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Janaine Isabela da Silva Rocha (✉ janainerocha@yahoo.com.br)

Universidade Estadual de Santa Cruz <https://orcid.org/0000-0002-1651-9689>

Gustavo Souza Cruz Menezes

Instituto Chico Mendes de Conservacao da Biodiversidade

Eliana Cazetta

Universidade Estadual de Santa Cruz

Pavel Dodonov

Universidade Federal da Bahia

Daniela Custódio Talora

Universidade Estadual de Santa Cruz

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Seed rain across fire-created edges in a Neotropical rainforest

Janaine Isabela da Silva Rocha^{1*}; Gustavo Souza Cruz Menezes²; Eliana Cazetta¹; Pavel Dodonov³; Daniela

Custódio Talora¹

¹ Department of biological Sciences, Universidade Estadual de Santa Cruz (UESC), Rodovia Ilhéus-Itabuna, Km. 16. Ilhéus, Bahia, Brazil. 42662-900;

² Chico Mendes Institute for Biodiversity Conservation, Ministry of Environment, Rod. BA 001, km 45, Una, BA, Brazil. 45690-000;

³ Institute of Biology, Federal University of Bahia. Rua Barão de Jeremoabo, 668, Ondina, Salvador, Bahia, Brazil. 40170-115.

*corresponding author: janainerocha@yahoo.com.br

Abstract

Human-induced wildfires are increasing in frequency in tropical forests, and their deleterious consequences for biodiversity include decreases in seed rain, which may be affected directly by fire or indirectly by the creation of edges between forest and non-forest environments. **Understanding seed rain is key to assess the potential for natural regeneration in plant communities. We assessed the impact of fire and fire-created edges on seed rain species richness, abundance, size, weight, and dispersal syndromes in Atlantic Forest remnants in Bahia, Brazil. We assessed seed rain at monthly intervals for an entire year** along seven 300 m-long transects placed perpendicular to the edge. We installed seed traps at the edge and at 20, 40, 60, 80, 100, and 150 m into the burnt area and into the forest from forest edge. We recorded a total of 9,050 seeds belonging to 250 morphospecies. **We did not observe edge influence; however, we detected a lower abundance and proportion of animal-dispersed seeds in the burnt than in the unburnt areas.** The seed abundance in the burnt areas was lower and seeds were smaller and lighter than those in the unburnt area. Seed rain in the burnt area was not greater near to the forest than far from it. The abundance and **richness** of seed rain was positively correlated with tree density. Our findings highlight the lack of seed rain in burnt areas and differences in **community composition** between the burnt and unburnt areas. **Collectively, these results indicate negative consequences on natural regeneration, which can lead to permanent secundarization and challenges for early regeneration of burnt areas, which will initially have impoverished forests due to low seed richness.**

Keywords: post-fire restoration, dispersal; edge influence; forest influence; tropical forest

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38 Introduction

39 Fires play a significant role in tropical ecosystems by influencing community structure and species
40 composition (Bond and Keeley 2005). In tropical forests, the geographic extent of forests may be limited by fires
41 as well as edaphic and climatic factors (Hoffmann and Moreira 2002; Russell-Smith et al. 2004). Even though
42 evolutionary history resulted in fire-resistant traits for some vegetation types (Hoffmann et al. 2003; Pausas et al.
43 2006; Maurin et al. 2014), anthropogenic wildfires are an increasing threat to biodiversity. In tropical forests,
44 wildfires used to be rare or absent (Thonicke et al. 2001; Chisholm et al. 2016; Barlow et al. 2020) but have become
45 a recurring disturbance (Armenteras et al. 2013; Granzow de la Cerda et al. 2012) in the last decades. Interactions
46 with other anthropogenic disturbances, such as climate change and deforestation, are changing fire intensity and
47 impacts (Kelly et al. 2020, Driscoll et al. 2021). In tropical rain forests, a single fire can release between 7.7 and
48 22,3 Mg C ha⁻¹, depending on land use history and previous fires (Cochrane et al., 1999; Balch et al., 2008). The
49 increase in the frequency of anthropogenic fires is expected to change forest structure (Cochrane et al., 2004). For
50 example, fires may result in the invasion of Atlantic forest fragments by the bracken fern *Pteridium* sp., which
51 may become the dominant species above ground and in the seed bank (Silva and Silva-Matos 2006, Menezes et
52 al. 2019).

53 Wildfires induce different levels of vegetation mortality, creating edges between stands of different
54 structural characteristics according to the burn severity (Parkins 2018) and between burnt and unburnt vegetation.
55 These edges may alter community structure and dynamics, which can consequently cause edge influence (Murcia
56 1995; Harper et al. 2005). Partial burning of vegetation and organic matter at fire-created edges modifies abiotic
57 attributes such as light, wind, and moisture (Harper et al. 2004; Harper et al. 2005). For example, edges between
58 forest and non-forest vegetation alter wind speed (Laurance and Curran 2008), with possible consequences for
59 seed dispersal by wind (anemochoric seeds; Augsperger and Franson 1987). Finally, such edges may affect animal
60 behavior by attracting animals (positive edge effect) or causing edge avoidance (negative edge effect, Potts et al.
61 2016). Consequently, fire-created edges may also affect seed dispersal by animals (zoochoric seeds; Freitas et al
62 2013; Ssali 2018). Thus, seed rain is likely to be affected by forest edges (Capellesso et al. 2018; Vespa et al. 2014)
63 and may consequently impact regeneration processes (Nathan et al. 2002).

64 Mature forest fragments near fire-affected areas are essential for seed inflow and may act as source areas
65 for restoration (Rodrigues et al. 2009). Closer proximity to undisturbed forest edges may increase the dispersal of
66 some vertebrate species, especially seed-dispersing birds (Casenavea et al. 1995; Ingle 2002). “Forest influence”
67 occurs when a forest fragment affects biotic or abiotic variables in the adjacent disturbed area (Baker et al. 2013).

