	94.3	0.00	0.336	0.17
	-	2	95.3	1.03	0.201	0.00
	PPI + WEI	4	95.9	1.65	0.147	0.23
<b>Sexual systems</b>						
Hermaphrodites	ARD	3	113.5	0.00	0.376	0.41
	ARD + GPI	4	114.2	0.66	0.270	0.48
Monoecious	-	2	82.7	0.00	0.374	0.00

	PPI	3	83.8	1.17	0.208	0.07
	WEI	3	84.5	1.87	0.147	0.04
Dioecious	ARD + GPI + PPI + WEI + ARD:GPI + ARD:WEI	9	51.1	0.00	0.930	0.94
<b>Reproductive systems</b>						
Self-compatible	-	2	76.9	0.00	0.393	0.00
	WEI	3	78.1	1.24	0.212	0.00
Self-incompatible (SI)	ARD + WEI + ARD:WEI	5	83.7	0.00	0.534	0.55
Outcrossing (SI+ D)	ARD + WEI + ARD:WEI	5	95.8	0.00	0.633	0.60
<b>Pollination systems</b>						
Birds	ARD + GPI + PPI + WEI	6	35.1	0.00	0.341	0.79
	GPI + PPI + WEI	5	35.1	0.04	0.335	0.70
Bats	ARD	3	75.4	0.00	0.288	0.19
	ARD + WEI	4	75.7	0.33	0.244	0.30
	WEI	3	76.1	0.71	0.202	0.16
Wind	-	2	13.3	0.00	0.344	0.00
	ARD	3	14.0	0.69	0.244	0.28
	WEI	3	14.8	1.49	0.163	0.18
Bees	ARD	3	101.9	0.00	0.463	0.26
Sphingids	ARD + WEI	4	27.7	0.00	0.490	0.70
	ARD + WEI + GPI	5	29.1	1.39	0.244	0.76
DSI	-	2	95.3	0.00	0.328	0.00
	PPI	3	95.8	0.45	0.262	0.11
Moths	GPI + PPI	4	26.9	0.00	0.389	0.43
	-	2	28.0	1.09	0.225	0.00
	GPI	3	28.4	1.47	0.187	0.16
Bettles	ARD + WEI	4	48.3	0.00	0.396	0.38
	ARD	3	49.0	0.66	0.284	0.22

Burtterflies	GPI + PPI + WEI	5	64.1	0.00	0.437	0.48
	WEI	3	65.6	1.44	0.212	0.20
All vertebrates	ARD + WEI	4	79.4	0.00	0.343	0.36
	ARD	3	80.3	0.89	0.219	0.22
	WEI	3	80.6	1.20	0.188	0.21
	WEI	3	80.6	1.20	0.188	0.21
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Generalist	ARD + GPI + PPI	5	116.1	0.00	0.217	0.38
	-	2	116.4	0.22	0.195	0.00
	ARD + GPI + PPI	3	116.4	0.22	0.194	0.13
	PPI	3	117.0	0.88	0.140	0.10
	GPI + PPI	4	117.0	0.90	0.138	0.23
	ARD + PPI	4	117.4	1.24	0.116	0.21
Specialist	ARD	3	102.3	0.00	0.480	0.32
	ARD + GPI + PPI	4	104.2	1.84	0.191	0.36
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<b>Fruit types</b>						
Generalist (dry)	ARD + GPI + WEI + ARD:WEI	6	163.6	0.00	0.242	0.60
	ARD + GPI + WEI + ARD:WEI	3	163.7	0.03	0.238	0.30
	ARD+ WEI	5	163.9	0.29	0.209	0.50
	ARD + GPI+ ARD:GPI	5	165.2	1.53	0.112	0.46
	ARD + WEI	4	165.2	1.54	0.112	0.36
Specialist (fleshy)	ARD + WEI	4	96.0	0.00	0.242	0.56
	ARD	3	96.1	0.06	0.235	0.48
	ARD + PPI + WEI	5	96.3	0.26	0.212	0.63
	ARD + WEI	4	97.1	1.13	0.138	0.53
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<b>Dispersal modes</b>						
Zoochory	ARD	3	94.6	0.00	0.489	0.49
	ARD + PPI	4	96.4	1.79	0.489	0.52

Autochory	-	2	86.1	0.00	0.445	0.00
Anemochory	-	2	71.6	0.00	0.241	0.00
	ARD	3	72.1	0.53	0.185	0.11
	WEI	3	72.2	0.61	0.178	0.10
	PPI	3	72.7	1.08	0.141	0.08
	ARD + PPI + WEI + ARD:WEI	6	72.7	1.13	0.137	0.48
	ARD + WEI + ARD:WEI	5	73.0	1.44	0.117	0.34
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Generalista (abiotic)	-	2	98.7	0.00	0.342	0.00
	ARD	3	100.1	1.38	0.172	0.06
	WEI	3	100.2	1.56	0.157	0.06
	ARD + WEI	5	100.3	1.67	0.148	0.32
Specialist (biotic)	ARD	3	94.6	0.00	0.489	0.49
	ARD + PPI	4	96.4	1.79	0.199	0.52
<b>Rao Q</b>	GPI + PPI	4	141.6	0.00	0.328	0.23
	GPI	3	142.3	1.32	0.237	0.07

663  $\Delta$ AICc represents the difference between the current and the best-supported models. Weight represents the relative probability of each model.

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