68 Seed rain may be subjected to forest influence by a series of mechanisms. For example, fruiting plants at edges
69 may be more abundant and attractive to some of the dispersing fauna, thus increasing animal movement along
70 edges (Pollock et al. 2017) and consequently seed dispersal to the disturbed areas. **Forest influence can thus
71 improve the recolonization and establishment of viable populations in the disturbed area via seed dispersal from
72 the forest edge or from surviving individuals within the burnt area (Baker et al. 2013).**

73 In this study, we explored gradients in seed rain across fire-created edges in the Brazilian Atlantic Forest.
74 **Our main objectives were i. to compare seed rain between the burnt and unburnt areas; ii. to evaluate the existence
75 of edge and forest influence on seed rain at fire edges; and iii. to assess whether variation in seed rain can be
76 explained by the structural characteristics of vegetation.** We assessed seed rain by evaluating seed abundance and
77 species richness, as well as different dispersal mechanisms. **We expected seed rain to differ between the burnt area
78 and the remaining forest and to be affected by edge proximity, with a gradient from higher richness and abundance
79 within the forest interior to lower richness and abundance within the burnt area. We also expected that zoochoric
80 seeds would be more abundant than non-zoochoric seeds in unburnt areas, as previously recorded for tropical
81 forests (Griz and Machado 1998; Jordano and Schupp 2000). We predicted that zoochoric seeds would be larger
82 and heavier in the forest interior (Tabarelli et al. 2010), than in the burnt area, representing edge avoidance by
83 large-bodied frugivores; and that non-zoochoric seeds would be more prevalent in the burnt area than in the intact
84 forest.**

85

86 **Materials and methods**

87 *Study area*

88 The study site is in a protected area, the Una Wildlife Refuge (Refúgio de Vida Silvestre de Una - Revis-
89 Una) (15°08'15" S, 39° 00'39" W), which is in the municipality of Una in southern Bahia, North-Eastern Brazil.
90 **The area is affected by anthropogenic impacts, especially those caused by deforestation for new agriculture fields,
91 poaching, and extraction of wood and other plant products by local dwellers (GSCM, pers. obs.).** The Revis-Una
92 is 23,404 ha in size and has a humid to sub-humid climate without a defined dry period, an annual rainfall of 1,600
93 to 1,800 mm, and an average yearly temperature of 23°C (SEI-BA 1998). The soil is yellow oxisols (Santos et al.
94 2011) with a mostly sandy soil texture (pers. obs). **The vegetation is 15 to 30 m tall and characterized by a large
95 abundance of lianas and vertically stratified plants, including an herbaceous layer with many saplings and, in some
96 areas, bamboos (Menezes et al. 2019).**

97 The wildfires in the area are likely a result of the use of fire for management of agricultural areas within
98 and around the Revis-Una, where fire can be used to prepare land for agriculture (Barlow et al. 2019). The area
99 underwent accidental soil and surface fires between December 2015 and February 2016. The duration of each of
100 the fires was approximately one month and the fires impacted different parts of the protected area (Menezes et al.
101 2019). The wildfires caused profound structural changes in burnt areas, which had lower basal area and density of
102 trees, saplings, lianas and herbaceous life-forms, but higher density of snags, logs (fallen trees) and pioneer species
103 (such as *Trema* spp., *Cecropia* spp., *Solanum* spp.) as well as graminoids, than the surrounding unburnt forest. The
104 bracken fern *Pteridium arachnoideum* (Kaulf.) Maxon dominated burnt areas, forming fronds with very high
105 height and cover (Menezes et al. 2019). Sampling started approximately a year and a half after the fires ended.

106

107 *Sampling design*

108 Within the protected area, we selected three partially burnt forest patches (Fig. 1a). All patches showed a
109 clear edge between the forest and the burnt area (Fig. 1b) and the sizes of the burnt areas were 28, 63.5, and 260
110 ha. Within these areas, we placed a total of seven transects, at least 100 m apart from each other, perpendicular to
111 the edge and extending from 150 m into the forest to 150 m into the burnt area. Along each transect we installed
112 13 seed collectors (Fig. 1c): at the edge (determined by the presence of charcoal on the soil) and at 20, 40, 60, 80,
113 100 and 150 m into the forest and into the burnt area from the edge. Thus, we used a total of 91 seed traps at the
114 seven transects. They were made of a 1 m x 1 m square piece of polyester mesh, with a 1 mm mesh size, nailed on
115 eight wooden sticks at a height of 1 m from the ground. This seed trap design is commonly used in seed rain studies
116 (Melo et al, 2006; Rother et al, 2015), especially to capture wind-dispersed seeds and those dispersed by birds,
117 bats and primates, but not seeds dispersed by ground vertebrates or invertebrates. The seed traps were visited
118 monthly from September 2017 to August 2018, and all the material within them was taken to the lab for sorting.
119 Next to each seed collector we placed a 20 m x 4 m transect (long side parallel to the edge) to sample vegetation
120 structure. In each transect we measured the diameter at breast height (dbh) of all trees and snags with a dbh of at
121 least 10 cm (detailed results for vegetation structure can be found in Menezes et al. 2019).

122

123 *Sorting and classification of the collected material*

124 In the lab, we first separated the fruits and seeds from the plant litter. We photographed the fruits and
125 removed the pulp to store the seeds. We then weighed, measured the width, and took pictures of all seeds,
126 separating them into morphotypes (which we treat here as morphospecies) where each new seed that was different

127 from previously collected ones was classified as a new morphotype. The morphospecies were classified into
128 dispersal types according to Van Der Pijl (1982) as follows: a) zoochoric: seeds with characteristics of animal
129 dispersal, especially fruits such as drupes or berries and seeds with aril; b) anemochoric: seeds with structures for
130 wind dispersal; and c) autochoric: seeds with explosive mechanisms. For data analysis, we grouped anemochoric
131 and autochoric seeds into a single non-zoochoric category.

132

133 *Data analysis*

134 We analyzed the following response variables: total seed abundance (number of seeds per trap); average
135 seed species richness (average number of morphospecies per month); total seed species richness (total number of
136 different morphospecies observed at a seed trap throughout the study); average seed width per seed trap; and
137 average seed weight per seed trap. We also calculated seed rain abundance and species richness separately for the
138 dispersal categories (zoochoric and non-zoochoric species). Finally, we used seed width and seed weight as
139 morphological traits important for zoochoric seeds (Moles et al 2005; Moran and Catterall 2010, Todeschini et al
140 2020) and non-zoochoric seeds (Traveset and Rodríguez-Pérez 2008), respectively. We excluded samples with no
141 seeds for average seed width and average seed weight. In some cases (0.2% of the total seeds collected), seed
142 weight was below the detection limit of our scales so we assigned a value of 0.0001 g to the average weight.

143 To assess differences between burnt and unburnt areas and the existence of edge-related gradients, we
144 created different generalized linear and additive mixed models (Zuur et al. 2009), including transect as a random
145 factor in all models. This analysis enabled us to simultaneously assess the differences between burnt and unburnt
146 areas, the existence of edge-related gradients, and the shape of these gradients when present. Thus, we created six
147 models for each response variable (Fig. 2): 1) a null (intercept-only) model representing the null hypothesis of no
148 difference between the burnt and unburnt areas and no edge or forest influence; 2) a categorical model, with
149 location (burnt area or unburnt forest) as an explanatory variable and with the edge being classified as unburnt
150 forest; 3) a categorical model, with location as an explanatory variable, and with edge being classified as burnt
151 area; 4) an additive model, with distance as an explanatory variable and the response variables modeled as a smooth
152 function of distance; 5) an additive model that also included distance as an explanatory variable, with the edge
153 being classified as unburnt forest; 6) an additive model that also included distance as an explanatory variable, with
154 the edge being classified as burnt area. In the additive models, the optimal degree of smoothing was determined
155 by cross-validation (Zuur et al. 2009), but we established a maximum smoothing of 4 effective degrees of freedom
156 to avoid overfitting.

157 For count variables (abundance and total seed rain species richness), we used the negative binomial
158 distribution. For average seed rain species richness we used the Gaussian distribution; for average weight and
159 width we used the gamma distribution. We then calculated Akaike's information criterion corrected for small
160 sample size (AICc; Burnham and Anderson 2002) for each model, and, for each response variable, selected the
161 simplest model among those with a $\Delta\text{AICc} \leq 2.0$.

162 We also compared the mean values of the response variables between burnt and unburnt areas (excluding
163 the collectors located at the edge) by means of a restricted-permutation t-test. The significance of the test was
164 assessed by randomizing the label ("Fire" or "Forest") between the collectors of each transect (Manly 2007). For
165 this test, we first calculated the difference in the mean values between the burnt and unburnt areas, then randomized
166 the data as explained above, and recalculated this difference for the randomized data. We used 9999 permutations
167 in addition to the original data, used the absolute value of the difference between the mean values as the test
168 statistic, and calculated significance as the proportion of absolute differences, which were at least as large as the
169 observed absolute difference. We also used bootstrap to calculate 95% confidence intervals for the values of the
170 response variables in the burnt area and forest, with 9999 pseudo samples in addition to the original data (Manly
171 2007). We restricted the bootstrap resampling to always consider the same number of elements from each transect.
172 As above, we removed the collectors located at the edge.

173 We performed a Non-metric Multidimensional Scaling analysis (NMDS) with two dimensions ($k = 2$) to
174 evaluate differences in species composition among areas (forests, edges and burnt areas). We used
175 presence/absence data and the Bray–Curtis dissimilarity index to perform the ordination based on similarities of
176 species composition. We further performed a PERMANOVA using Bray-Curtis distances and 4999 permutations
177 to assess whether the two areas differed significantly.

178 To assess the effects of vegetation structure on seed rain, we performed Spearman correlations between
179 seed abundance and seed rain species richness (average zoochoric and non-zoochoric) and two structural variables:
180 number of live trees (dbh>10 cm) and number of snags.

181 We performed all analyses in R 3.4.4 (R Core Team 2017) with the packages mgcv (Wood 2011), nlme
182 (Pinheiro et al. 2017), bbmle (Bolker and R Development Core Team 2017), lme4 (Bates et al. 2015), gamm4
183 (Wood and Sheipl 2020) and vegan (Oksanen et al. 2009). The data and codes are available as supplementary
184 material 1 and 2, respectively.

185

186 **Results**

187 We collected a total of 9,050 seeds belonging to 295 morphospecies during the study year (12 months),
188 with 4,404 seeds (191 morphotypes) characterized as animal-dispersed and 4,646 seeds (104 morphotypes) wind-
189 or self-dispersed (autochoric). Seed abundance was highest in the forest, followed by the burnt area and the edge
190 (0.39, 0.19 and 0.12 seeds.m⁻².day⁻¹, respectively). Tree abundance increased from the burnt area (958 trees / ha)
191 to the forest (8,360 trees/ha). In contrast, snag abundance was greater in the burnt area (449 trees/ha) than in the
192 forest (145 trees / ha).

193 Average seed width varied from 0.01 to 36.6 mm (Fig. 3a); 84% (7598) were classified as small, 15%
194 (1399) as average, 0.5% (47) as large and only 0.08% (7) as very large. Of the zoochoric seeds (Fig. 3b), 47%
195 (3,564) were classified as small, 19% (828) as average, 0.5% (24) as large and 0.1% (6) as very large. Seed average
196 weight varied from below our scales' detection limit of 0.001 g to 30.47 g, with the largest seed being found 100
197 m inside the forest from the edge (Fig. 3c-d).

198 We observed significant differences between burnt and unburnt forest for all response variables, as the
199 null model always presented $\Delta AICc > 6$ (Table 1). Furthermore, the restricted permutations revealed differences
200 between burnt and unburnt area for all variables ($p < 0.02$). All response variables had higher values in the unburnt
201 forest than in the burnt area (Fig. 3-5). In the forest, independent from edge distance, there were 2.2 times more
202 seeds than in the burnt area (2.4 and 2.1 times for total abundance of zoochoric and non-zoochoric seeds,
203 respectively) (Table 2). Similarly, the average and total seed rain species richness in the forest were on average 2.5
204 times higher than in the burnt area (3 times for zoochoric and 2 times for non-zoochoric) (Table 2). Seed average
205 weight and seed weight was 1.3 times and 2.7 times, respectively, higher in the forest than in the burnt area (Table
206 2).

207 We did not observe evidence of edge influence, as the best model was categorical for all variables
208 independent of distance from edge (Table 1). For the total abundance of non-zoochoric species, the best model
209 was the additive and categorical, but the simpler categorical model had a $\Delta AICc$ higher than the null model,
210 indicating that performance is similar to that of a more complex alternative (Burnham and Anderson 2002).

211 The comparison of two models, one in which edge was classified as forest and the other as burnt area,
212 enabled us to assess to which environment the edge was more similar. The $\Delta AICc$ between these two models was
213 higher for the null model (Table 1). The seed abundance and average richness at the edge were more similar to the
214 burnt area than the forest, but total richness at the edge was more similar to the forest. These results were consistent
215 for all seeds, whether zoochoric or non-zoochoric (Table 1; Fig. 3 and 4). The mean seed weight and width and

216 the mean weight of non-zoochoric seeds at the edge were more similar to the forest than the burnt area, but the
217 mean width of zoochoric seeds was more similar to the burnt area than the forest (Table 1; Fig. 5).

218 The first two axes of the NMDS had a stress value of 0.20. The second axis showed a partial separation
219 between the unburnt forest and burnt areas, whereas the group formed by the edge was more widely distributed
220 (Fig. 6). We found a significant result in the PERMANOVA ($p < 0.001$), confirming the difference in species
221 richness among groups and suggesting that species composition varied by location. The ordering axes of the seed
222 rain species richness matrices segregated the forest areas, then the burnt areas and the edges.

223 Total seed rain abundance was positively correlated with tree abundance ($r = 0.42$, $p < 0.001$).
224 Furthermore, zoochoric and non-zoochoric seed abundance were strongly and positively correlated with live trees
225 abundance ($r = 0.46$ and $r = 0.29$, $p < 0.001$, respectively). Seed rain species richness was also positively correlated
226 with live tree abundance ($r = 0.56$, $p < 0.001$), as well as zoochoric and non-zoochoric seed richness ($r = 0.57$ and
227 0.48 , $p < 0.001$, respectively). There was no correlation between seed abundance and richness with snags ($r = 0.10$
228 and $r = 0.15$; $p > 0.05$, respectively).

229

230 Discussion

231 Our results highlight a strong contrast in seed rain between intact forest and burnt areas. Seed rain species
232 richness and seed abundance were higher in the forest than in the burnt areas, as well as seed size and width,
233 independent of seed dispersal mode. Contrary to our expectations, we did not find a gradient in seed dispersal via
234 seed rain from the edges to the interior of either the burnt areas or the unburnt forest, regardless of seed dispersal
235 type, seed width or seed weight. Interestingly, abundance and mean richness at edges were more similar to forest
236 than burnt areas, but total richness at the edge was more similar to the burnt area than the forest. Collectively, our
237 results may indicate that seed rain is compromised after fires, which can consequently impair initial natural forest
238 regeneration after burning.

239 We found a two-fold (or more) decrease in abundance of seeds, both zoochoric and non-zoochoric, in the
240 burnt areas as compared to the unburnt forest. This result is similar to what has been observed in other studies in
241 the Atlantic Forest of southern Bahia (Martini and Santos 2007) and Amazonia (Cury et al. 2020). It is known that
242 fire negatively affects sexual reproduction (and therefore seed production) even in fire-prone environments such
243 as savannas (Dodonov et al. 2018; Hoffmann 1998), and this decrease is expected to be even greater in moist
244 forest. In addition, we found that seed rain abundances (total, zoochoric and non zoochoric) were positively
245 correlated to vegetation structure, indicating that areas with higher tree density also have greater seed rain. This

246 correlation reinforces the hypothesis that seed rain is reflecting forest structural changes promoted by fire. In the
247 same burnt areas we investigated, a previous study revealed lower densities and basal areas of trees, saplings and
248 lianas, and also higher values of snag density, snag basal area, and log density than the unburnt contiguous forest
249 areas (Menezes et al. 2019).

250 Seed rain in the burnt areas was impoverished, with fewer species, large and heavy seeds, and zoochoric
251 seeds as compared to the forest. In fact, the morphospecies composition in the seed rain was different between the
252 burnt and unburnt areas, indicating that generally seeds are not moving among areas. Hence, we can assume that
253 seed rain is sourced from propagules of neighboring trees, with few exchanges between burnt and unburnt areas.
254 Previous studies have revealed that forest interior areas had more median and large seeds than forest edges (Melo
255 et al. 2006; Piotto et al. 2019), which may be due to the autochthonous seed rain, representing the species found
256 at each site. This probably occurs because the local composition of the vegetation may indicate the composition
257 of the seed rain (Drake 1998; Jensen 1998), as most seeds fall near the parent plants (Burrows 1994). The few trees
258 that were present in burnt areas produced many small seeds, which is characteristic of pioneer species (Levey
259 1988) that were responsible for most seed rain abundance.

260 The forest environments also had higher and heavier seeds than in the burnt area, generally related to
261 zoochoric dispersal. In general, higher and heavier seeds are characteristic of late-successional plant species of the
262 forest interior (Ehrlén and Lehtilä 2002) and their dispersal might depend on forest specialist frugivores. Our
263 observation of large seeds exclusively in the forest interior suggests there was low mobility of large seeds to the
264 burnt area, indicating that larger-body frugivores tend to avoid open areas (Guariguata and Pinard 1998). The
265 possible lack of large dispersers may have also hindered the dispersal of these seeds beyond the forest edge (Galetti
266 and Dirzo 2013; Tabarelli et al. 2004); however, the use of burnt areas by dispersers should be tested in future
267 studies.

268 The lack of a gradient in seed rain from the edge to the forest interior was not expected, but followed the
269 structural patterns found in the same areas (Menezes et al. 2019). **This result differs from other studies that
270 indicated edge influence on seed rain in the Atlantic Forest (Melo et al. 2006; Vespa et al. 2014); however, contrary
271 to our studies, which were carried out at regenerating edges, these studies were performed at maintained edges
272 (sugarcane and commercial tree plantations, respectively). Thus, the lack of edge gradients observed in our study
273 may be explained by forest edge age (burnt areas were approximately 2 years old) so some effects, such as
274 increased tree mortality (Laurance 2000; Menezes et al. 2019), that can significantly reduce local seed production
275 (Benítez-Malvido and Martínez-Ramos 2003), may not have manifested yet. Thus, it is possible that stronger**

276 gradients from the edge into the unburnt forests will be observed as the edge develops because edge influence
277 often changes with time (Chabrierie et al. 2013; Harper et al. 2005). Conversely, the opposite may occur, with the
278 forest and burnt area becoming more similar as the burnt area recovers from the disturbance. The absence of
279 gradients within the burnt area may also be explained by avoidance of the burnt area by seed dispersers or from a
280 lower flux of abiotic dispersed seeds from the forest to the burnt area because the strength of the winds within the
281 forests is generally low. Forest structure affects wind flow, and dispersal distances in forests are considerably
282 shorter than in open areas (Nathan et al. 2002, Vespa et al. 2018).

283 **Even though we observed significantly more seeds in unburnt than burnt forests**, our results showed that
284 a relatively large number of seeds also reached the burnt areas, but they were mainly small and light, typically
285 from pioneer species. This may be due to drastic structural change in the burnt areas, the presence of surviving
286 trees post- fire, and post-fire regeneration of some pioneer and fast-growing species, such as *Miconia mirabilis*,
287 *Trema micranta*, *Cecropia sp.*, *Solanum crinitum* and *Henriettea succosa* that were found throughout the burnt area
288 (Menezes et al. 2019). These species are common in burnt areas and favored by disturbances such as fire because
289 they are adapted to secondary forests and edges (Barlow and Peres 2004) and are present in early successional
290 stages after fire (Martini and Santos 2007). They are characterized by high seed production and seeds dispersed
291 by common generalist frugivorous species, such as bats or small birds (Laurance 2007), or wind (Whitmore 1983).
292 The surviving trees can also provide shelter for the dispersing fauna and natural perches, which contribute to seed
293 dispersal beneath tree canopies (Holl 2002). The NMDS results corroborate this idea as they indicate that
294 morphospecies from seed rain have distinct composition in unburnt and burnt areas. These shifts in species
295 composition can converge towards early successional communities (Berenguer et al. 2018) that can become
296 functionally more similar to secondary forests over time (Arroyo-Rodríguez et al. 2017; Howe, 2016), especially
297 if wildfires become more frequent.

298 Our findings reveal that edges were more similar to forests concerning abundance and mean richness but
299 were more similar to the burnt area for total seed rain species richness. We previously discussed the lack of edge
300 gradient; however, we cannot exclude possible effects when distance to edge is equal to zero. Therefore, effects
301 might be present very close to the edge and did not penetrate into the forest. Indeed, short-distance edge effects,
302 limited to the first meters from the edge or even to the immediate edge, are not uncommon (Dodonov et al. 2013;
303 Harper et al. 2005) and have been observed for some characteristics of vegetation structure at our study site
304 (Menezes et al. 2019). In our study, such edge effects limited to the immediate edge were observed for total seed

305 abundance, average seed rain species richness, and the mean width of zoochoric seeds, which may indicate that
306 seed-dispersing fauna avoid the immediate edge as well as the burnt area.

307

308 Conclusion

309 In our study, seed rain was dominated by small and zoochoric seeds and was not affected by edge
310 influence. We observed differences in abundance, richness and seed dispersal syndromes between the forest and
311 burnt areas. **Our results indicate a decrease in large-seeded species and increase of small-seeded species in the**
312 **burnt areas, which can impair or retard plant recruitment and restoration processes.** Importantly, seed rain was not
313 greater near remaining forest patches; instead, the decrease in seed rain was homogeneous throughout the burnt
314 areas. Because forest fire disturbance reduces plant diversity, it compromises future forest regeneration, thus
315 regeneration from seed rain to a burnt area may be less diverse. The decrease in seed diversity is of particular
316 concern because trees are the major component of the diversity, structure, and function of tropical rain forests
317 (Denslow 1987).

318 **We acknowledge some potential limitations of our study. For instance, our study was designed for a single**
319 **year of observation so we did not consider possible intra-annual variation in seed rain. Furthermore, our sampling**
320 **occurred a few years after fire, thus, our results are related to the early regeneration process and could differ with**
321 **increased time-since-fire.** Following the natural successional pathways, the prevalence of small seeds typically
322 from pioneer species found in our study area would be expected during this successional stage (Chazdon 2014).
323 However, it is important to consider the underrepresentation of large seeds in the study area because it suggests
324 that initial regeneration can be impoverished with mostly small seeds of few species. **Fires are an ever-increasing**
325 **disturbance in tropical forests and burnt areas are more prone to new fires. Consequently, future monitoring is**
326 **critical to determine if active restoration actions might be needed for recovery of the burnt Atlantic forest areas.**

327 .

328 Declarations

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337

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339 No conflict to declare.

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342 *Code availability*

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344 *Authors' contributions*

345 All authors contributed to the study conception. Material preparation, data collection and analysis were performed
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348

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552 landscape. *Ecography* 22:715-728

553 **Table 1.** Model selection results showing the differences in the corrected Akaike's information criterion ($\Delta AICc$)
 554 values for each model for each response variable.

	Model					
	Null	Categoric - edge as forest	Categoric - edge as fire	Gradient	Gradient and categoric - edge as forest	Gradient and categoric - edge as fire
Total abundance	20.36	6.77	0.00*	16.11	11.25	3.43
Total abundance – zoochoric	13.90	4.11	0.00*	8.71	8.08	4.51
Total abundance - non-zoochoric	16.62	6.90	0.68*	16.82	9.59	0.00
Average seed rain species richness	44.06	6.54	0.00*	14.21	10.57	4.53
Average seed rain species richness – zoochoric	50.94	8.59	0.00*	10.26	7.74	2.04
Average seed rain species richness - non-zoochoric	17.90	2.53	0.00*	14.71	5.33	1.39
Total seed rain species richness	46.34	0.00*	6.29	24.72	4.24	9.49
Total seed rain species richness – zoochoric	47.74	0.00*	4.71	23.23	2.45	5.86
Total seed rain species richness- non-zoochoric	29.76	0.00*	4.74	16.80	3.86	9.19
Mean width	8.86	0.00*	2.44	3.10	3.86	5.14
Mean weight	15.28	0.00*	9.35	9.70	4.54	11.75
Mean width – zoochoric	6.40	3.01	0.00*	4.90	6.81	4.59
Mean weight - non-zoochoric	12.67	0.00*	10.06	5.36	2.77	NA

555 *Model selected for each response variable corresponding to the model with the lowest AICc.

556

557 **Table 2.** Mean values and 95% confidence intervals (calculated by restricted bootstrap with 9999 random samples
558 plus the original data) for the fire and forest seed collectors and the statistical of this difference (assessed by a
559 restricted randomizations t-test, with 9999 randomizations plus the original data).
560

	Mean (and confidence interval) - burnt area	Mean (and confidence interval) - unburnt forest	Significance of the difference
Total abundance	64.2 (44.3 - 84.7)	143.7 (115.1 - 174.7)	0.0006
Total abundance – zoochoric	29.4 (18.1 - 42.8)	71.7 (55.5 - 90.8)	0.0004
Total abundance - non-zoochoric	34.8 (23.4 - 47.8)	72 (49 - 99.2)	0.0139
Average seed rain species richness	0.9 (0.7 - 1.2)	2.4 (2.2 - 2.6)	0.0001
Average seed rain species richness – zoochoric	0.5 (0.4 - 0.6)	1.4 (1.3 - 1.6)	0.0001
Average seed rain species richness - non-zoochoric	0.5 (0.4 - 0.6)	0.9 (0.8 - 1.1)	0.0001
Total seed rain species richness	7.6 (6.2 - 8.9)	19.7 (18.4 - 21.2)	0.0001
Total seed rain species richness – zoochoric	4.1 (3.2 - 4.9)	12.6 (11.5 - 13.7)	0.0001
Total seed rain species richness- non-zoochoric	3.5 (2.9 - 4.2)	7.1 (6.4 - 7.9)	0.0001
Mean width	3.3 (3 - 3.7)	4.2 (3.9 - 4.5)	0.0018
Mean weight	0.03 (0.02 - 0.05)	0.08 (0.06 - 0.10)	0.0004
Mean width – zoochoric	4.1 (3.5 - 4.8)	5.1 (4.7 - 5.5)	0.0156
Mean weight - non-zoochoric	0.009 (0.005 - 0.015)	0.028 (0.017 - 0.042)	0.0013

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567 **Fig. 1** Map of the study area depicting the three partially burnt patches within the Una Wildlife Refuge in southern
568 Bahia, Brazil

569 **Fig. 2** Description and graphical visualization of the six models adjusted for each response variable. Although in
570 this figure the values for all (except the null) models are lower in the burnt area, the models could also show the
571 opposite pattern. The horizontal axes represent distance along the transects, with the burnt area on the left; the
572 vertical lines represent the edge; the solid lines are the expected values for each model and the dashed lines are the
573 confidence intervals

574 **Fig. 3** Seed rain showing the average number of seeds (a), average weight of seeds (b), and average width of seeds
575 (c) recorded in each survey in burnt and forest areas in the Atlantic Forest from Brazil. Surveys were performed
576 monthly from September 2017 to August 2018. Negative values represent the burnt area and positive values forest
577 areas. Each one of the seven transects were represented for each distance. Lines represent the mean value for each
578 area

579 **Fig. 4** Seed rain results showing seed rain species richness: average seed rain species richness (a), total seed rain
580 species richness (b), average zoochoric seed rain species richness (c), total zoochoric seed rain species richness
581 (d), average non-zoochoric seed rain species richness (e), and total non-zoochoric seed rain species richness (f)
582 recorded in each survey and for the seven transects in burnt and unburnt (forest) areas in the Atlantic Forest, Brazil.
583 Surveys were performed monthly from September 2017 to August 2018. Negative and positive values represent
584 the burnt areas and unburnt areas, respectively. Lines represent the mean value for each area

585 **Fig. 5** Zoochoric seed width (a) and non zoochoric seed weight of (b) in burnt and unburnt areas, Una, Bahia, Brazil.
586 In the x-axes, positive and negative values represent unburnt and burnt areas, respectively. The dots and lines
587 represent transects and average values, respectively

588 **Fig. 6** Ordination diagram produced by Nonmetric multidimensional scaling (NMDS) for seed rain composition
589 in forest, edges and burnt areas in Una Wildlife Refuge in southern Bahia, Brazil. STRESS value = 0.20, k = 2

590

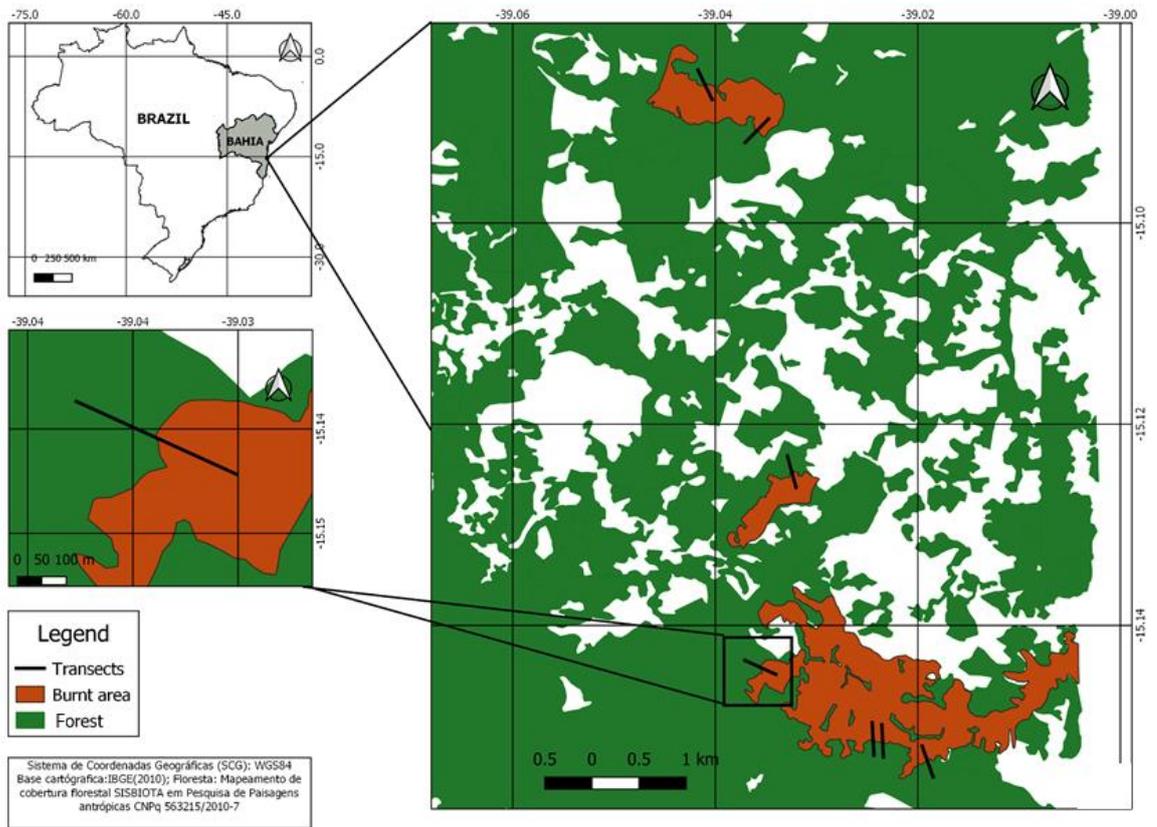
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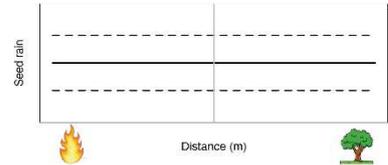
Model

Description

Visualization

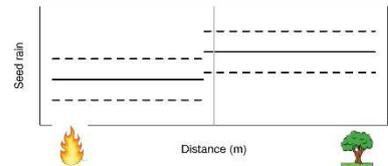
Null

No gradients and no differences between the burned area and the unburned forest.



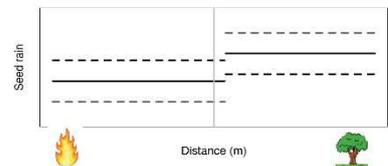
Categorical, edge classified as forest

Mean values differ between the burned area and the unburned forest; edge is similar to the unburned forest.



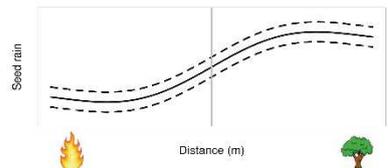
Categorical, edge classified as burned area

Mean values differ between the burned area and the unburned forest; edge is similar to the burned area.



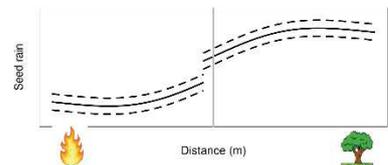
Additive

Gradual variation in the response variable along the transect.



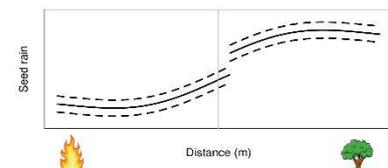
Additive and Categorical, edge classified as burned area

Gradual variation in the response variable along the transect with additional differences in mean values between the burned and unburned area; edge is similar to the unburned forest.



Additive and Categorical, edge classified as forest

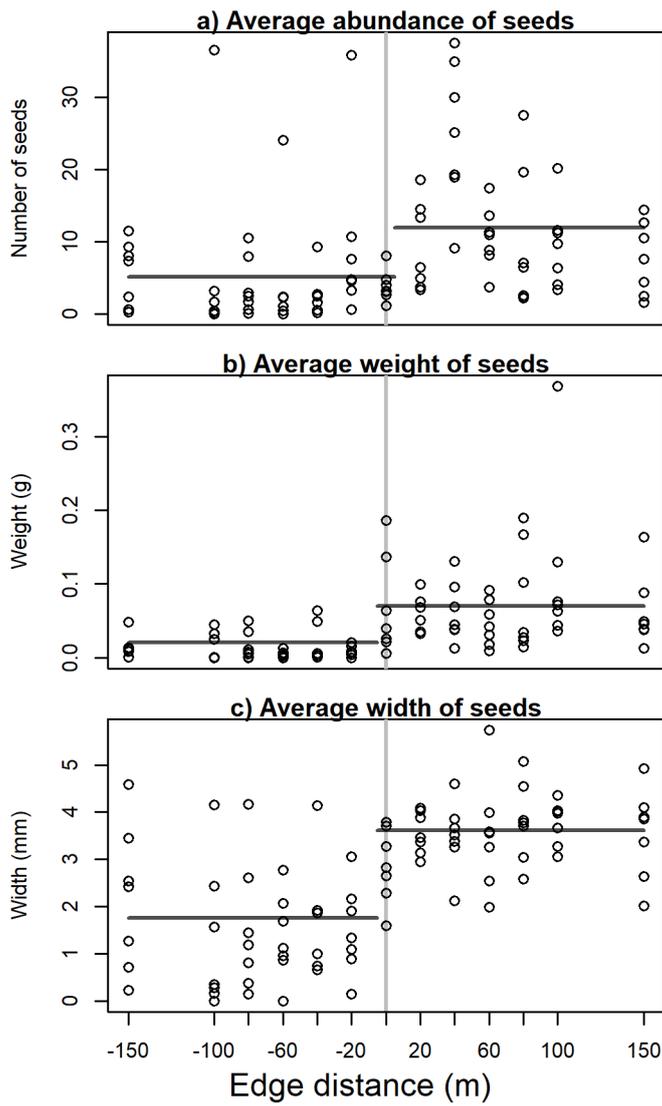
Gradual variation in the response variables along the transect with additional differences in mean values between the burned forest and the unburned area; edge is similar to the burned area.



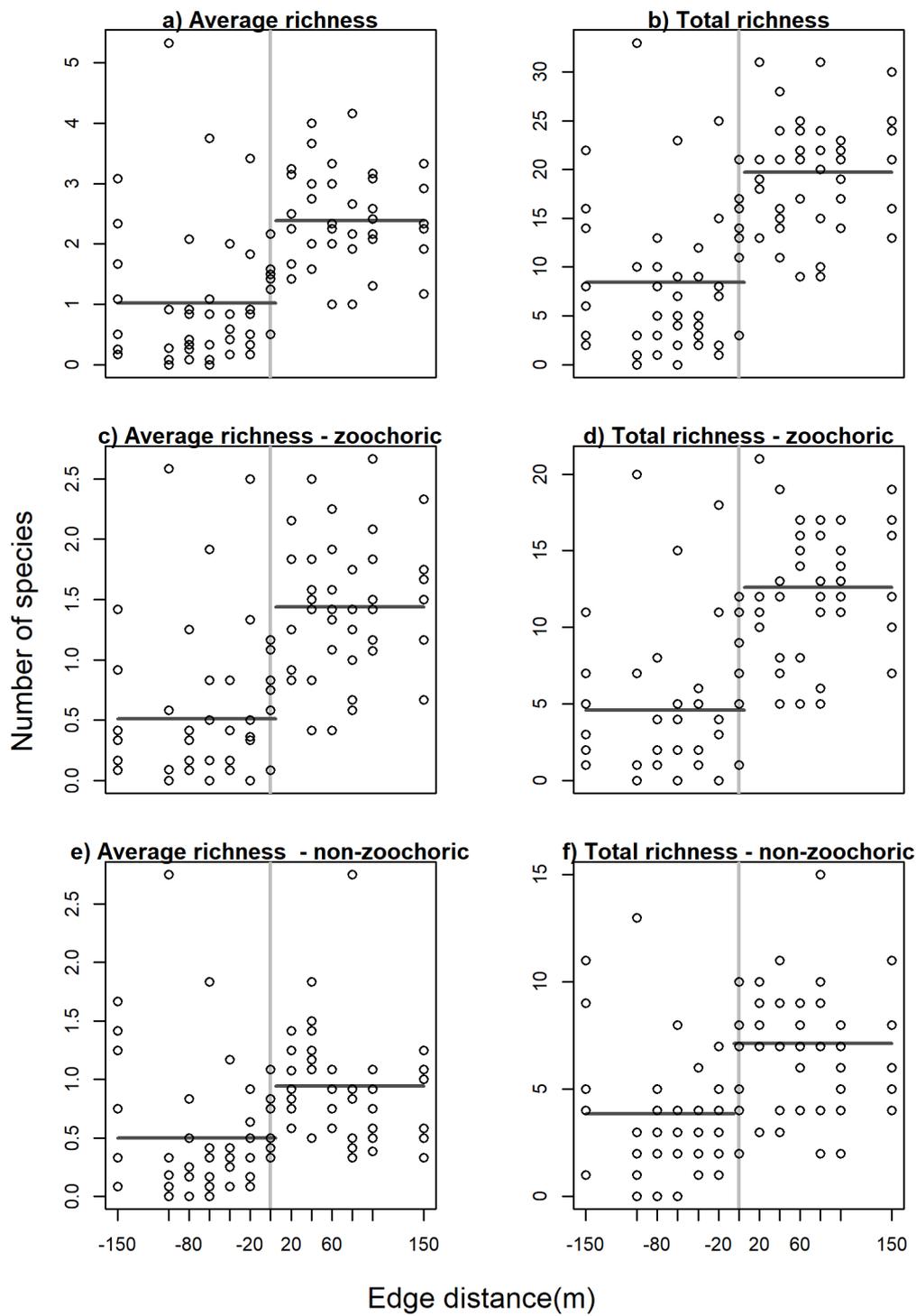
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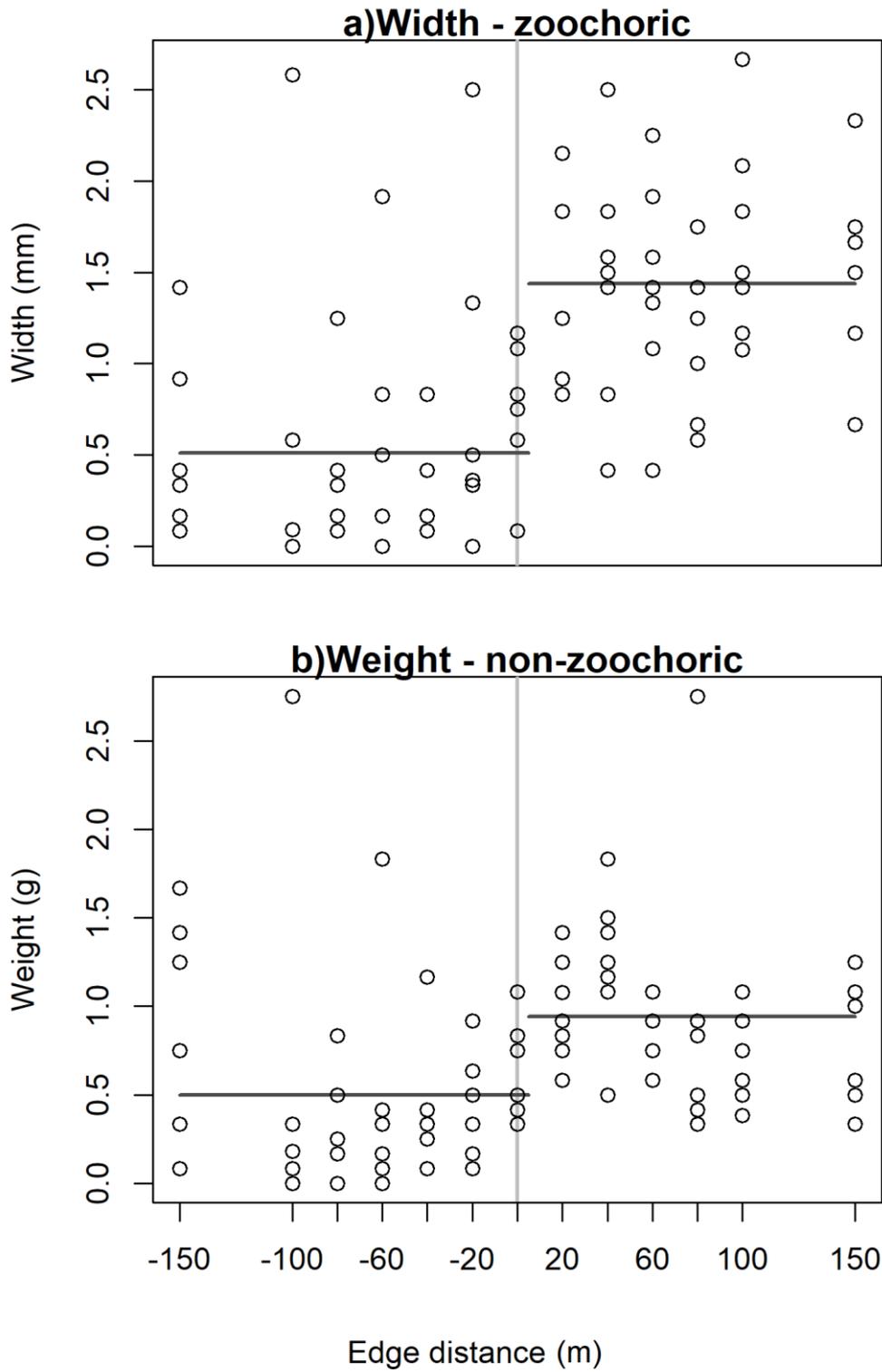
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